

Processing of one, two or four natural scenes in humans: the limits of parallelism

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Abstract

The visual processing of objects in natural scenes is fast and efficient, as indexed by behavioral and ERP data [Nature 381 (1996) 520]. The results from a recent experiment suggested that such fast routines work in parallel across the visual field when subjects were presented with two natural scenes simultaneously [Nature Neurosci. 5 (2002) 629]. In the present experiment, the visual system was driven to its limits by presenting one, two or four scenes simultaneously. Behavior and ERP reveal a clear cost in processing an increasing number of scenes. However, a parallel-late selection model can still account for the results. This model is developed and discussed with reference to behavioral, single-unit and ERP data.

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1. Introduction

Our ability to face complex and unpredictable environments seems to rely on several mechanisms involving fast and parallel visual routines. The very rapid categorization of briefly presented pictures (Biederman, 1972; Potter, 1976) could well rely on neurons in higher order areas such as infero-temporal cortex (IT) that have been shown to fire selectively and very rapidly to a wide range of complex stimuli, both in monkeys (Gross, Bender, & Rocha-Miranda, 1969; Perrett, Rolls, & Caan, 1982; Tanaka, 1996; Vogels, 1999) and in humans (Allison, Puce, Spencer, & McCarthy, 1999; Kreiman, Koch, & Fried, 2000). Other evidence comes from studies using event-related potentials (ERP) that indicate that the discrimination of isolated stimuli might start at about 120–150 ms after stimulus onset (Jeffreys, 1996; Rossion et al., 2000; Schendan, Ganis, & Kutas, 1998; Vogel & Luck, 2000). Whether such fast mechanisms can apply in

parallel across the visual field is still very controversial. Indeed, many models of visual processing assume that after an early parallel encoding of object features, there is a computational bottleneck that prevents more than one set of features at a time from forming ‘high-level’ object representations (Treisman, 1998; Wolfe, 1998). However, single-unit recordings in monkeys have shown that when more than one object is present within the receptive field of IT neurons, they can all affect the response of the cell, although there is evidence that the different stimuli compete for control of the neuronal response (Chelazzi, Duncan, Miller, & Desimone, 1998; Olson, 2001). Such phenomena have also been seen in the context of natural scenes (Sheinberg & Logothetis, 2001). Nevertheless, it is clear that relatively little is known about the degree of parallelism in the processing of natural objects and even less in the context of natural scenes where several objects are typically present simultaneously. In previous studies, we showed that in 150 ms the human brain has accumulated enough information to start to categorize a natural scene as containing or not an animal (Fabre-Thorpe, Delorme, Marlot, & Thorpe, 2001; Thorpe, Fize, & Marlot, 1996) or a non-biological category such as a means of transport (VanRullen & Thorpe, 2001). This rapid categorization of natural scenes

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already suggests some degree of parallel processing in the visual system. In a recent experiment, we tried to challenge the visual parallelism by requiring from human subjects the simultaneous processing of two different natural scenes. The results strengthen the idea that such fast routines can work in parallel across the visual field (Rousselet, Fabre-Thorpe, & Thorpe, 2002). Compared with a single scene condition, human subjects were shown to be just as fast at detecting animals when they had to process two different natural scenes flashed for 20 ms on each side of a central fixation point, with the images centered on the horizontal meridian. Over contralateral occipital electrodes, ERPs on correct go trials diverged from ERPs on correct no-go trials at 150 ms in both conditions. This pattern of differential activity suggests that some high-level object properties are accessed in parallel during natural scene processing. But the brief presentation of images in the left or the right hemifield had induced an initial lateralization of the visual inputs to the contralateral hemisphere so that each hemisphere could independently process one of the two different scenes. However, it is not known whether this result would extend to a situation in which the two images would be presented in the same hemifield, hence entering into an intra-hemisphere competition.

In the present experiment the visual system was driven to its limits by tackling both inter- and intra-hemispheric parallel processing. The task required subjects to respond as fast and accurately as possible each time there was an animal in a briefly (26 ms) presented visual display. This display contained one, two or four photographs of natural scenes appearing simultaneously centered at 4.9° from a central fixation point, in 1–4 of the quadrants. When two pictures were presented, they could appear in the upper or the lower visual field or in the left or the right visual hemifield.

In addition, some aspects of the paradigm used in the present experiment might give us better insights as to the actual mechanisms generating the differential activity. This point will be addressed in the last part of the electrophysiology result section.

Here we present the behavioral performance and electrical scalp surface recordings from 16 human subjects.

2. Experimental procedures

2.1. Subjects

The 16 adult volunteers in this study (7 women, all right-handed, 9 men, 2 left-handed, mean age 28 ranging from 21 to 50) gave their informed written consent. All subjects had normal or corrected to normal vision.

2.2. Stimuli

We used photographs of natural scenes taken from a large commercial CD-ROM library (Corel Stock Photo Libraries). From this data bank, 3360 distracters and 960 targets were selected. Horizontal photographs (384 by 256 pixels, sustaining about 7.8° by 5.2° of visual angle) were chosen to be as varied as possible. Animals included mammals, birds, fish, insects and reptiles... There was no a priori information on the size, position, or number of targets in any particular photograph. There was also a very wide range of distracter images that included outdoor or indoor scenes, natural landscapes (mountains, fields, forests, beaches...) and street scenes, pictures of food, fruits, vegetables or plants, buildings, tools or other man-made objects...

2.3. Task and set-up

Subjects sat in a dimly lit room at 100 cm from a computer screen (resolution: 1024×768 , vertical refresh rate: 75 Hz) piloted from a PC computer. Stimulus presentation and behavioral response recording was achieved using the Presentation software application (<http://nbs.neuro-bs.com/>). To start a block of trials, subjects had to place their finger on a response pad for one second. Stimulus displays were composed of 1, 2 or 4 images that appeared centered at the corners of an imaginary rectangle. The distance between the center of each image and the central fixation point was 3.7° vertically and 4.9° horizontally. In the 1-image condition, the photograph could appear in four possible locations and be either a target (T) or a distractor (D). In the 2-image conditions, the scenes could appear either (1) on each side of the vertical meridian, whether in the upper or the lower visual field (inter-hemifield condition), or (2) above and below the horizontal meridian, whether in the left or the right hemifield (intra-hemifield condition). In all cases the 2 images were either two distractors or a target and a distractor. The 4-image condition involved the presentation of either one target among three distractors on target trials or four distractors otherwise.

A trial was organized as follows: a 300–600 ms fixation point (about 0.1° of visual angle) appeared in the middle of the screen after which a display composed of one, two or four photographs was presented for two frames, i.e. 26 ms. Participants had to raise their finger as quickly and as accurately as possible (go response) each time an animal was present. Responses were detected using infrared diodes. Subjects had 1000 ms to respond, after which their response was considered as a no-go response. This maximum response time delay was followed by a 300 ms black screen before the reappearance of the 300–600 ms fixation point, resulting in a random 1600–2200 ms inter-trial interval. When the photographs contained no animal, subjects had to keep

their finger on the pad for at least 1000 ms (no-go response). An experimental session consisted of 20 blocks of 96 trials in which target and distractor trials were equally likely in each condition. To prevent learning, each image was seen only once by each subject. On any of the four target trials (1-image, 2-image inter, 2-image intra and 4-image trials), the target image could be shown in each of the four quadrants, resulting in a total of 16 target conditions. On distractor trials, the position of a given distractor was not considered in the analysis, thus resulting in 9 distractor conditions (4 conditions in the 1-image trials in which the distractor could appear in each of the quadrants, 2 conditions in each of the 2-image trials in which both distractors could appear in one -upper/lower or left/right- hemifields and 1 condition in the 4-image trials). The design was counterbalanced so that overall, each image was presented the same number of times in all the different conditions. Subjects were given two training series before the test session. Training images were not used in the test session. Task effects on behavioral measurements were assessed by ANOVA with a Greenhouse–Geisser correction for non-sphericity. Post-hoc analyses were performed using paired *t*-tests with a Bonferroni correction or Wilcoxon tests.

