European Journal of Neuroscience, Vol. 21, pp. 2007–2018, 2005

Rapid categorization of achromatic natural scenes: how robust at very low contrasts?

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Keywords: animal categorization, EEG, human performance, low contrast, magnocellular, natural images

Abstract

The human visual system is remarkably good at categorizing objects even in challenging visual conditions. Here we specifically assessed the robustness of the visual system in the face of large contrast variations in a high-level categorization task using natural images. Human subjects performed a go/no-go animal/nonanimal categorization task with briefly flashed grey level images. Performance was analysed for a large range of contrast conditions randomly presented to the subjects and varying from normal to 3% of initial contrast. Accuracy was very robust and subjects were performing well above chance level ($\approx$ 70% correct) with only 10–12% of initial contrast. Accuracy decreased with contrast reduction but reached chance level only in the most extreme condition (3% of initial contrast). Conversely, the maximal increase in mean reaction time was $\approx$60 ms (at 8% of initial contrast); it then remained stable with further contrast reductions. Associated ERPs recorded on correct target and distractor trials showed a clear differential effect whose amplitude and peak latency were correlated respectively with task accuracy and mean reaction times. These data show the strong robustness of the visual system in object categorization at very low contrast. They suggest that magnocellular information could play a role in ventral stream visual functions such as object recognition. Performance may rely on early object representations which lack the details provided subsequently by the parvocellular system but contain enough information to reach decision in the categorization task.

Introduction

There is a huge literature concerning the sensitivity of the visual system as a function of contrast, but the vast majority of these studies have involved electrophysiological or behavioural responses to relatively simple visual stimuli such as static, moving or flickering gratings and bars (De Valois *et al*., 1974; Kaplan & Shapley, 1982; Schiller *et al*., 1990; Sclar *et al*., 1990; Shapley, 1990). A few studies have looked at particular visual tasks such as letter and figure recognition, conjunction search or reading (Legge *et al*., 1987; Strasburger *et al*., 1991; Strasburger & Rentschler, 1996; Nasanen *et al*., 2001; Cheng *et al*., 2004). Complex objects and human faces at different contrasts were used in two studies. In the first one, the authors used a limited set of hand drawings at four different contrasts and showed that accuracy performance remained high above 10% contrast. Moreover, the response along the ventral stream brain areas became increasingly contrast-invariant (Avidan *et al*., 2002). The second study used a simple detection task and contrast was at most divided by two, with a marginal effect on reaction time (Lewis & Edmonds, 2003). To our knowledge, no other study involved high-level object recognition and scene processing as a function of contrast. This is unfortunate given that object recognition in natural scenes is one of the most important functions of the visual system.

Under normal visual conditions, human beings can be extremely fast in extracting the meaning of natural visual scenes (Potter, 1976; Intraub, 1981; Keysers *et al*., 2001). In a go/no-go categorization task in which subjects have to determine whether or not a photograph of a natural scene contains a target object (e.g. an animal or a means of transport) they are able to score $\approx$94% correct, with early motor responses appearing before 300 ms (Thorpe *et al*., 1996; VanRullen & Thorpe, 2001a). However, in everyday life, visual conditions are often far from being optimal; at dusk or dawn, for example, luminance and contrast can be very low and conditions might not allow the processing of colours. When faced with such challenging everyday conditions our visual system still appears very efficient. To what extent is high-level scene categorization possible when the contrast of the image is severely reduced, as in the case of a natural phenomenon such as fog?

Low contrast and luminance prevent information about colour from being used efficiently, and it might be thought that the absence of colour would have a major impact on performance. Indeed, there have been a number of studies showing that colour can have an early important role for high-level visual tasks (Gegenfurtner & Rieger, 2000; Delorme *et al*., 2004), but previous studies from our laboratory have also demonstrated that removing of colour information in rapid visual categorization tasks has remarkably little effect (Delorme *et al*., 2000). Specifically, the influence of colour cues on the onset of correct 'go' responses towards targets is not visible before 400 ms, at which point more than 50% of the responses have already been produced. An achromatic object representation can thus be sufficient to trigger an adequate motor response. Because the achromatic magnocellular information reaches V1 $\approx$20 ms before the chromatic parvocellular information (Maunsell & Gibson, 1992; Nowak *et al*., 1995; Schmolesky *et al*., 1998), this result had led us to propose that the magnocellular achromatic pathway could have a crucial role to play in

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Received 6 September 2004, revised 31 January 2005, accepted 2 February 2005

doi:10.1111/j.1460-9568.2005.04029.x

early object processing. However, in such cases this representation is presumably very coarse. Because magnocellular ganglion cells in the macaque retina are eight times less densely packed than parvocellular cells (Silveira & Perry, 1991), with more convergence from photoreceptors (Dacey & Brace, 1992; Dacey & Petersen, 1992; Sun, 2001), magnocellular spatial resolution is relatively poor. Nonetheless, such coarse representations might be sufficient for some forms of object categorization.

The present experiment was specifically designed to determine the robustness of human performance in an animal vs. nonanimal rapid visual categorization task using achromatic natural images and large reductions of contrast.

In addition, we can use the different contrast sensitivities of the different visual pathways to address another question. In the cat's retina, parvocellular (X) cells stop responding below 10% contrast whereas magnocellular (Y) cells can still fire at residual contrasts of 2–3% (Enroth-Cugell & Robson, 1966). Similar results have been found in the macaque retina (Kaplan & Shapley, 1986) and in the lateral geniculate nucleus (Shapley *et al*., 1981; Derrington & Lennie, 1984). Thus, the present experiment could also provide clues about a possible role of magnocellular pathways in object vision at very low contrasts.

Materials and methods

Subjects

Twenty-four subjects (12 males and 12 females) aged 22–52 years (mean 30) performed the experiment. All participants had normal or corrected-to-normal vision. They volunteered for the study and gave their written informed consent. The study conformed to the Code of Ethics of the World Medical Association. Reaction times and accuracy were recorded as well as brain electrical activity using a 32-channel electrocap and a Synamps system.

Go/no-go rapid visual categorization task

The methods were similar to those used in a number of previous studies (e.g. Fabre-Thorpe *et al*., 1998; Delorme *et al*., 2000). Subjects were seated ≈40–50 cm in front of a tactile computer screen in a dimly lighted room. They had to place their fingers on a response pad (a plate with photodiodes) to trigger image presentation. An image was then flashed at the centre of the screen for only 28 ms to prevent ocular exploration. The subjects were verbally instructed to perform a go/no-go animal/nonanimal visual categorization task as quickly and as accurately as possible. When a photograph that contained a target was flashed, subjects had to lift their hand and touch the screen in < 1 s (go response). The reaction time was measured between the onset of the visual stimulus and the finger lift from the response pad. When the trial was a distractor, subjects had to keep their finger(s) on the button (no-go response). To avoid behavioural anticipations, the interstimulus interval time was randomly selected between 1.6 and 2 s (mean 1.8 s). Subjects were given online feedback of results: correct responses, both go and no-go, were indicated by a brief sound.