2.4. EEG analysis

Electric cortical activity was recorded from 32 tin electrodes mounted in an elastic cap in accordance with the 10–20 system (Oxford Instruments) with the addition of extra occipital electrodes and using a Synamps amplifier system (Neuroscan Inc.). The ground electrode was placed along the midline, ahead of Fz. Impedances were systematically kept below 5 k Ω . Signals were digitized at a sampling rate of 1000 Hz (corresponding to a sample bin of 1 ms) and low-pass filtered at 100 Hz. Potentials were on-line referenced to electrode Cz and averaged-referenced off-line. Baseline correction was performed using the 100 ms of pre-stimulus activity. Two artifact rejections were applied over the [–100 ms; +400 ms] time period: on frontal electrodes with a criterion of [–80; +80 μ V] to reject trials with eye movements, and on parietal electrodes with a criterion of [–40; +40 μ V] to remove trials with excessive activity in the alpha range. Only correct trials were averaged except when specified in the text. ERP components were further low-pass filtered at 40 Hz before analysis. Sixteen differential activities (one for each target condition) were computed by subtracting evoked potentials for distractor trials from evoked potentials for target trials. Analysis concentrated on three groups of electrodes where distinct differential activities were clearly identified: occipital (left: P3', T5, O1', O1, CB1, CB1'; right: P4', T6, O2', O2, CB2, CB2'), frontal (left: FP1, F3, F7; right: FP2, F4, F8) and parietal (P3, P3', Pz, Pz', P4, P4')

electrodes. These groups of electrodes were selected based on our previous experiment on parallel processing (occipital and frontal electrodes: Rousselet et al. (2002); parietal electrodes: Rousselet et al. (unpublished data)). Among the occipital electrodes, O1&O2 pertain to the 10–20 system. The additional occipital electrodes have the following spherical coordinates (theta/phi): O1' = –92/54, O2' = 92/–54, CB1 = –115/54, CB2 = 115/–54, CB1' = –115/72, CB2' = 115/–72, P3' = –74/61, P4' = 74/–61. Note that CB1–CB2, O1'–O2' and P3'–P4' are part of the 10–10 system where they appear respectively as PO9–PO10, PO7–PO8 and PO3–PO4. The parietal electrode Pz' is also referred as POz in the 10–10 system.

Electrophysiological measurements were entered in omnibus ANOVAs with five within-subject factors: image (4 levels), upper/lower visual field, left/right visual field, left/right hemisphere electrodes (occipital and frontal differential activities only), and electrodes (occipital and parietal = 6 levels, frontal = 3 levels). A Greenhouse–Geisser correction for non-sphericity was applied when necessary. Post-hoc analyses were performed using paired *t*-tests with a Bonferroni correction.

The onset at which the ERP amplitude on target trials significantly diverged from that on distractor trials was evaluated by performing paired *t*-tests (15 d.f., $p < 0.05$) at each time bin, i.e. every ms with a 1000 Hz sample rate. In our previous experiment paired *t*-tests were considered significant only when $p < 0.0001$ (Rousselet et al., 2002). In the present study, because of the large number of different conditions, the signal to noise ratio was lower justifying the use of a threshold at $p < 0.05$ to index differential activity latencies. However, in order not to underestimate those latencies, we fixed an arbitrary threshold of 20 successive significant *t* values to index a differential effect rather than the 15 steps previously used. Thus, a given differential activity latency reported in this paper is the time at which the two conditions start to differ for at least 20 ms.

3. Behavior

In this behavioral section, we will first focus on the comparison between the conditions with 1, 2 and 4 images. The comparison between the intra- and inter-hemifield 2-image conditions will be the subject of a second part. Finally, laterality effects will be approached.

3.1. Comparing the 1-, 2- and 4-image conditions

Despite the very challenging nature of the task, a good level of performance was reached (Table 1, Fig. 1). Mean accuracy decreased as a function of the number of images to process ($F(1.6, 23.3) = 167, p < 0.0001$) (Figs.

Table 1
Summary of behavioral results: 1 vs. 2 vs. 4 images

Behavior	1 image	2 images	4 images
Accuracy (%)			
Mean accuracy	80.7 (1.1)	74.7 (0.9)	67.6 (0.9)
Model predictions	n.a.	76.9 (1.1)	70.8 (1.3)
Correct go	74.1 (2.2)	68.2 (1.8)	67.4 (1.4)
Correct no-go	87.4 (1.3)	81.2 (1.8)	67.7 (2.0)
RT (ms)			
Mean	477 (11)	493 (11)	504 (12)
Median	457 (11)	469 (11)	475 (12)
Min RT (10 ms bins)	310	320	350

Data shown here have been pooled over quadrants for clarity. Standard error is indicated in brackets. A simple parallel model of processing was used to estimate from the 1-image results the accuracy reduction due to the addition of distractor images (second row). This model (Rousselet et al., 2002) postulates that each of the two simultaneously presented images is processed by a separate and independent mechanism whose accuracy is adjusted to the one reached in the 1-image condition; the two outputs are then pooled together. In the 2-image condition, a correct no-go response on a distractor trial with two different distractors (no-goDD) is only obtained when both distractors are correctly ignored: $\text{no-goDD} = (1 - p(\text{FA}))^2$. For target trials, in which a target is simultaneously presented with a distractor, a correct go response (goTD) is produced either by a hit in response to the target or by a false alarm to the simultaneously presented distractor: $\text{goTD} = 1 - (1 - p(\text{Hit})) \times (1 - p(\text{FA}))$. As target and distractor trials are equiprobable, the overall probability of correct responses if both images are processed in parallel should be: $(\text{no-goDD} + \text{goTD})/2 = ((1 - p(\text{FA}))^2 + 1 - (1 - p(\text{Hit})) \times (1 - p(\text{FA}))) / 2$. The same logic was applied to predict the results with 4 images, with $\text{no-goDDDD} = (1 - p(\text{FA}))^4$ and $\text{goTDDD} = 1 - (1 - p(\text{Hit})) \times (1 - p(\text{FA}))^3$. Thus, the probability of correct responses with 4 images is: $((1 - p(\text{FA}))^4 + 1 - (1 - p(\text{Hit})) \times (1 - p(\text{FA}))^3) / 2$.

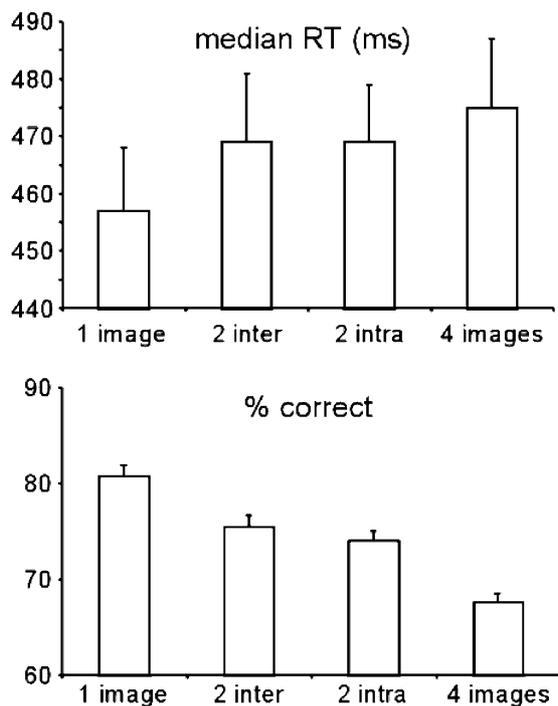


Fig. 1. Median reaction times and mean accuracy with the associated standard errors in the 1-image, 2-image intra- and interhemifield and 4-image conditions.

1 and 2). A higher accuracy was reached in the 1-image condition (80.7%) than in the 2- and 4-image conditions, the 2-image condition (74.7%) being in turn associated with better performance compared to the 4-image condition (67.6%) (Wilcoxon tests, all $z < -3.5$, all $p < 0.0001$). Across conditions, accuracy was better for

distractors (no-go responses: 78.8%) than targets (go responses: 70.0%), reflecting a common bias of human subjects ($F(1, 15) = 11.7$, $p = 0.004$). However, this was not true for the 4-image condition in which accuracy on no-go responses was not different from accuracy on go responses (interaction between go/no-go and image factors, $F(1.4, 21.1) = 18.0$, $p < 0.0001$). The number of simultaneously presented photographs affected both the proportion of correct go responses ($F(1.5, 22.6) = 9.1$, $p < 0.003$) and the proportion of correct no-go responses on distractors ($F(1.3, 19.5) = 175$, $p < 0.0001$). Accuracy on targets was significantly better with 1 image (74.1%) than with 2 images (68.2%) and 4 images (67.4%) (Wilcoxon tests, both $z < -2.5$, both $p < 0.02$). But the comparison between the 2- and the 4-image conditions failed to reach statistical significance. The accuracy on distractors was also better in the 1-image condition (87.4%) than in the 2- (81.2%) or 4- (67.7%) image conditions, the two last conditions being also significantly different from one another (Wilcoxon tests, all $z < -3.44$, all $p < 0.001$).

We assessed whether the general drop in accuracy due to the increasing number of pictures to process was accounted for by a simple parallel model of processing (as in Rousselet et al., 2002). In this model, each of the simultaneously presented images is processed by a separate and independent mechanism, each mechanism converging on a single output system (see Table 1 caption for details). In our task, a prediction for the accuracy in the 2-image condition can be made on the basis of hit rate and false alarm rate obtained in the 1-image condition. A prediction was computed for each subject. The expected average result (76.9%) is very close to the value observed in the 2-image condition (74.7%). How-

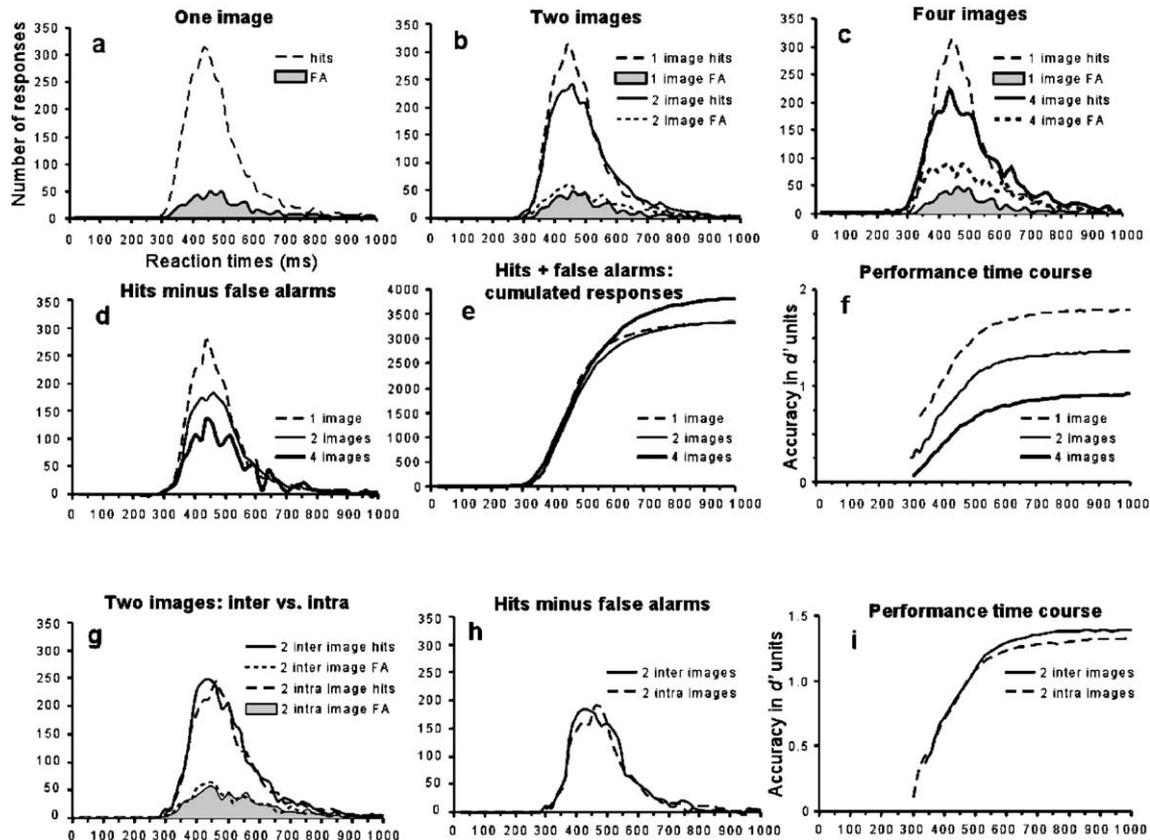


Fig. 2. Reaction time distributions and performance time course. The top two rows compare the behavioral results associated with the 1-, 2- and 4-image conditions. The 2-image curves result from the averaging of the intra and inter-hemifield 2-image conditions. These two conditions are directly compared in the bottom row. In all RT distributions (a, b, c, d, g, and h), the number of correct (hits) and incorrect go-responses (false alarms: FA) are expressed over time, with time bins of 20 ms. As targets and distractors were equally likely in the task, the difference between hits and FA allowed a careful examination of how accuracy varies over time. The RT distributions obtained in the 1-image condition and shown in (a) are also plotted in b and c to allow better comparison with the 2- and 4-image conditions. In panel (d), FA have been subtracted from hits to allow direct comparisons of mean accuracy over time. The cumulated response curves in panel (e) illustrate that subjects tended to produce more go-responses in the 4-image condition. Performance was also analyzed over time using a dynamic d' calculated from the cumulative number of hits and FA at each successive 20 ms time bin. Plateau values correspond to the d' values calculated on global results and were affected by the number of images to process. Comparing the intra- and inter-hemifield 2-image conditions in the bottom row shows that RT distributions were very similar and that the accuracy reached a somewhat higher level when the two images were presented in different hemifields rather than in the same (left or right) hemifield (i).

ever, this difference between the model and the actual data was significant, showing that subjects performed on average 2% worse than expected by our very simple model of parallel processing (Wilcoxon test: $z = -2.4$; $p < 0.02$). In the 4-image condition, the prediction from the 1-image results also tended to be more optimistic (70.8%) than the observed results (67.6%) (Wilcoxon test: $z = -2.8$; $p < 0.005$). Overall, this simple parallel model gives a relatively good account of the observed data but tended—on average—to overestimate performance significantly. However, it has to be noted that this was not true for every subject, given that out of 16 subjects, 5 subjects in the 2-image condition and 4 subjects in the 4-image condition performed better than expected by the model.

Mean and median reaction times increased with the number of images presented, (respectively $F(1.3, 19.7) = 17.5$, $p < 0.0001$; $F(1.3, 19.5) = 10.7$, $p = 0.002$). All

comparisons for the mean RT values (respectively 477, 493 and 504 ms for the 1-, 2-, and 4-image condition) were significant (paired t -tests: all $p < 0.02$). This pattern was also true for median RT values (respectively 457, 469 and 475 ms) ($p < 0.01$) but the difference between the 2- and the 4-image conditions was not significant. To evaluate how fast subjects can perform the task, we also used as an index the minimal processing time defined as the latency of the bin at which correct go-responses started to significantly outnumber incorrect go-responses in the RT histogram (Fig. 2; χ^2 tests on cumulated data at each 10 ms time bin, $p < 0.01$). The minimal processing time needed to correctly respond with 1-image was 310 ms (Table 1, Fig. 2). The temporal cost induced by the addition of one distractor image was 10 ms but increased to 40 ms when four images had to be processed simultaneously.

3.2. The 2-image condition: comparing inter- vs. intra-hemifield competition

In the previous section, the three main conditions in this experiment were compared. Clear evidence was found for a strong competition when four images were presented in the visual field, but some competition was also present with only two simultaneously presented images. However, the global results of the 2-image condition average two different cases. In the first one the two images are presented in different (left and right) hemifields and can be processed independently by each hemisphere, whereas in the second case the two images are presented in the same hemifield and have to be processed by the same hemisphere. Comparing these two cases was important to address the issue of the level of interference between two competing images in our task. If this competition mainly took place within hemispheres, we expected better performances in the inter- than in the intra-hemifield condition. If competition mainly took place at a higher level of integration, for example at a decision stage in frontal areas, then no difference between the two conditions would be expected.

No reliable difference was found in the global mean accuracy (Fig. 1, Table 2) obtained in the inter- and intra-hemifield 2-image conditions (75.5% vs. 74.0%). However when considering separately the accuracy on distractors and targets we found that although the proportion of correct no-go responses on distractors was similar (80.4 vs. 81.9%), go accuracy was significantly higher when the two images were presented in separate hemifields (70.5 vs. 66.0% respectively for inter- and intra-hemifield conditions; interaction between inter/intra and go/no-go factors, $F(1, 15) = 7.3$, $p < 0.02$). However, this effect did not concern the earliest responses triggered in the two conditions (RT < 500 ms, Fig. 2i). Processing speed was remarkably similar between the two conditions: mean, median and minimal RT were virtually identical and did not present any

reliable differences. Similarly, the RT distributions had very close profiles (Fig. 2g, h).

3.3. Hemifield comparisons: left vs. right and upper vs. lower

Although it was not the main purpose of this experiment, it was interesting to examine possible bias between the different hemifields. Accuracy on go responses did not present any reliable effect for the left/right and upper/lower comparisons. On the other hand, processing speed presented some reliable effects. Median RT was slightly shorter in response to targets that appeared in the right visual field (466 ms) compared to those appearing in the left visual field (469 ms) ($F(1, 15) = 6.0$, $p < 0.03$), a difference that was not present at the level of mean RT (right = 491 ms, left = 492 ms, n.s.). The difference between lower and upper visual field targets was more pronounced. Targets presented in the upper visual field were processed significantly faster than targets presented in the lower visual field (mean RT: upper = 488 ms, lower = 497 ms, median RT: upper = 463 ms, lower = 472 ms). Both differences were significant using an ANOVA with images (4 levels), upper/lower and left/right visual field within-subject factors (respectively, $F(1, 15) = 9.8$, $p < 0.007$; $F(1, 13) = 11.3$, $p < 0.004$). This effect was not seen for the earliest responses as minimal RT was the same in both cases (349 ms) and did not interact with other factors.

3.4. Behavior: discussion

In the present study we investigated the capacity of the human visual system to categorize natural scenes at a superordinate level using a very challenging task in which one, two or four images were briefly and simultaneously flashed in different quadrants of the visual field. The main question we wanted to address was whether there was any evidence for parallel processing in such a demanding task.