Stimuli

For the present experiment, 1728 grey-level photographs of natural scenes were used in eight different contrast conditions (13824 stimuli). All images came from a large commercial database (Corel photo library) and were chosen specifically to be as varied as possible (see Fig. 1) with one or more animals of many different kinds and sizes as target images: mammals, fish, reptiles and birds. Distractors were also highly varied with landscapes, trees, flowers, objects of all kinds, human constructions and cars. Subjects had no clues concerning the next photograph and when it contained a target they had no information concerning the viewpoint, the size, the number, the location and the possible occlusion of the target(s).

Images resolution was 384 × 256 pixels and the 17-inch tactile screen was set at a resolution of 800 × 600 pixels. The apparent size of the pictures was 15 × 10° and most images (75%) were horizontal. The 1728 images in 16 million colours were converted to 256 grey levels using Corel photo CD lab software, and then processed using Adobe Photoshop to generate seven other exemplars of each image in which the normal original contrast (N) of the photograph was divided by 4, 8, 10, 12, 14, 16 and 32 (N, N/4, N/8, N/10, N/12, N/14, N/16, N/32). This contrast reduction was done with mean luminance of the image kept constant and corresponds to a division of the standard deviation of the pixel luminance values. Each subject saw each image in a single contrast condition over 18 blocks of 96 images (1728 trials). All contrast conditions for an image were counterbalanced across the group of subjects ($n = 24$) so that any given image was seen at each contrast condition by three different subjects. Contrast conditions and targets and distractors for a given contrast condition were all equiprobable in each testing block and subjects were instructed to try to respond on about half of the trials in each testing condition. Prior to testing, all subjects performed a 50-trial training session using a different set of photographs.

Image statistics

If we consider that the original normal contrast of the image is at 100% contrast, the N/4, N/8, N/10, N/12, N/14, N/16, N/32 stimuli obtained with contrast reduction have, respectively, residual contrast levels of 25, 12.5, 10, 8.3, 7.1, 6.2, and 3.1%.

This residual contrast is a strong overestimation of the overall local contrasts of the test photographs. Classically, contrast studies have used regular sine wave gratings or checkerboard patterns but this type of artificial stimulus is very different from natural images. Local contrasts of natural scenes hardly ever reflect the optimal 100% Michelson contrast that could be achieved with a checkerboard stimulus, as pixels with maximum and minimum values are virtually never placed next to each other. We analysed the local contrast distribution of the images by calculating, for each pixel value converted in luminance intensity of the screen (in candelas per square meter), the mean and maximum absolute Michelson contrast values with the eight surrounding pixels (Fig. 2A and B). Relatively to simpler psychophysical stimuli, maximal local contrasts in natural images seldom reach 100%; nearly 90% of the photographs had < 3% of their maximum local contrast values > 90% Michelson contrast.

Two contrast values, namely 10% and 3%, are of special interest as they correspond to the maximal contrast sensitivity usually attributed to, respectively, the parvocellular and the magnocellular pathways. In the original images, only 41% of the mean pixel-based contrast values were > 10% threshold. This proportion was strongly reduced to 5.9, 0.82 and 0.26 in the N/4, N/8 and N/10 conditions, a proportion that dropped to 0.02 for N/16. For the hardest conditions, N/14, N/16 and N/32, only 4.2, 3.12 and 0.26% of the mean local contrasts were > 3%. Considering the optimal 256 grey level values that were used for the normal condition, subjects could only rely on a maximum of 32 consecutive grey levels for N/8, 25 for N/10, 18 for N/14 and 16 for N/16. These local contrast statistics on the image set show that the visual system had to deal only with local contrasts < 10% for all contrast conditions below N/8 or N/10. The distributions of local contrasts obtained with our set of images were similar to those from

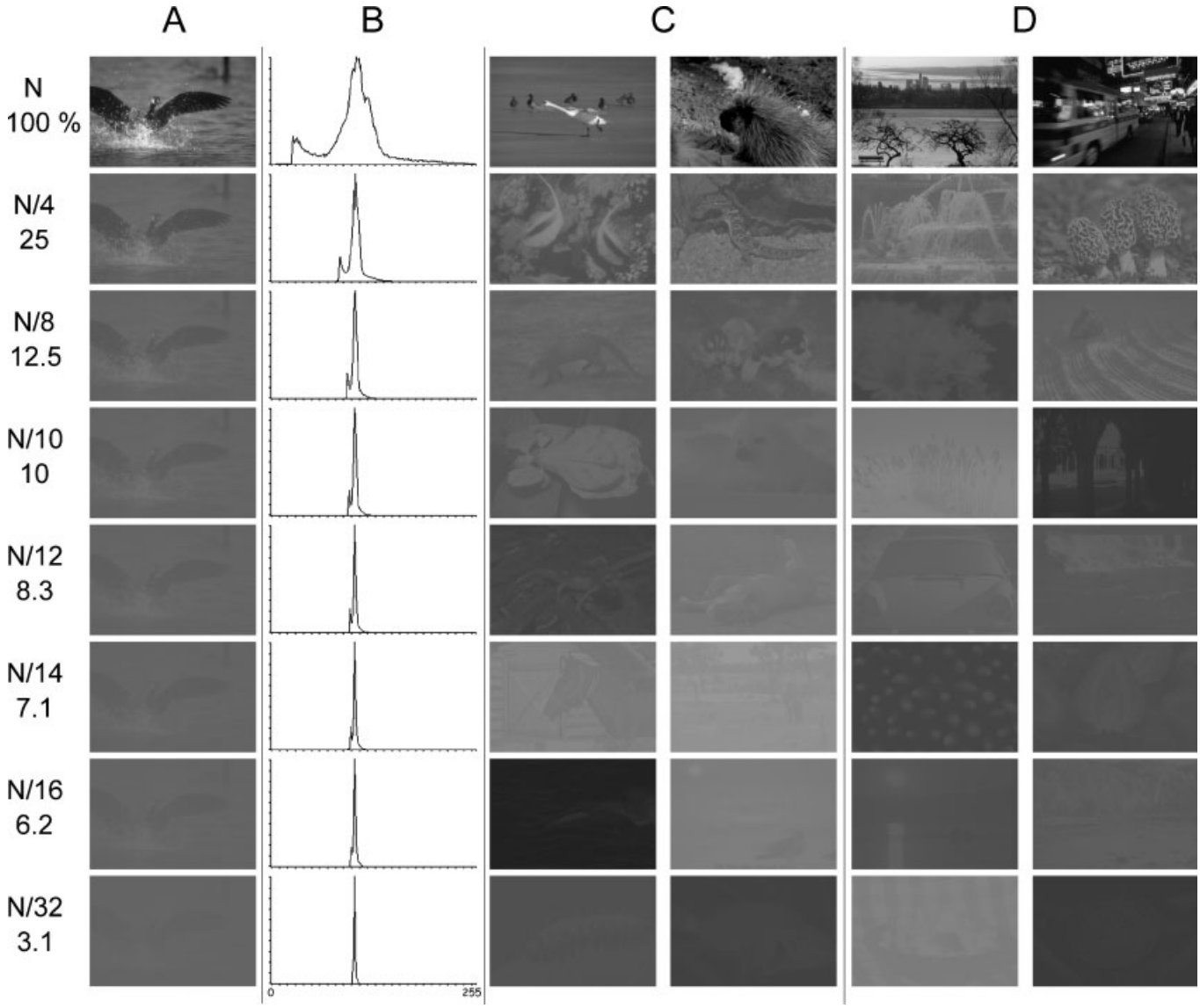

FIG. 1. Examples of stimuli for the eight contrast conditions. From N to N/32, the residual contrast calculated from an initial image considered at 100% contrast in the N condition is indicated below. (A) The same target image is shown in the eight different contrast conditions and (B) the associated distribution of pixel luminance corresponding to the various grey levels (0–255) is shown. Note that the distributions are centred on the same mean luminance value. (C and D) Various examples of target (C) and distractor (D) images for each of the eight contrast conditions are shown.