First of all, it is worth noting that the task used in the present experiment was much more challenging than the one used in our previous report (Rousselet et al., 2002). Monitoring up to four quadrant images instead of one or two images presented along the horizontal meridian had a dramatic impact on subjects' performances: in the 1-image condition, accuracy decreased by 10%, median reaction time (RT) increased by 66 ms and minimal RT increased by 50 ms compared to the former experiment. This discrepancy might be due to an increase in spatial uncertainty in the present experiment because the target could appear in one of four locations instead of one between two in the former experiment. However, such explanation is very unlikely in the light of the results from a previous experiment testing large eccentricities (Thorpe, Gegenfurtner, Fabre-Thorpe, & Bühlhoff,

Table 2
Summary of the 2 image behavioral results: 2 inter- vs. 2 intra-hemifield image conditions

Behavior	2 inter-images	2 intra-images
Mean accuracy (%)	75.5 (1.1)	74.0 (0.9)
Model predictions	76.9 (1.1)	76.9 (1.1)
Correct go	70.5 (2.1)	66.0 (1.9)
Correct no-go	80.4 (1.8)	81.9 (1.8)
RT (ms)		
Mean	491 (12)	495 (10)
Median	469 (12)	468 (10)
Minimal RT (10 ms bins)	320	320

Data shown here have been collapsed over quadrants for clarity. Standard error is indicated in brackets.

2001). In that experiment, subjects had to perform the same go/no-go animal/non-animal task used here, but with photographs of natural scenes centered at up to 70° from the fixation point along the horizontal meridian. Despite the very high spatial uncertainty, subjects still responded correctly on 90% of the trials at 13° of eccentricity. Thus, a more likely explanation for the drop of accuracy in the 1-image condition between the two experiments relies on a change of decisional strategy. This bias might have been introduced by the random presentation of 1-, 2- and 4-image conditions in the same series.

To test this hypothesis, 16 additional subjects who had not participated in the original experiment were tested in two control behavioral studies (8 subjects per study). Different subjects were tested in these two experiments because not enough images were available to avoid stimulus repetition. In the first experiment, subjects were only presented with the 1-image condition and the scene could appear in one of four quadrants. In the second experiment, they were only presented with the 4-image condition. The experimental conditions were identical to those in the original experiment except that subjects performed 15 series of 96 trials in the 1-image experiment and 8 series of 96 trials in the 4-image experiment. Results show that even when subjects were tested with a constant image set size, their performance was not better than when all conditions were mixed together.

In the 1-image experiment the 8 subjects (3 women, 5 men, mean age 25.6 ranging from 21 to 31, 3 left handed) scored 75.8% on average (individual range [69.9–81.6]), which is below the 80.7% obtained with the 16 original subjects. Accuracy was 84.0% [71.7–97.8] on distractors, 67.6% [42.1–84.2] on targets. Mean RT was only 10 ms slower compared to the original data, reaching 487 ms [380–591].

In the 4-image experiment, the 8 subjects (3 women, 5 men, mean age 24.1 [21–29], 2 left handed) performed almost exactly like the 16 original subjects. Mean accuracy was 67.3% [58.6–72.1], reaching 69.6% [50.5–85.7] on distractors and 65.0% [50.8–74.2] on targets. Mean RT was 503 ms [401–643].

These data collected with two control experiments suggest that the results obtained in the present study cannot be explained by response biases due to the random alternation of all the different experimental conditions within the same series. It also suggests that human observers are worse at categorizing animals in natural scenes in visual quadrants than along the horizontal meridian. This issue clearly deserves further investigation.

We now turn to the effects of processing an increasing number of pictures in this task. Compared to the 1-image condition, the addition of a second image in the opposite hemifield (inter-hemifield condition) decreased

accuracy and increased RT significantly. In keeping with the idea that even a parallel model of visual processing with unlimited capacities predicts impairments because of the presence of distractors (Kinchla, 1992; Palmer, 1998), the decrease in accuracy was in large part accounted for by a very simple model of parallel processing. However, the increase in RT obtained in the present study contradicts our previous null effect on RT when the images were presented along the horizontal meridian (Rousselet et al., 2002). This might be taken as evidence that the search was not truly parallel in this task, at least not in the sense of Treisman (1998), where parallelism is defined by flat visual search functions. It is important to note here that the animal categorization task used in the present experiment cannot be directly compared to classic visual search tasks. Indeed, searching for animals in one natural scene already relies on some form of parallelism. Hence processing 4 natural scenes is considerably more challenging than searching for one target object among three distractor objects. Despite this qualitative difference in the nature of the stimuli, VanRullen, Reddy, and Koch (in press) showed recently with stimulus set sizes ranging from 1 to 16 natural scenes, that the animal/non-animal categorization task used in our experiment cannot be performed in parallel, i.e. RT increased with the number of distractors, mirroring the effects found with simple forms. Surprisingly, the animal task can be performed without focal attention, in the periphery, while subjects are concentrated on a demanding central task (Li, VanRullen, Koch, & Perona, 2002). The puzzling contrast between the experimental results found in the visual search task and in the dual-task paradigm has led VanRullen et al. (in press) to hypothesize that natural scenes are processed pre-attentively but not in parallel. While the term “parallel” refers to low-level segmentation mechanisms that can extract odd objects from an array, the term “pre-attentive” implies the existence of neurons in the ventral pathway coding for high-level representations of objects in natural scenes that can be activated without focused attention. These representations would be built through our interaction with the world. Such high-level object “filters” might allow the detection of objects in the dual task used by Li et al. However, these representations would not be immune to local competition in the ventral pathway, which typically occurs in natural scenes as a consequence of the presence of multiple objects (Chelazzi et al., 1998). Thus, a possible explanation for the ‘parallel’ processing presented in our previous report might be due to the fact that neurons responding to complex objects in the occipito-temporal areas are strongly biased toward contralateral stimuli, receiving virtually no interference from ipsilateral stimuli (Chelazzi et al., 1998). Consequently, more competition was expected in the 2-image intra-hemifield condition.

Presenting the distractor in the same hemifield as the target had the same consequences as those reported in the inter-hemifield condition, except that the capacity to detect targets decreased. This effect could indeed reflect intra-hemisphere competition. Alternatively, as we have suggested previously, this competition might rather take place at a higher level of integration, for example in frontal areas (Rousselet et al., 2002). Teasing these two hypotheses apart is rather difficult on the basis of behavioral data. The next section provides electrophysiological evidence that favors the second alternative. But already, the 4-image results are providing cues. The fact that there was a further drop in performance with 4 images compared to the 2-image condition seems to fit with the classic view that IT neuronal receptive fields cover the entire visual field, so that three distractor images would normally be expected to increase the competitive effects on the visual processing of the target image. Paradoxically, in the next section we develop an opposite argument: because IT receptive fields have recently been reported not to cover the entire visual field (Op De Beeck & Vogels, 2000; Rolls, Aggelopoulos, & Zheng, 2003) and appear typically biased toward the contralateral hemifield (Chelazzi et al., 1998), the performance drop between the 2-intra image and the 4-image conditions might be due to a competition taking place at a higher level of integration, possibly in prefrontal cortex.

4. Electrophysiology

Differential activities were computed by subtracting correct no-go trial ERPs from correct go trial ERPs. In the go/no-go paradigm used here, this technique has been shown to allow access to task related effects independently of non-controlled low-level differences (Macé, Rousselet, Sternberg, Fabre-Thorpe, & Thorpe, 2002; VanRullen & Thorpe, 2001) and without the need to make assumptions about putative links between ERP components and underlying sources (Makeig et al., 2002). In previous experiments, the onset latency of the differential activity as proved to be a good indicator of processing speed in categorization tasks (Delorme, Rousselet, Macé, & Fabre-Thorpe, in press; Fabre-Thorpe et al., 2001; Rousselet et al., 2002). In addition, the amplitude of the differential activity has been found to increase with subject accuracy, somehow reflecting the quality of processing (Fabre-Thorpe et al., 2001; Rousselet et al., 2002; Thorpe, Bacon, Rousselet, Macé, & Fabre-Thorpe, 2002). Two components, one occipitotemporal and one frontal, were isolated. Their topography was identical to the one presented in our previ-

ous report (Rousselet et al., 2002). They are analyzed in Sections 4.1 and 4.2.