Ruderman (1994), Brady & Field (2000) and Tadmor & Tolhurst (2000) with small discrepancies which could be explained by differences in image sets.

Evoked-potential recording and analysis

Brain electrical activity was recorded from 32 electrodes mounted in an elastic cap in accordance with the 10–20 system and completed by additional occipital electrodes connected to a Synamps amplifier system (Neuroscan Inc., El Paso, TX, USA). The ground electrode was placed along the midline, ahead of Fz. Impedances were kept < 5 kΩ. The signal was sampled at 1000 Hz and low-pass filtered at 100 Hz with a notch filter at 50 Hz. Potentials were on-line referenced relative to electrode Cz and average re-referenced off-line. Baseline correction was performed using the 100-ms prestimulus interval. Two artefact rejections were applied over the −100 ms to +400 ms time period, the first on frontal electrodes FP1 and FP2 with a criterion of −50 to +50 μV to reject trials with eye movements, and the second on parietal electrodes Oz and Pz with a criterion of −30 to +30 μV to remove trials with excessive alpha rhythms. Only correct trials were averaged. Statistical tests were performed on the original data and the electroencephalogram (EEG) signal shown on figures is low-passed at 30 Hz. Event-related potentials (ERPs) were computed separately for correct target trials and correct nontarget trials and a differential activity was calculated by subtracting the distractor signal from the target signal. This 'differential cerebral activity' was calculated to focus on the differences between the two kinds of trials. It has been shown to reflect successively three different stages of processing. Whereas its early phase, starting ≈ 75 ms post stimulus onset, appears linked to low-level differences between image sets, and its late phase (after 250 ms) to the motor response on target trials, the intermediate phase in the 150–250 ms time window develops in relation with task performance (VanRullen & Thorpe, 2001b; Rousselet *et al*., 2004) and was the focus of the present experiment. As the differential activity

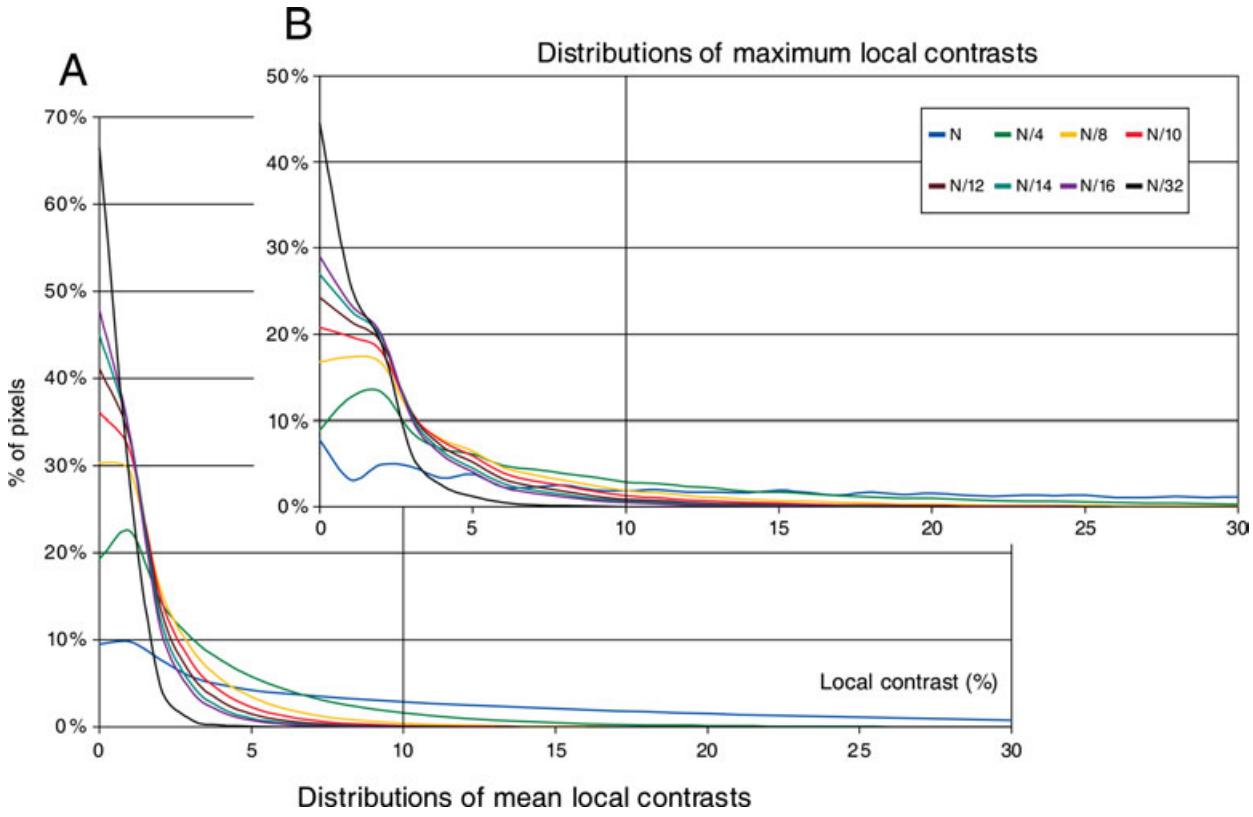

FIG. 2. Distribution of local contrasts (bin size 1%) in all the stimuli and for each condition from N to N/32. The percentage of pixels is plotted in relation to the percentage of (A) mean or (B) maximum Michelson local contrast [Michelson contrast: (Lmax − Lmin)/(Lmax + Lmin)]. The vertical line at 10% corresponds to the contrast commonly given as the parvocellular contrast sensitivity threshold measured in the LGN.

was delayed in extreme contrast conditions, its peak amplitude and peak latency were measured in a much larger time window, 220–320 ms, which included the task-related differential activity in all contrast conditions. To look for the onset of this differential activity a 130–320-ms time window was considered. Following Rugg *et al.* (1995), the onset value of this differential activity is evaluated by applying paired *t*-tests every ms at each scalp location. Normally, the *t*-tests values have to result in probabilities < 0.01 for at least 15 consecutive bins; however, in the present study, because of low signal-to-noise ratio in extreme contrast conditions, an estimation of the onset value is given using a significant *t*-test value < 0.05 for 10 consecutive steps.

Results

Behaviour

Accuracy

We evaluated behavioural performance in terms of accuracy and reaction time for each condition. A χ^2 test between correct and incorrect responses determined whether accuracy was above chance level, set at 50% as targets and distractors were equally likely. For the 100% contrast condition, the mean accuracy was > 88%, a score that is slightly below the accuracy obtained previously (Delorme *et al.*, 2000) with grey level photographs categorized among coloured photographs (93% correct) and closer to the value (91.4% correct) obtained in a challenging categorization experiment when grey level images were followed by a strong mask after 100 ms (Bacon-Mace *et al.*, 2005). As expected, we observed a significant accuracy decrease with contrast reduction (Fig. 3A and Table 1). Compared to the N condition, accuracy dropped by 7% in the N/4 condition where subjects scored 81.2% correct. Each contrast reduction induced a statistically significant drop in accuracy relatively to the preceding contrast condition (Fig. 3A). However, for intermediate conditions (N/8, N/10 and N/12), accuracy remained at a good level (72.4, 67.4 and 62.7% correct) even though the visual system was faced with images where virtually all the mean local contrast values were < 10%. Even at more extreme conditions N/14 and N/16, accuracy, although very poor, was still above chance (N/16: 56%, $\chi^2 = 93.982$, d.f. $= 1$, $P < 0.001$). In fact, chance level was not reached until the hardest task condition in which contrast was divided by 32 (49% correct).

Reducing contrast did not affect all images equally. In particular, it appears that the amount of local image contrast is important. When the 864 target images were classified into three equal groups of 288 images, according to their average value of local contrasts (using either maximum or mean local contrasts), there was no difference in accuracy between the three groups when the contrast was normal (condition N). However, with reduced contrast, there was a clear accuracy advantage for the group with the largest amount of local contrast. The maximal accuracy bias was observed in the N/12 condition with 17% more correct responses for the photographs with highest local contrasts.

Subjects were instructed to try and keep responding on ≈ 50% of the trials in all contrast conditions. Overall, they succeeded well because they responded on 51.0% of trials. However, the response rate depended on the condition with a bias towards not responding at low contrasts (below N/12) and a tendency to over-respond at higher

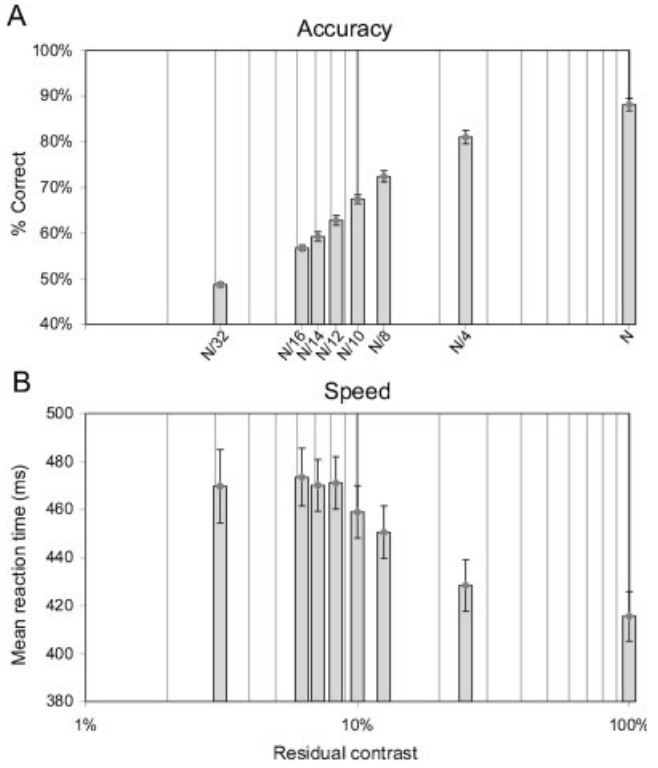

FIG. 3. Average (A) accuracy and (B) speed of performance illustrated by the mean reaction time for the group of 24 subjects and across all contrast conditions as indicated on graph A (from N to N/32). The horizontal axis represents the residual contrast computed with the N condition at 100% contrast and expressed on a logarithmic scale. Error bars are ± SEM. Note that the accuracy takes into account correct responses on target and distractor trials whereas RT values are only obtained with correct go responses on target trials.

contrasts. Interestingly, despite these variations, the false alarm rate remained remarkably constant across all contrast reduced conditions (mean 18%, range 15–19.7% of the total trials). As a consequence, the main effect of reducing contrast was on the proportion of correct hits which decreased from 47% for condition N to 14.1% of the total number of trials at N/32 (see Table 1).

Speed

Mean and median reaction times were also affected by the reduction of contrast but this effect was limited to the first few conditions only. From the N condition [mean reaction time (RT) 416 ms] and up to the N/12 condition (mean RT 473 ms), the increase in mean RT was progressive to reach a maximum of 57 ms (Fig. 3B). Each contrast reduction induced a statistically significant increase (see Table 1). There was virtually no more increase when contrast was further reduced (N/14, N/16 and N/32 compared to N/12). This plateau could suggest that maximal processing of the available information had been done so that any further delay was unable to provide more evidence for decision making.

This increase in reaction time can be seen in the RT distributions computed for each contrast condition (Fig. 4A). The shape of the distribution compared to the 100% contrast condition was nearly unaffected for N/4. As contrast decreased, the distribution was more and more flattened and shifted towards longer latencies. All responses were affected including the earliest ones. As subjects were explicitly required to produce their responses as fast as possible, these early responses are of great interest and can set the minimum input–output processing time. This minimum RT can be defined as the latency at which correct go responses start to statistically outnumber incorrect ones. Table 1 clearly shows that this minimum latency regularly increased with contrast reduction. Calculated on the cumulative number of go responses, it increased from 280 ms for the original N condition to 410 ms for N/16, suggesting that the minimum amount of information used to trigger the earliest responses is available later and later when contrast is reduced.

Electrophysiology

Event-related potentials

The visual and cognitive processing of target and distractor images can be reflected in the electrical activity recorded while the subjects are performing the task. It is assumed that early ERP components are heavily dependant on the physical characteristics of the stimuli and that more and more cognitive processing is reflected by components with longer latencies (Halgren *et al.*, 1994; Foxe & Simpson, 2002; Liu *et al.*, 2002; Proverbio *et al.*, 2002). The effect of contrast reduction was present on the earliest recorded ERP components with the occipital P1 wave being significantly delayed by ≈ 20 ms when

TABLE 1. Accuracy and speed of performance in each of the testing conditions from N to N/32

	N	N/4	N/8	N/10	N/12	N/14	N/16	N/32
Accuracy (%)								
Overall	88.1 ± 6.6	81.0 ± 7.3	72.4 ± 6.0	67.4 ± 4.6	62.7 ± 5.3	59.2 ± 5.2	56.7 ± 2.9	48.7 ± 2.5
Correct go	47.8 ± 1.8	46.0 ± 4.0	40.8 ± 5.0	37.1 ± 6.1	32.3 ± 6.7	28.7 ± 5.5	25.2 ± 8.4	14.1 ± 4.0
Correct no-go	40.3 ± 7.4	35.0 ± 5.4	31.5 ± 4.8	30.3 ± 5.5	30.4 ± 6.0	30.5 ± 5.8	31.5 ± 9.1	34.6 ± 4.5
Go-response rate	57.5 ± 7.1	61.0 ± 8.0	59.3 ± 7.5	56.9 ± 8.6	51.9 ± 10.3	48.2 ± 11.5	43.7 ± 10.9	29.5 ± 17.3
RT (ms)								
Mean	416 ± 50	430 ± 53	452 ± 54	462 ± 54	473 ± 54	472 ± 53	476 ± 59	476 ± 75
Median	407 ± 52	417 ± 53	441 ± 54	450 ± 54	459 ± 52	458 ± 56	459 ± 63	464 ± 73
Minimum RT (ms)								
10-ms bin	280	310	330	370	410	NS	NS	NS
Cumul. 10-ms bin	280	300	320	340	350	370	410	NS

Accuracy and RT values are ± SD. The average overall accuracy is given for the group of 24 subjects together with the relative accuracy on target (go responses) and distractors (no-go responses). As subjects were instructed to respond on half of the trials, the response rate obtained in each testing condition is also indicated. The mean and median RT (in ms) are averages of the 24 individual mean and median RTs. The minimum RT was calculated for each condition with all subjects pooled together. It was computed for noncumulated and cumulated data over 10-ms time bins. A minimum of three consecutive significant χ^2 tests at $P < 0.01$ was required to be confident that the performance was over chance level.