4.1. Effect of processing an increased number of images on occipital ERP

The left row of Fig. 3 shows the event-related potentials recorded over occipital electrodes. Independently of image status (target or distractor), there was a strong effect of image condition on the amplitude of the overall electrophysiological signal. This effect was certainly due to the large physical differences between experimental conditions. Differential activities were thus used to get access to task related effects independently of these physical differences. Occipital differential activities were almost superimposed in the 1-image condition and the two 2-image conditions. With four images, the differential activity tended to have a later onset and its amplitude was clearly reduced compared to the three former conditions. Paradoxically, the onset latency of the differential activity was significantly longer with one image (175 ms) than with two images presented in both the inter- (155 ms) or intra-hemifield (164 ms) conditions. The longest onset latency was found in the 4-image condition (190 ms). This result is at odds with our previous findings showing either no differences in differential activity onset as a function of behavioral RT (Thorpe et al., 1996) or an earlier onset associated with shorter RT (Delorme et al., in press). This result might be due to a higher variability in the electrophysiological data in this experiment compared to the previous ones probably because of task difficulty. Therefore, we used several other measurements to assess the task effects on visual processing. First, we analyzed the latency and the amplitude of the peak of the differential activity. As in our previous results (Fize, Fabre-Thorpe, Richard, Doyon, & Thorpe, in revision; Rousselet et al., 2002), the occipital differential activity was strongly biased toward sites contralateral to the target (as shown by an interaction between the laterality and the hemisphere factors, $F = 30.8$, $p < 0.0001$), thus the analysis concentrated exclusively on contralateral posterior electrodes. Regardless of the 1-, 2- or 4-image conditions, the differential activity reached its peak at the same latency, around 250 ms (Figure 3). However, its amplitude tended to decrease with task difficulty and thus with error rate ($F = 5.4$, $p = 0.008$). The peak amplitude in the 4-image condition was significantly lower than in each of the three other conditions (all $p < 0.03$). However, peak amplitude in these three other conditions did not differ from one another. Post-hoc comparisons performed separately on each posterior electrode also failed to reveal differences between these conditions. Mean amplitude between 200 and 250 ms post-stimulus presented the same pattern, with two occipital sites at which there was a significant effect of

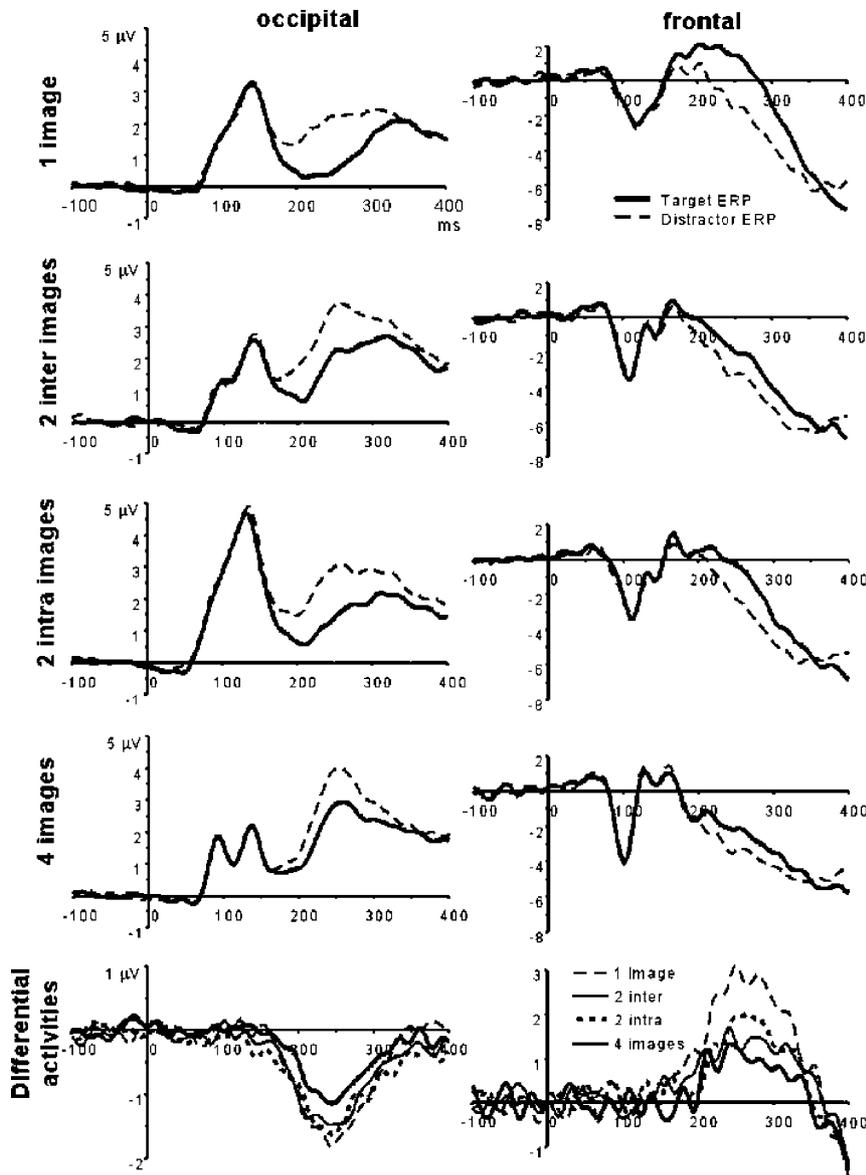


Fig. 3. ERPs and differential activities. ERPs on correct target (plain line) and distractor (dotted line) trials are shown for each condition of presentation at occipital sites contralateral to the target and frontal sites ipsilateral to the target. Occipital signals were characterized by an initial positive deflection followed by a negative going potential. This negativity was increased on target trials, giving rise to a differential activity between target and distractor trials in the 150–350 ms time window. Frontal signals presented the reverse pattern. Data are shown by pooling signals over quadrant and hemisphere dimensions from contralateral electrodes CB1–CB2 (occipital) and FP1–FP2 (frontal).

the number of images (CB1–CB2 and CB1'–CB2', respectively $F = 5.3$, $p = 0.007$; $F = 7.3$, $p = 0.002$), the amplitudes associated with the processing of the three conditions with 1 or 2 images being higher than the one associated with the processing of 4 images (paired t -test, all $p < 0.03$). No mean amplitude differences were found in the 150–200 ms interval. Thus it appeared that one or two images, whether presented in the same or different hemifields, were processed to the same extent in posterior visual areas. It is only in the four-image condition that target processing suffered significantly from the competition induced by the distractors.

4.2. Effect of processing an increased number of images on frontal ERP

Frontal differential activity was higher over sites ipsilateral to the presentation ($F = 5.5$, $p = 0.034$) and therefore analysis concentrated on ipsilateral anterior electrodes. This was expected given recent evidence showing that the signal recorded over frontal electrodes in tasks requiring the categorization of a central image can be explained in large part by dipoles situated in the ventral pathway (Delorme et al., in press). Thus, with one image, the frontal activity seems to partially mirror

with a reverse polarity, the contralateral activity recorded over occipital electrodes. However, we found recently a dissociation between these two activities, frontal electrodes capturing in addition signals related to late stimulus evaluation (Rousselet et al., 2002; see also Hopf & Mangun, 2000; Lange, Wijers, Mulder, & Mulder, 1998; Potts, Liotti, Tucker, & Posner, 1996; Potts & Tucker, 2001). In the present experiment, focusing on ipsilateral electrodes was thus intended to highlight differences between occipital and frontal signals.

Frontal differential activity onsets were found to present a pattern similar to the pattern found at the occipital level. The shortest differential activity in the 1-image condition appeared at 183 ms, which was before 2-intra hemifield images (194 ms) and 4-images (203) but after 2-inter hemifield images (174 ms).

As in the case of the occipital differential activity, the frontal peak latency (around 260 ms, Fig. 3) was not significantly different between the four conditions. Its amplitude was affected by the image factor ($F = 4.9$, $p = 0.017$) but with a different pattern from the one found at occipital sites. The largest amplitude was found in the 1-image condition (Fig. 3, bottom right). It diverged significantly from that obtained in the intra-hemifield 2-image condition ($p = 0.016$) and the 4-image condition ($p = 0.024$) but not from the amplitude in the inter-hemifield 2-image condition. Those three last conditions did not differ from one another. When performed on each frontal electrode, post-hoc analysis showed the same effects (although the comparison between 1-image and 2-image inter-hemifield activities just failed to reach statistical significance, $p = 0.051$ on electrodes FP1–FP2). From 250 to 300 ms post-stimulus, the differential activity mean amplitude reached in the 1 image condition surpassed the mean amplitude in the 3 other conditions at sites FP1–FP2 (all $p < 0.025$).

4.3. ERP results: discussion

In this experiment, ERPs were used to get a better insight into the mechanisms involved in the simultaneous processing of two and four photographs of natural scenes. In particular, the mean amplitude of the differential activity in the different experimental conditions provided a measure of processing as a function of time before behavioral responses were triggered.