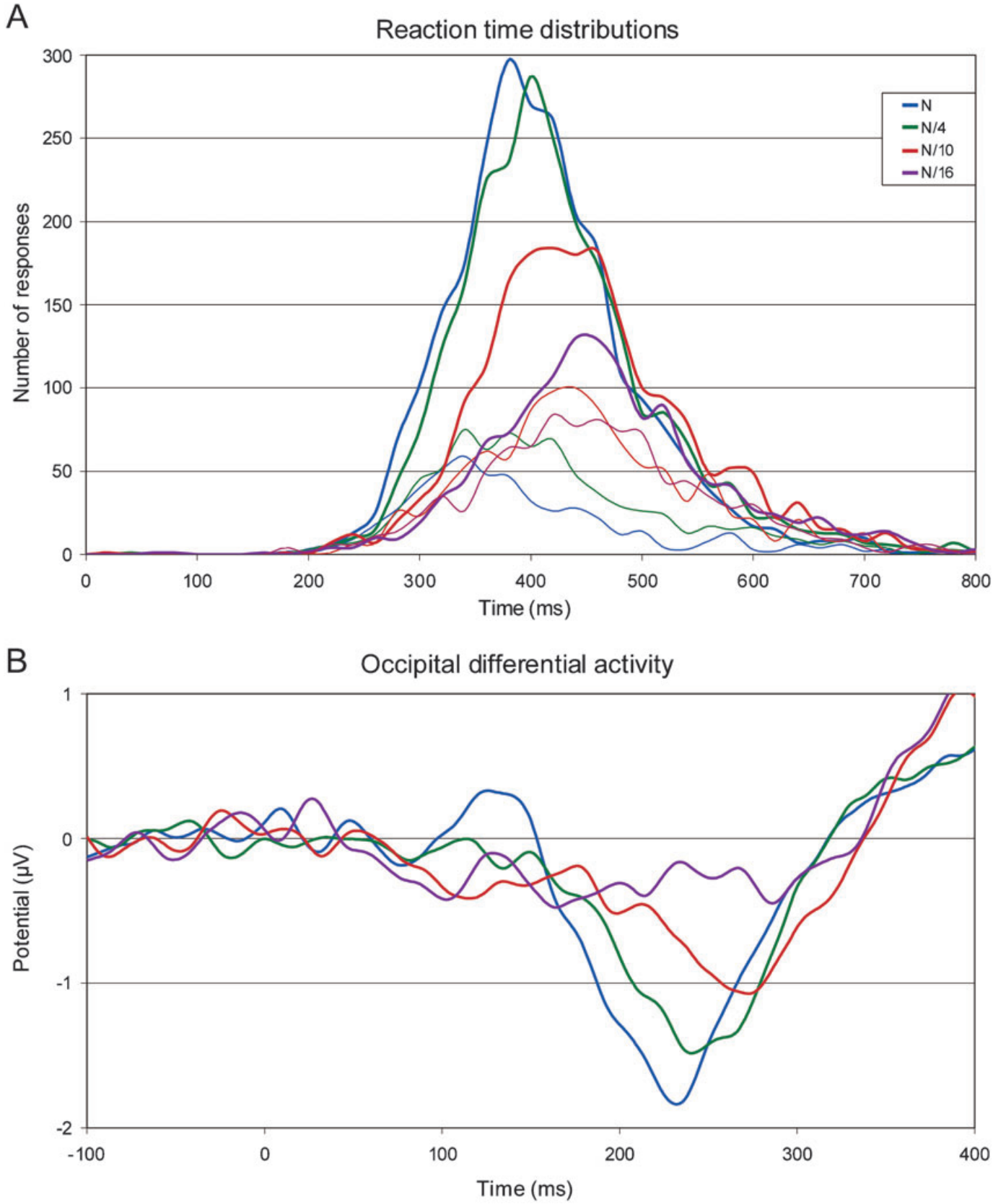

FIG. 4. (A) Reaction time (RT) distributions for the 24 subjects in four of the eight contrast conditions: N (blue), N/4 (green), N/10 (red) and N/16 (purple); time bins are 10 ms. RT distributions of correct go responses on targets are shown in thick lines and RT distributions of false alarms on distractors in thin lines. (B) Differential activity between target and distractor ERPs are averaged from seven occipital electrodes (O1, O2, PO7, PO8, O9, O10 and Oz) for the same four contrast conditions.

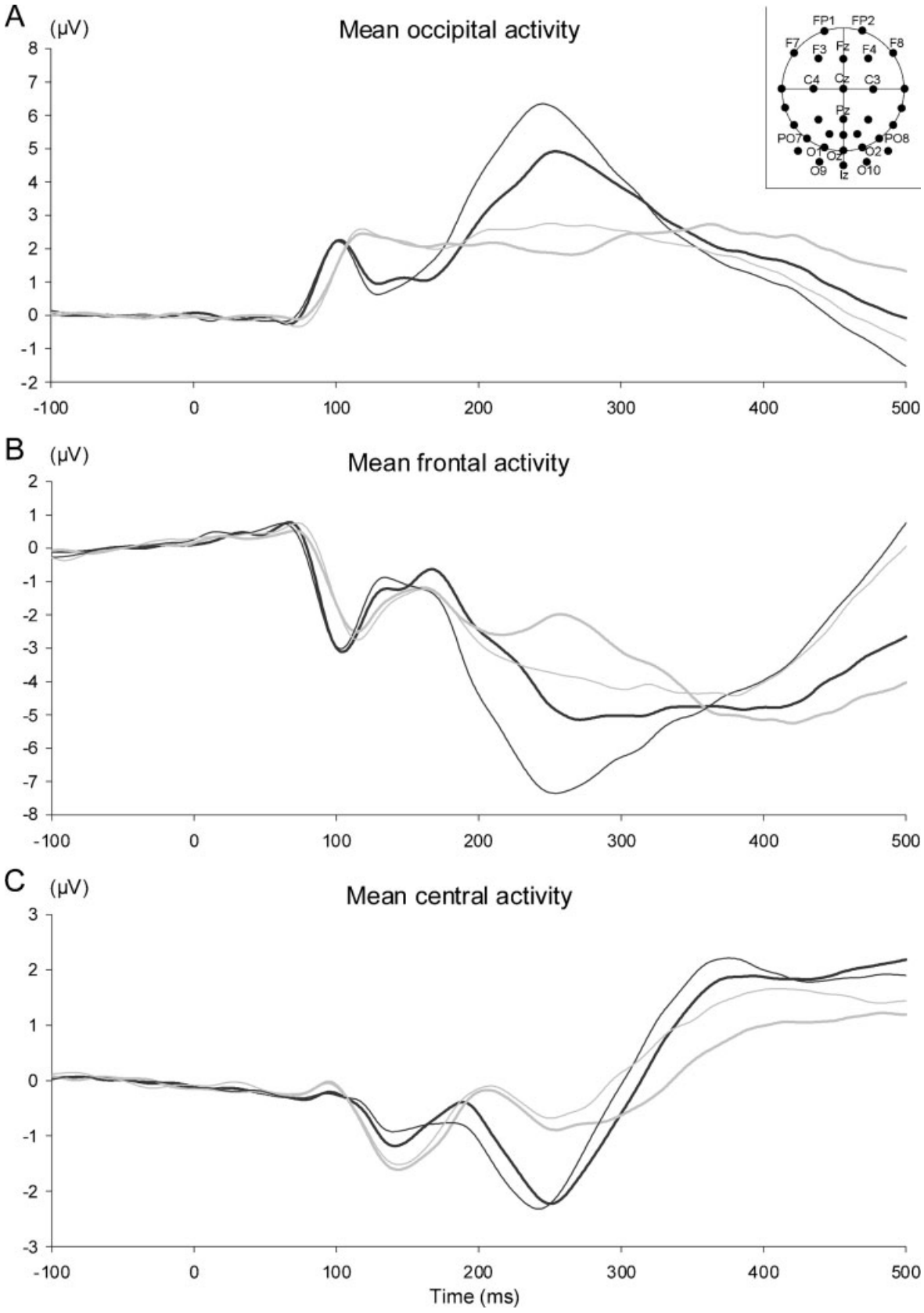

FIG. 5. Mean ERP signal in two contrast conditions, N and N/8; N condition in black, N/8 condition in grey. Targets, thick traces; distractors, thin traces. (A) Average signal from seven occipital electrodes (O1, O2, PO7, PO8, O9, O10 and Oz). (B) Average from five central electrodes (C3, C4, P3, P4 and Pz). (C) Average from seven frontal electrodes (FP1, FP2, F3, F4, F7, F8, Fz). The location in the 10–20 system of all cited electrodes is shown in the top right-hand corner.

TABLE 2. Average onset latency, peak latency and peak amplitude of the differential activity (DA) obtained by subtracting the grand average signal obtained on correct distractor trials from those obtained on correct target trials (24 subjects)

	N	N/4	N/8	N/10	N/12	N/14	N/16
Seven occipital electrodes							
DA onset (ms)	166	171	206	208	221	230	257
Peak latency (ms)	231	240	263	269	270	282	292
Peak amplitude (μV)	−1.94	−1.65	−1.15	−1.26	−0.71	−0.59	−0.75
Seven frontal electrodes							
DA onset (ms)	162	184	217	211	260	227	247
Peak latency (ms)	240	260	263	283	281	281	302
Peak amplitude (μV)	3.11	2.66	2.16	2.20	1.12	1.14	1.45

The grand averages were computed from seven occipital electrodes (O1, O2, PO7, PO8, O9, O10 and Oz) and from seven frontal electrodes (FP1, FP2, F3, F4, F7, F8 and Fz) for the seven contrast conditions from N to N/16.

contrast was divided by 4. However, no further delay was seen with enhanced contrast reductions (Fig. 5). Many studies have shown that with contrast reductions, information flow through the ventral visual system is slowed down due to longer integration times [retina, Shapley & Victor, 1978; lateral geniculate nucleus (LGN), Kaplan *et al*., 1987; Hartveit & Heggelund, 1992; Maunsell *et al*., 1999; V1, Albrecht & Hamilton, 1982; Lupp *et al*., 1976; Maunsell & Gibson, 1992; see also Albrecht *et al*., 2002, for a review]. With contrast reduction, the increased P1 peak latency could partly reflect the increase in neuronal firing latencies in the visual pathway although no scaling effect was observed with increasing contrast reductions.

Differential activities

ERPs were analysed separately for target and distractor correct trials. Target ERP and distractor ERP grand averages were computed for the whole group of subjects. The differential activity was always calculated by subtracting the signal recorded on distractors from the signal recorded on targets. Studies that aimed at localizing the brain generators involved showed that > 90% of the occipital and frontal differential activities could be explained by two dipoles located ventrally and laterally in the extrastriate cortex (Rousselet *et al*., 2002; Delorme *et al*., 2004). In the present experiment, statistically significant differential activity could be observed on occipital sites in all contrast conditions with the exception of the N/32 condition in which subjects performed at chance level.

The early differential activity which has been shown to reflect physical differences between the image sets (VanRullen & Thorpe, 2001b), can be observed on occipital electrodes in the highest contrast condition at ≈ 100 ms. With increasing contrast reductions, this early differential activity disappears progressively as low level differences between target and distractor images become less prominent.

On the other hand, the large differential activity building up after 250–300 ms corresponds to the differential motor activation between correct go and no-go responses. In the present study the effect related to motor activation was also evaluated by comparing left and right EEG signals in right-handed subjects. Whereas there was no asymmetry between left and right occipital and frontal recorded signals, an important lateralization effect was seen when comparing ERPs recorded on central electrodes C3 and C4. This motor activation developed over the left hemisphere at a latency that was never earlier than 250 ms across all contrast conditions. Such left–right asymmetry limited to central electrodes and developing at longer latencies than the task-related signal shows that, despite its large amplitude, the motor activation cannot contaminate the categorization-related activation. This has also been clearly stated by others (Antal *et al*., 2000 and Johnson & Olshausen, 2003), who showed that the sign of the 150–250 ms differential activity remained unchanged after an inversion of the motor response (i.e. no-go on previous targets and go on previous distractors).

Now, focusing on the categorization-related differential activity that appears in normal contrast conditions in the 150–250 ms window after stimulus onset, an effect of contrast reduction could be seen across all task conditions, both on the latency of the differential activity and on the amplitude and latency of its peak (cf Table 2). Concerning the latency from which the differential activity develops on occipital sites (averaged on seven occipital sites: O1, O2, PO7, PO8, O9, O10 and Oz), there was a pronounced increase with contrast reduction from 166 ms in the N condition to 257 ms for N/16 (see Table 2 and Fig. 4B). The delayed onset of the differential activity was associated with a significant reduction in its amplitude. At occipital sites, the peak amplitude was reduced by more than a half between conditions N and N/16 (Fig. 4B). Finally, this drop in amplitude was also associated with an increase in the latency at which it peaks, from 231 ms to 292 ms. Similar results were observed on frontal sites (Table 2).

Correlations between behaviour and electrophysiological recordings

In the original study (Thorpe *et al*., 1996) it was proposed that the differential activation between go and no-go trials could reflect inhibitory mechanisms on no-go trials. Indeed, the lack of correlation found between the onset latency of the differential effect and the behavioural reaction times -recently confirmed (Johnson & Olshausen, 2003) was consistent with such a hypothesis. However, generators for this differential activity were subsequently found in the extrastriate visual areas. Moreover, we recently showed (Rousselet *et al*., 2004) that ERPs associated with missed target trials were similar to ERPs on distractor trials whereas a differential activity could clearly be seen between ERPs on false alarms and ERPs on distractor trials. It is reasonable to imagine that a behavioural response can be triggered once a sufficient number of neurons tuned to animal features are recruited (correctly or erroneously) by the visual stimulation. For a discussion about the possible origins of this differential activity, see Rousselet *et al*. (2004).