One of the main outcomes of this analysis was that the pattern of differential activities in the 2-image inter-hemifield condition replicated the dichotomy found previously between occipital and frontal sites (Rousselet et al., 2002). With a single scene, the differential activity recorded over frontal sites has been shown to mirror in large part the occipital differential activity (Delorme et al., in press; Fize et al., in revision; see also Anllo-Vento, Luck, & Hillyard, 1998; Kenemans, Lijffijt, Camfferman,

& Verbaten, 2002). However, when two different scenes presented in a different hemifield have to be processed simultaneously, an additional mechanism is reflected in the frontal differential activity (Rousselet et al., 2002). Specifically, we found evidence in our previous study and in the present one that the amplitude of the frontal differential effect was reduced when two images were presented despite there being no effect whatsoever on the peak latency and the peak amplitude of the differential effect at occipito-temporal sites. This result is in keeping with the behavioral literature (Friedman & Campbell Polson, 1981; Sereno & Kosslyn, 1991) as well as studies in patients (Luck, Hillyard, Mangun, & Gazzaniga, 1994) showing that each hemisphere might act as an independent resource limited visual processor. In our experiments using photographs of natural scenes, it seems that the occipital areas in each hemisphere were working independently. This was probably due to the brief and lateralized image presentations, each hemisphere being first stimulated by the contralateral image. Furthermore, single-unit recordings in monkeys suggest that the interference between two stimuli presented in two different hemifields does not appear to take place in the ventral pathway, despite the existence of trans-callosal connections (Chelazzi et al., 1998). We thus reiterate our initial conclusion that much of the interference in the 2-image inter-hemifield condition might arise at the level of prefrontal cortex; a proposition compatible with a two-stage competitive model of visual processing (Chun & Potter, 1995). Indeed, the present results seem to fit with the idea of a bottleneck located close to the response output stage. The fact that the differential neuronal activity at frontal electrodes was higher on average for one-image trials than for 2-image inter-hemifield trials suggest the existence of a competition taking place at an integration stage at which object representations processed in occipito-temporal areas would compete to gain control of the unique response output, which is a kind of mechanism well documented in prefrontal cortex (Bichot, Chenchal Rao, & Schall, 2001; Freedman, Riesenhuber, Poggio, & Miller, 2001; Rao, Rainer, & Miller, 1997; Schall & Thompson, 1999; Tanji & Hoshi, 2001). In keeping with this idea, previous studies have suggested that ERP signals recorded over frontal electrodes might reflect a frontal activity related to stimuli evaluation and behavioral response choice (Hopf & Mangun, 2000; Lange et al., 1998; Potts et al., 1996; Potts & Tucker, 2001).

Another major outcome of this experiment was that adding a second image in the same hemifield as the target (intra-hemifield condition) had virtually the same consequences as those reported in the inter-hemifield condition. It was only at the behavioral level that a main difference between the two 2-image conditions appeared, the capacity to detect targets slightly decreasing in the intra-hemifield condition relatively to the inter-hemifield

condition, as already mentioned above. This could be the hallmark of intra-hemisphere competition, as suggested by data showing that competition takes place mainly between stimuli presented in the contralateral visual hemifield (Chelazzi et al., 1998; Hopf et al., 2000). However, we found again that the major source of interference might happen in the prefrontal cortex rather than in the ventral pathway. So it does appear that two images might be processed concurrently in the same hemisphere without much interference. However, it might be that our ERP recordings were not able to capture an occipital effect between the inter- and intra-hemifield conditions because of insufficient signal to noise ratio. A difference between these two conditions could also be expected at the level of the frontal differential activity, where neurons involved for instance in visual-motor decisional mechanisms seem to preserve retinotopic (Moore & Armstrong, 2003; Schall & Thompson, 1999) or hemisphere preferences (Barcelo, Suwazono, & Knight, 2000). Further experiments, perhaps with many more experimental trials to improve the signal to noise ratio, will be necessary to capture these putative signal differences in frontal and occipital activity.

It was only in the 4-image condition that a significant effect was found on the occipital differential activity. The clear impact seen on its amplitude with four simultaneously presented images compared to the 2-image conditions might indicate that the competition in one hemisphere integrated information from both hemifields due to the large receptive fields of IT neurons or to competition involving trans-callosal connections. However, there are two reasons why such conclusion cannot be drawn from this result. First, contrary to popular belief, IT neuronal receptive fields do not typically cover the entire visual field and can instead be rather small (Op De Beeck & Vogels, 2000); they may even be particularly small in size in response to objects in the context of natural scenes as opposed to blank backgrounds (Rolls et al., 2003). Second, there is evidence that ipsilateral stimuli do not enter into competition with contralateral stimuli because IT neurons are strongly driven by contralateral stimuli (Chelazzi et al., 1998). This is also evident in patients suffering from visual extinction after frontal and/or parietal lesions (Driver & Vuilleumier, 2001). When two objects are presented to the two hemifields of these patients, the one contralateral to the side of the lesion tends not to be perceived consciously because it enters in competition with the other one. However, there is evidence that this competition is not taking place (or only partially) in the ventral pathway because the extinguished object seems to be recognized implicitly on the basis of neuronal responses in occipito-temporal areas classically responding to objects (Driver & Vuilleumier, 2001). Hence, as an alternative to the idea that the competition observed with 4 images is

taking place in IT, we suggest that the effect of the 4-image condition on occipital activity might be due to feedback from prefrontal cortex that integrates evidence from the two hemispheres to make a category related decision (Freedman et al., 2001; Rainer, Asaad, & Miller, 1998). This hypothesis fits with the existence of first frontal activations as early as 80 ms after stimulus onset, suggesting that feedback loops have enough time to take place very early during visual processing (Foxe & Simpson, 2002). It also fits with the recent demonstration of frontal modulations at 125 ms on occipital ERPs (Barcelo et al., 2000).

The 4-image condition being so challenging probably led to a very slow and less efficient accumulation of evidence, explaining the later onset and lower amplitude of the differential activity in this condition compared to the 1- and 2-image conditions. However, we do not want to overstate this conclusion, which is only plausible if one assumes that the differential activity recorded over occipito-temporal electrodes reflects at least to some extent the direct involvement of high-level object mechanisms implemented in the ventral pathway. In a similar vein, complementary experiments with high-density electrode recordings will be necessary to isolate precisely the origin of the interference when human subjects are presented with several images simultaneously. Until careful source analyses are performed in this kind of task, the present conclusions are only speculative, but provide a realistic account of the data obtained so far.

5. Some insights into the origin of the differential activity

Although it is not yet possible to draw definitive conclusions regarding the patterns of differential activities recorded in the present task, our experimental protocol can provide some evidence about where in the visual system the target-distractor interference occurred and what is the origin of the differential activity.

5.1. Differential activity on non-correct trials

In this experiment, because of task difficulty, a sufficient number of incorrect responses were available to evaluate the cerebral activity associated with false alarms and missed targets. This analysis was thought to provide a better understanding of the relationship between differential activity amplitude and decision mechanisms underlying response selection. The differential activity presented so far in this paper was calculated by subtracting the mean ERP associated with correct no-go distractor trials from ERP recorded on correct go target trials. Using the ERP on correct no-go distractor trials as a reference, we determined the differential responses produced by incorrect go trials (false

alarms) and by incorrect no-go trials (target misses). To this aim, the signal associated with the correct no-go distractor trials was subtracted separately from the signal associated with each of the two incorrect trials. This produced a false alarm differential activity and a target miss differential activity respectively. The mean amplitudes of the correct, target miss and false alarm differential activities were determined for occipital, frontal and parietal electrodes with time windows of 50 ms (Fig. 4). There was no evidence for a differential activity associated with missed targets, while a clear differential activity was seen with false alarms. The false alarm differential activity was conspicuous and shared the same time course as the classical differential activity but with a smaller amplitude (see Fig. 4 for details and statistical results).

In summary, the cerebral activity elicited by target-images in which the subjects did not detect the target did not diverge from those induced by distractor images. Inversely, when a subject responded incorrectly to a distractor image as if it contained an animal (false alarm), the cerebral activity diverged from other distractor images as in the case of target-images.

5.2. Upper versus lower visual fields

Finally, as the upper and lower hemifields do not have the same cerebral representation (Tootell, Hadjikhani, Mendola, Marrett, & Dale, 1998), the data were analyzed separately for each hemifield and compared. When an image containing an animal was presented in the upper or lower visual field, it defined respectively upper and lower target trials. Results were entered in an ANOVA with five within-subject factors: image (4 levels), upper/lower visual field, left/right visual field, left/right hemisphere electrodes, electrodes (6 levels). The data presented below have been collapsed over the image, left/right visual field and hemisphere dimensions for simplicity. This was possible given that these three factors did not interact with the upper/lower factor.

The occipital differential activity onsets were virtually identical in upper (169 ms) and lower (173 ms) visual fields, but the peak latency presented a reliable advance when the targets appeared in the upper visual field compared to the lower visual field, consistent with the 9 ms behavioral effect ($F = 16.7$, $p = 0.001$, upper = 240 ms, lower = 253 ms). On the other hand, the peak amplitude of the differential activity was higher when targets appeared in the lower visual field ($F = 5.8$, $p = 0.029$). Although this effect seems to contradict the behavioral results, it differed significantly depending on the electrodes ($F = 36.2$, $p < 0.0001$). As depicted in Fig. 5, there were no significant differences between upper and lower signals at the temporal T5–T6 sites and the more posterior CB1'–CB2' and CB1–CB2 sites. At sites medial to T5–T6 and anterior to CB1–CB2 and

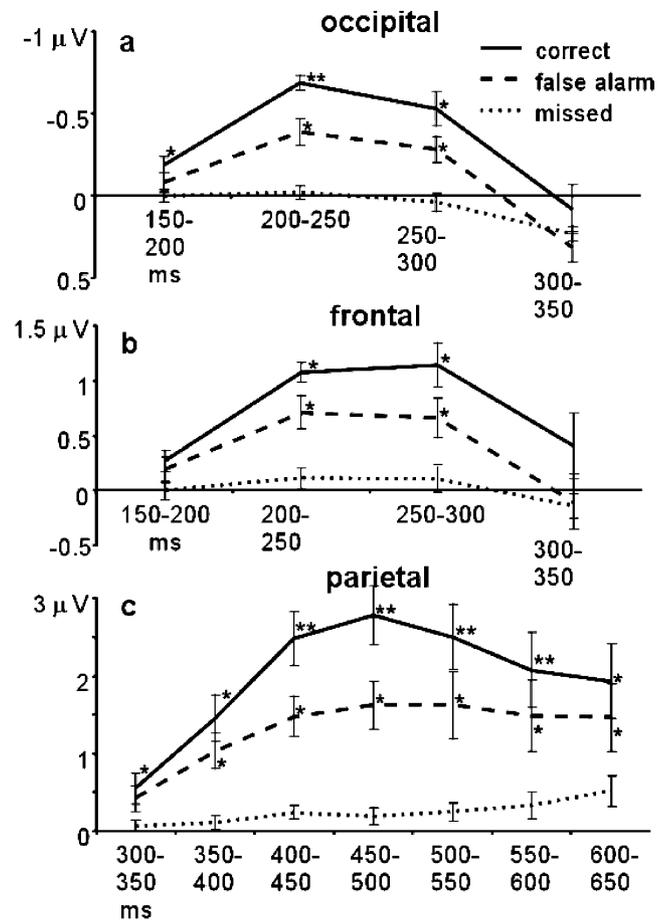


Fig. 4. Mean amplitude of the differential activity to false alarms and missed targets. Note that the differential activity was negative at occipital sites and positive at frontal and parietal sites. Data with associated standard errors are pooled across the image and the quadrant factors using 50 ms time windows. Data were first entered in omnibus ANOVAs with 6 within-subject factors: correct/false alarm/missed, image, upper/lower visual field, left/right visual field, left/right hemisphere electrodes, electrodes (6 levels). Small stars indicate significant post-hoc two by two comparisons (all $p < 0.05$). A single star over the classical or the false alarm differential activity mean amplitude indicates that it differed significantly from the differential activity to missed targets. Two stars over the classical differential activity amplitude indicate that it differed significantly from the amplitude reached in the false alarm and the target missed conditions. At those occipital sites where accuracy effects were larger (CB1–CB2 & CB1'–CB2', 150–200 ms: $F = 4.3$, $p = 0.008$; 200–350 ms: all $F > 12.0$, all $p < 0.0001$) post-hoc analysis revealed that a higher amplitude was also associated with correct trials compared to FA trials in the 150–200 ms time window (CB1'–CB2', $p = 0.046$) and in the 250–300 ms time window (CB1–CB2, $p = 0.013$; CB1'–CB2', $p = 0.014$). At those frontal sites where accuracy effects were stronger (FP1–FP2, $F = 4.7$, $p = 0.006$) this effect was nearly significant in the 250–300 ms time window ($p = 0.052$). Note that parietal effects are plotted on a different time scale and that this delayed effect probably reflects motor response generation.

CB1'–CB2', differential activity was significantly higher for lower visual field targets when compared to upper visual field ones (P3'–P4': $F = 22.5$, $p < 0.0001$; O1'–O2': $F = 9.0$, $p = 0.009$; O1–O2: $F = 34.0$, $p < 0.0001$). A

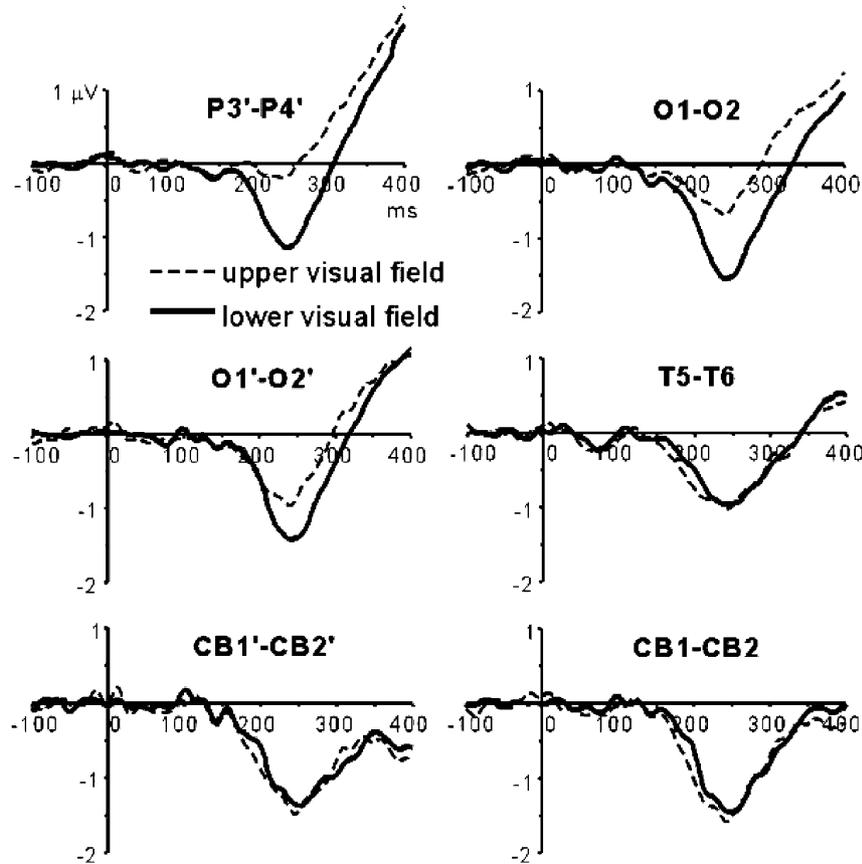


Fig. 5. Upper vs. lower occipital differential activities. Occipital differential activity is shown at each of the six posterior electrode pairs where it was recorded: CB1–CB2 and CB1'–CB2', O1–O2, O1'–O2' and T5–T6 and P3'–P4'. Data are pooled across image, left/right field and hemisphere factors.

study of the mean amplitude of the differential activity between 150 and 350 ms with time windows of 50 ms revealed that the interaction between position and electrode factors was already present in the first time window (150–200 ms: $F = 10.0$, $p < 0.0001$) and in all the following ones (all $F > 9.6$, $p < 0.001$). At frontal sites, these effects were more difficult to assess because of the lower electrode coverage. Differential activity peak amplitude presented a borderline interaction between the hemifield and the electrode factors ($F = 3.7$, $p = 0.057$). This effect was significant between 200 and 350 ms when analysis was performed on mean amplitude in 50 ms time windows (all $F > 3.7$, all $p < 0.05$). This was due to a higher amplitude of the differential activity with upper hemifield targets at the most anterior sites (FP1–FP2) and a higher differential activity amplitude with lower targets at more lateral and dorsal frontal sites (respectively F7–F8 and F3–F4). However, post-hoc analysis on each electrode failed to reach significance.

5.3. Origin of the differential activity: discussion

When the original study on differential ERP effects related to animal categorization was published, the cause of the differential activity was unclear (Thorpe

et al., 1996). The differential activation could reflect the activity of neural mechanisms selectively responding to animals. Alternatively, it could reflect inhibitory mechanisms specific to no-go trials. Indeed, some of the results, and in particular the fact that there was no correlation between the onset latency of the differential effect and behavioral reaction time, as recently confirmed by Johnson and Olshausen (2003), were consistent with such a hypothesis (Thorpe et al., 1996). This activity might also be related to the decision that an animal is present, a decision being made in the ventral pathway, in cortical areas such as V4 and IT, or at a higher level of integration, like in the prefrontal cortex where explicit categorization is thought to take place.

In the present experiment, we were able to test more directly these various hypotheses. The absence of differential activity for missed targets and the presence of a reliable differential activity effect associated with false alarms is consistent with the hypothesis that this activity could reflect the activation of neurons tuned to animals or animal features. It is reasonable to imagine that once a sufficient number of these neurons are recruited by the visual stimulation, their activity triggers a behavioral response, whether the target was really there or not. Although this conclusion might provide us with a simple

account of the origin of the differential activity, an additional argument suggests that it might not be related directly to the activation of populations of “animal detectors”. Indeed, we have argued above that the pattern of occipital differential activity in the 4-image condition speaks rather in favor of the involvement of feedback from prefrontal cortex to the ventral pathway in generating such activity. According to this stance, the differential activity would reflect late stages in the target selection process. Given the very indirect way by which this conclusion is reached, we do not want to make a strong case of it. Further experiments are strongly needed to strengthen or falsify this hypothesis. One piece of evidence that strengthens the idea that the occipital differential effects result from feedback related phenomena comes from recent data using a choice saccade task in which two images were presented simultaneously to the left and right of the fixation point and the subjects were required to make an eye movement to the side that contained an animal. Remarkably, the fastest behavioral responses occurred between 130 and 150 ms, that is to say, before the onset of the main differential ERP effect at occipital sites (Kirchner, Bacon, & Thorpe, 2003).