It is thus of great interest to look for correlations between behaviour and the various features of the recorded task-related differential activity.

First, across the different contrast conditions, the decrease in accuracy was highly correlated with the decrease in the peak amplitude of the differential activity. In the case of the occipital and the frontal grand averages, the Pearson R^2 correlation indexes were, respectively, 0.93 and 0.88 (Fig. 6A).

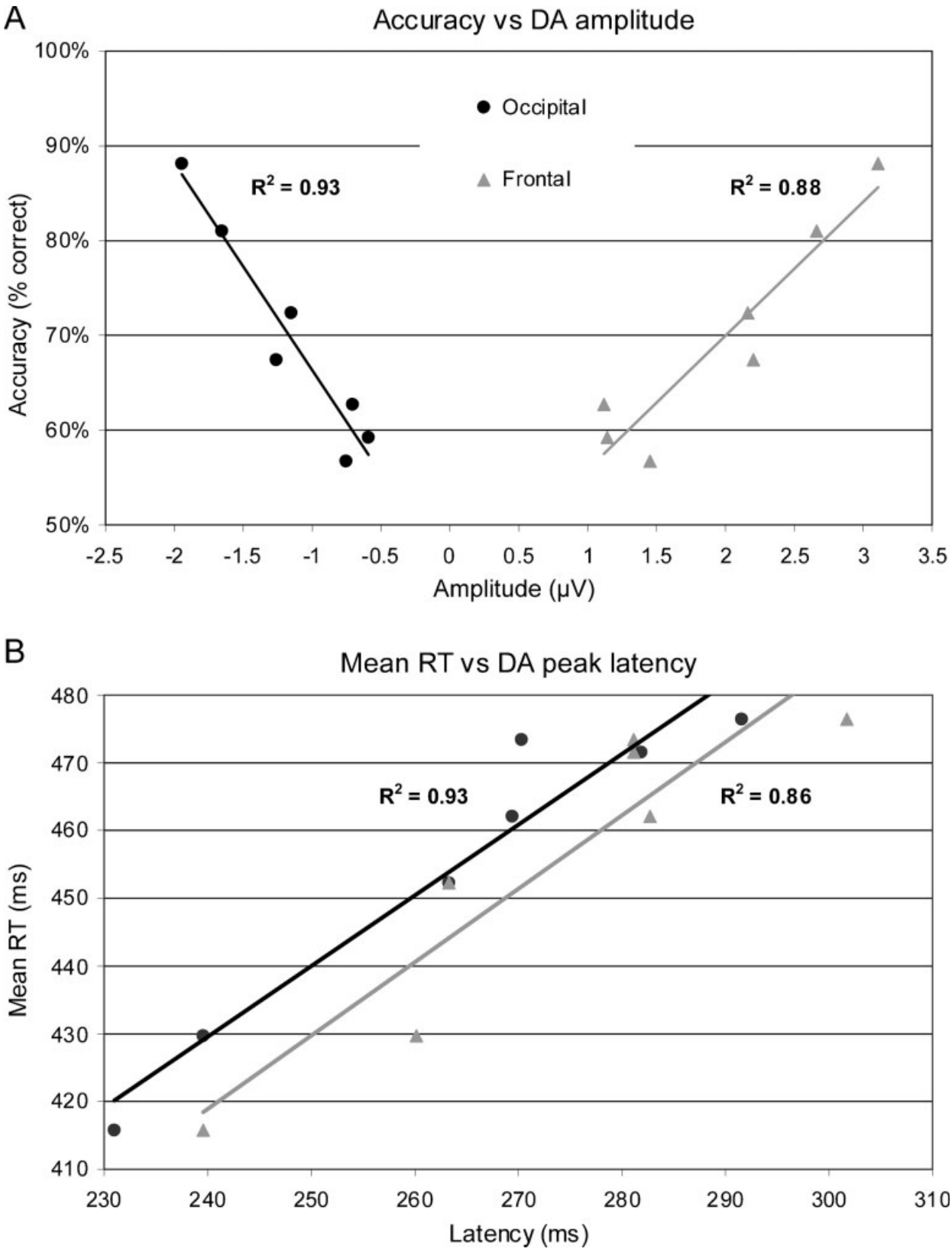

FIG. 6. Correlations between behavioural results and the ERP differential activity (DA) data on occipital (●) and on frontal (▲) electrodes. Mean values were averaged on seven occipital electrodes (O1, O2, PO7, PO8, O9, O10 and Oz) and on seven frontal electrodes (FP1, FP2, F3, F4, F7, F8, Fz). (A) Correlation between the behavioural accuracy in each of the seven contrast conditions and the peak amplitude of the ERP differential activity (expressed in μV). (B) Correlation between the mean reaction time (RT) and the latency of the DA peak (both in ms). R^2 indexes are Pearson's correlation coefficients. Note that the RT values are obtained with correct go responses on target trials whereas the DA signal reflects the difference between ERPs recorded on correct target and distractor trials.

Second, a high correlation (0.93 for occipital electrodes and 0.86 for frontal ones) was also found between the peak latency of the differential activity and the mean reaction time observed in all task conditions (Fig. 6B); the N/32 condition was excluded as no differential activity could be observed and subjects responded at chance level. It is worth noting that the regression curves of occipital and frontal signal correlations are virtually parallel and separated by ≈20 ms, a delay which could reflect the intervention of a second mechanism, presumably more frontal but nevertheless time-linked to the occipital activation.

Discussion

The main result of this study concerns the high robustness of the human visual object recognition system under extreme conditions of stimulus contrast. Subjects still score above chance level with achromatic natural photographs in which only 6–7% of the original contrast is left. In such degraded images, they have to base their responses on a very limited amount of information. In the original N condition, where 256 grey levels were available, 90% of the images used > 200 grey levels but only 3% used the full range of grey levels. When contrast was decreased, the image sharpness dropped dramatically as the number of grey levels was very limited (≤ 25 in the N/10 condition).

The results reported here are the first to specifically address the question of the human visual system efficiency at low contrast with natural image stimuli. In a recent study, Avidan and collaborators presented line drawings of complex objects and faces at different contrasts (Avidan *et al*., 2002) and reported a drop in performance below 10% contrast. Using fMRI, they also showed increasing contrast invariance from V1 to the lateral occipital complex (LOC) in the ventral visual pathway. They stressed the fact that contrast invariance is higher in areas in which neuronal activity is related to complex object representations. Such impressive invariance in high level visual areas to large modifications of contrast has also been stressed in monkeys (Rolls & Baylis, 1986) with natural stimuli such as photographs of faces. Other series of studies have mainly used digits and letters. Strasburger and collaborators (Strasburger *et al*., 1991; Strasburger & Rentschler, 1996) investigated the accuracy of human subjects in a high-level visual categorization task where the contrast of the stimuli was reduced. They found impressive performance levels at low contrast but only when the task was performed centrally, as performance dropped rapidly with eccentricity. The effect of contrast reduction has also been studied in cognitive visual tasks such as visual search for an uppercase character among digits (Nasanen *et al*., 2001), or reading (Legge *et al*., 1987). In these tasks, contrast reduction had a large effect on speed and it also increased the number of eye fixations necessary to perform the task as low contrast impairs peripheral vision.