The analysis of the upper versus lower bias in the present results also provides evidence that favors a late account of the differential activity. The fact that the distribution and amplitude of the differential activity depended on the retinal location of the images might be taken as evidence that the structures involved in its generation are themselves retinotopically organized. In contrast with this point of view, if the differential activity would reflect directly the activation of a unitary decision mechanism, there would be no reason for it to show differences depending on where the target is located. Luck, Girelli, McDermott, and Ford (1997) made a similar deduction about the N2pc, an ERP component registered over posterior electrodes contralateral to the target in a visual search task. They found that the N2pc was larger for lower compared to upper visual field targets, in agreement with the hypothesis that this activity was generated in a human area V4 homologous to the monkey area V4. In monkeys, V4 is organized so that most of the lower visual field is represented dorsally, while the upper visual field is represented ventrally (Gattass, Sousa, & Gross, 1988). If we make the plausible assumption that this organization is preserved in humans, neuronal activity originating in V4 would be more easily recorded by posterior electrodes following the presentation of lower visual field targets, because these electrodes would be situated closer to the putative dorsal representation of the lower visual field. Given that we found the same pattern of results in the present experiment, it seems unlikely that the effects reported here are produced in areas homologous to monkey IT cortex. Indeed, while neuronal responses in IT preserve some retinotopic information (DiCarlo & Maunsell,

2003; Kline, Amador-Garza, McAdams, Maunsell, & Sereno, 2003), the population of IT neurons as a whole does not present a bias such as the one found in V4 in its anatomical organization. The idea of the involvement of an area like V4 in generating the differential activity is further strengthened by the lack of interference between two images presented in the same hemifield, as discussed previously. Furthermore, we have already argued that the decrease of the occipital differential activity amplitude in the 4-image condition is not likely to reflect the involvement of IT cortex in the generation of the differential activity.

If we now suppose that intermediate level areas are involved, equivalent to V4 for example, there are various options. One is that neurons at this level in the visual system are already capable of showing category specificity at the moment they start firing. But the relatively late (150 ms) latency for the start of this activation seems rather too long for feed-forward V4 activation. An alternative would be to suppose that the differential activation of intermediate level structures could result from the activation of back-projections from structures such as IT and possibly prefrontal cortex. One reason for such reactivation might be to form a more detailed visual representation of the selected object. We must also leave open the possibility that the categorization of animals in natural scenes, as indexed by the differential activity, does not rely on “high-level” representations, but rather on features of intermediate complexity that might be more diagnostic for this kind of task (Rousselet, Macé, & Fabre-Thorpe, 2003; Ullman, Vidal-Naquet, & Sali, 2002). This would leave more time for interactions in the ventral pathway to occur. Alternatively, or in addition, the differential activity might reflect the spatial selection of a target based on its component features. This spatial selection might require interactions between prefrontal cortex and the ventral pathway (e.g. Barcelo et al., 2000; Gehring & Knight, 2002; Moore & Armstrong, 2003). This proposal is very similar to the one made by Luck and colleagues using visual search of relatively low-level properties (Hopf et al., 2000; Luck, Girelli, et al., 1997) and follows the lines of evidence showing that visual discrimination might rely on spatial selection before a response can be produced (Chelazzi, 1999).

However, it is not clear for the moment whether the differential activity reported in studies from our group can be directly compared to the N2pc reported by Luck and colleagues. The N2pc typically has an onset at about 180 ms post-stimulus and is proportionally larger for increasingly difficult searches, for example when distractors share more and more features with the target, and is absent for simple search tasks (Luck & Hillyard, 1994). It is larger for conjunction targets than for single-feature pop-out targets (Luck, Girelli, et al., 1997). It is also larger for a target and a distractor placed close

together in one hemifield than when a target and a distractor are in different hemifields (Luck, Girelli, et al., 1997) and appears to reflect the attenuation of distractor interference (Hopf, Vogel, Woodman, Heinze, & Luck, 2002). Together with the finding of a larger N2pc when subjects are required to foveate the target (Luck, Girelli, et al., 1997), this suggests a close link between this occipital modulation and spatial attention. The generators of this component seem to be in lateral occipito-temporal regions, with an additional contribution from posterior parietal cortex when the task is particularly challenging (Hopf et al., 2000). This pattern of results directly links the N2pc component to single-unit attention effects observed in areas IT and V4 of the macaque (Chelazzi et al., 1998; Chelazzi, Miller, Duncan, & Desimone, 2001; Luck, Chelazzi, Hillyard, & Desimone, 1997) as discussed in Luck, Girelli, et al. (1997).

The problem is that we never manipulated all these factors in our own experiments with natural scenes. Moreover, the amplitude of the differential activity was almost systematically larger with higher accuracy. In fact, most of the time the amplitude of the differential activity appears to be inversely proportional to the difficulty of the task as stated in the introduction and as shown in the present experiment. New experiments are required to further understand the relationship between the differential activity and the N2pc, but it would be surprising if the two components reflected totally different mechanisms.

Alternatively, the differential activity reported here might be more related to the occipito-temporal N1 component, which shares a similar latency and distribution to the differential activity effects seen in our task. Interestingly, the mechanism reflected by the N1 seems to be a discrimination process (Mangun & Hillyard, 1991; Vogel & Luck, 2000) that takes place within the focus of spatial attention (Luck, Fan, & Hillyard, 1993; Luck & Hillyard, 1995; Luck et al., 1994). But contrary to the finding that the amplitude of the N1 discrimination effect is unaffected by the difficulty of the task (Vogel & Luck, 2000) we found in the present experiment and repeatedly in previous experiments from our group that the amplitude of the differential activity is modulated by the task difficulty (Delorme et al., in press; Fabre-Thorpe et al., 2001; Thorpe et al., 2002).

For the moment it is not clear how the differential activity reported here and in previous experiments from our lab is related to the N2pc component and N1 discrimination effects. But at the same time it is striking to see how all these studies converge on the conclusion that the discrimination of a target stimulus, be it in a visual search task or a foveal discrimination task, systematically relies on some sort of spatial selection. A similar conclusion has been reached from the studies of patients suffering from hemineglect following a parietal lesion. Despite an intact ventral pathway ipsilateral to the le-

sion that allows object processing up to the semantic level, these patients are not conscious of and cannot act upon stimuli contralateral to the lesion (Driver & Vuilleumier, 2001). It has been suggested that even if objects are processed in parallel in the ventral pathway, the parietal cortex, probably in relation with the frontal cortex, might trigger a final shift of spatial attentional resources toward the potential target in order to make an explicit judgment about it (Chelazzi, 1999). In difficult conditions, when signal to noise ratio associated with the target can be relatively low, this shift of spatial resources is also thought to amplify the outcome of the target selection by a parallel competitive mechanism in the ventral pathway (Chelazzi, 1999). Thus, whether the ventral pathway works in parallel or not, there may well be a serial stage in visual processing that is needed to explicitly select a stimulus representation. This might be what is reflected by the differential activity reported here.

If this hypothesis is true, it would provide stronger temporal constraints for models of visual object processing than was assumed previously. Specifically, feedforward models of the ventral visual system might be able to account for the initiation of the spatial selection of targets in natural scenes in 150 ms. This view is also consistent with several innovative models of visual processing in which high level units interact very rapidly with low level units in order to refine and/or select object representations, possibly by an interplay between ventral and dorsal visual pathways (Bullier, 2001; de Kamps & van der Velde, 2001; Deco, Pollatos, & Zihl, 2002).

6. Summary

This experiment investigated the limits of parallelism in a task requiring human subjects to detect animals in one, two or four photographs of natural scenes presented briefly and simultaneously in different quadrants. At the behavioral level, accuracy decreased and reaction times increased with the number of images to process. Thus, animals did not “pop-out” from natural scenes. However, a simple parallel model of visual processing provided a relatively good fit of the accuracy data obtained. At the electrophysiological level, the subtraction of distractor ERPs from animal ERPs revealed a differential activity whose amplitude seemed to be related to behavioral accuracy, whereas no correlation could be found between its latency and the behavioral reaction times. Occipital differential activities suggested a parallel processing of two natural scenes, whether they were presented in different hemifields or in the same hemifield. Both behavioral and electrophysiological data suggested that the main interference in this task was not due to intra-hemisphere competition. Furthermore,

based on the literature reporting single-unit and neuro-psychological data, the drop in behavioral performance and in amplitude of the occipital differential activity observed in the 4-image condition was interpreted as being due to feedback from prefrontal cortex. This hypothesis is strengthened by the finding that the major source of interference was found at the level of frontal electrodes, and not occipital electrodes, a dissociation taken as evidence for a late selection account of the behavioral data. More generally, additional analyses suggested that the occipital differential activity reflects late stages in the target selection process, involving feedback from higher-level areas on retinotopically organized areas such as V4. During the rapid categorization of objects in natural scenes, the occipital differential activity could reflect a final shift of attentional resources within the ventral pathway towards a potential target.

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