Unlike the present study where we used a complex object recognition task in which the targets can have a wide range of unpredictable forms and sizes, the results using letters and digits were obtained with a limited number of simple form elements and we could have expected here a dramatic effect of contrast reduction. Although we indeed observed an accuracy decrease, this decrease was very progressive and contrast had to be divided by 32 before subjects reached chance level. Together with the decrease in accuracy, there was a progressive increase in mean reaction time that reached a plateau at N/12. Finally we also observed an increase in the minimum processing time, which could well reflect the fact that subjects need more and more time to gather information about the image features before they had accumulated enough to trigger their behavioural response. This idea can be linked to the model of information accumulation proposed by Schall (2001). Furthermore, this idea of information accumulation is also supported by the results of a masking study using the same sort of go/no-go animal categorization task that showed how performance drops off progressively as the stimulus–mask interval is decreased (Bacon-Macé *et al*., 2005).

In our data, we could relate this accumulation of information to the peak amplitude and latency of the EEG differential activity associated with the task. With contrast reduction we observed a decrease in its amplitude, which may reflect the fact that less and less evidence is available to discriminate targets from distractors (Rousselet *et al*., 2004). This amplitude was indeed highly correlated with the subject's accuracy. Such correlations are interesting as they suggest a direct relation between brain activity and performance level. This differential EEG activity between target and distractor trials is barely visible when subjects performed very poorly (56% correct) in condition N/16, and totally disappears in condition N/32 in which subjects responded at chance level. The slope of the differential activity, less and less steep across the different contrast conditions, may also reflect the speed at which information about the visual scene accumulates over time.

These electrophysiological observations can be discussed in relation to neuronal responses to different contrast conditions. Contrast is a very critical factor for both the strength and the latency of neuronal responses: firing rate is decreased and response onset is greatly delayed when contrast is reduced (Albrecht *et al*., 2002). In the cat retina and LGN, reducing contrast for sinusoidal gratings from 40% to detection threshold leads to a 15–25-ms increase in onset latency (Sestokas & Lehmkuhle, 1986; Sestokas *et al*., 1987). In the striate cortex, a decrease in contrast from 100% to 5–10% generally induces a latency increase of 30–50 ms (Carandini & Heeger, 1994; Albrecht, 1995; Gawne *et al*., 1996; Reich *et al*., 2001). While the effects of contrast on latency up to V1 are relatively modest, they are much more dramatic at higher levels of the visual system. Only one study has reported a value for the increase in onset latency for neurons in the superior temporal sulcus and the infero-temporal cortex (IT) with decreasing contrast (Oram *et al*., 2002). This study used grey level drawings or photographs of various objects at different contrast and showed an increase in latency of up to 150 ms when the contrast is reduced from 100% to 6% (see also Xiao *et al*., 2001). This value is in the same range as the 130 ms increase in minimum processing time observed here on behavioural reaction time between 100% and 6.25% contrast (corresponding to N and N/16; see Table 1). The similarity between the results reported in the present experiment and illustrated in Fig. 4 and the neuronal response curves illustrated in Fig. 6 of the Oram *et al*. (2002) paper is especially striking and argues in favour of a strong relationship between neuronal responses in higher order visual areas, differential EEG activity and psychophysical results. On the other hand this processing delay is not as marked for the mean behavioural reaction times (60 ms) or for the peak latency of the EEG differential activity (61 ms). These two parameters are tightly correlated across all contrast conditions, providing further evidence for a relation between the accumulation of information and the behavioural responses. These latencies increase less than the minimum reaction time as they might reflect the average time needed to process the total amount of available information, an amount that is more and more limited when contrast is reduced.

A role for the magnocellular pathway in early processing for object recognition?

In the rapid animal/nonanimal categorization task used here, subjects could still perform largely above chance level with very low

luminance contrast photographs which might only activate magnocellular cells. Commonly, 10% contrast is considered the minimum contrast value to activate parvocellular retinal cells. The proportion of pixels over this 10% contrast threshold drops below 1% from condition N/8 (see image statistics). Thus, the activation of the parvocellular system might be very low from the N/8 condition with the task being performed in the near-absence of parvocellular inputs at more extreme contrast conditions. Some behavioural (Merigan & Eskin, 1986; Schiller *et al*., 1990) and electrophysiological (Blasdel & Fitzpatrick, 1984; Hubel & Livingstone, 1990) studies have argued for a high parvocellular sensitivity which could result from 'probability summation' in V1 (Watson, 1992). Nevertheless, there is evidence that the significant contrast sensitivity advantage of the magnocellular ganglion cells cannot be totally suppressed by cortical integration (Kaplan *et al*., 1990; for a review see Vidyasagar *et al*., 2002).

Most experiments performed to dissociate the role of the ventral visual system from the dorsal visual system have concentrated on tasks that typically rely on visual features processed by the parvocellular pathways. Even though Sherman (1985) proposed that the parvocellular system could provide high acuity capacity to a coarse magnocellularly driven form of vision, only a few studies have taken into account this possibility (Kruger *et al*., 1988; Strasburger & Rentschler, 1996; Bullier, 2001). A recent study Sugase *et al*. (1999) showed a biphasic response of IT neurons to faces with a first phasic component related to face recognition and a second late tonic component related to finer computations about facial characteristics (such as its expression). Some authors have proposed an influence of the dorsal magnocellular stream over the ventral pathway (Bullier, 2001; Vidyasagar, 1999). However, as magnocellular projections might account for as much as half of the information in the ventral pathway (Ferrera *et al*., 1992; Nealey & Maunsell, 1994), such interactions could also take place within the ventral stream itself (Sherman, 1985; Nakamura *et al*., 1993). The rapid preprocessing of magnocellular inputs could thus guide, in an intelligent way, the detailed visual processing of the slower parvocellular information.

In the present study, the latency of the earliest correct go-responses that appear at $\approx$280 ms set a severe constraint on the input–output processing time. In such a short delay, early motor responses to visual scenes should mainly be based on the coarse processing of the first wave of magnocellular visual information (VanRullen & Thorpe, 2002; Thorpe & Fabre-Thorpe, 2001).

Overall, the robustness of the categorization performance at very low contrast suggests that early object representations underlying behavioural performance in our rapid categorization task are very coarse. They could rely on magnocellular visual information and be subsequently refined by parvocellular inputs. Such coarse transient representations might only be unveiled in tasks using severe time constraints or forced-choice responses.

Acknowledgements

This work was supported by the Integrative and Computational Neuroscience ACI program of the CNRS. Financial support was provided to M.J-M.M. by a PhD grant from the French government. Many thanks to Nadège M. Bacon-Macé for improvements in the manuscript. The authors declare that they have no competing financial interests.

Abbreviations

EEG, electroencephalogram; ERP, event-related potential; IT, infero-temporal cortex; LGN, lateral geniculate nucleus; RT, reaction time.

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