

Contextual guidance of attention

Human intracranial event-related potential evidence for feedback modulation in anatomically early, temporally late stages of visual processing

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Summary

We investigated attentional guidance in early visual areas in the brain by recording event-related potentials directly from the surface of visual cortex. Patients performed a contextual cueing task in which attentive search to targets was guided by implicitly learned spatial context information. The earliest activity in striate cortex (area V1) was not modulated by contextual cueing, whereas later activity beginning at ~200 ms was enhanced by

contextual cueing in V1, V2 and other portions of extrastriate cortex. These results suggest that context can enhance visual processing by temporally late top-down modulation of activity in anatomically early areas of visual cortex. Together with anatomical and neurophysiological studies in animals, these results suggest an excitatory feedback mechanism acting on apical dendrites of pyramidal cells in V1 and other areas of visual cortex.

Keywords: event-related potential; attention; context; top-down modulation; visual cortex

Abbreviations: AUC = area under the curve; ERP = event-related potential; FG = fusiform gyrus; IOG = inferior occipital gyrus; ITG = inferior temporal gyrus; V1 = visual cortex

Introduction

How does the visual system determine where to look? This has been a central question of visual attention research, and various factors have been found to facilitate detection of a target amongst distractors in visual search tasks. Bottom-up influences that guide the deployment of attention are salient features (Bravo and Nakayama, 1992), abrupt onsets (Yantis and Jonides, 1984) and singleton features (Treisman and Gormican, 1988). Top-down, or knowledge-based factors that can guide attention, are novelty (Johnston *et al.*, 1990), familiarity (Wang *et al.*, 1994) and expectancy (Shaw and Shaw, 1977; Shaw, 1978; Miller, 1988). Here, we focus on how top-down contextual information directs attention. Recently, it has been shown that learned spatial context information can guide attention to important locations (Chun and Jiang, 1998; Chun, 2000). Contextual guidance of attention facilitates detection of targets amongst distractors in visual search tasks, reflecting top-down processing based

on implicit memory traces of past views. How do memory-based representations guide attention and search? Does modulation occur at an early stage of visual processing or later?

Early or late modulation by attention?

Researchers have investigated the first point of attentional modulation in the visual processing pathway. Many different studies found that spatial attention modulates extrastriate areas but not striate cortex (V1), using a variety of techniques such as single-cell recording in monkeys (Luck *et al.*, 1997), recording blood flow or electrical activity in humans (Heinze, 1994; Mangun *et al.*, 1997; Hillyard and Anllo-Vento, 1998; Kastner *et al.*, 1998; Mangun *et al.*, 1998), or optical imaging in humans (Gratton, 1997).

However, more recent studies suggest that spatial attention

may modulate V1 activity (Roelfsema *et al.*, 1998; Vidyasagar, 1998; Watanabe *et al.*, 1998; Gandhi *et al.*, 1999; Ito and Gilbert, 1999; Martinez *et al.*, 1999; Somers *et al.*, 1999). Interestingly, some of these studies suggest that attentional modulation occurs by a temporally late mechanism. For instance, attention affects processing in macaque V1 at 100–200 ms (Vidyasagar, 1998), later than the initial sensory processing in macaque V1 at 34–94 ms (Schmolesky *et al.*, 1998). A similar conclusion was reached using both functional MRI and scalp event-related potentials (ERPs) in humans (Aine *et al.*, 1995; Martinez *et al.*, 1999). These findings suggest an important point: attentional modulation may occur in an anatomically early area by a temporally late mechanism.

Temporally late modulation in an anatomically early area can be taken as evidence for re-entrant processing. Top-down attentional guidance may be one common cognitive operation that uses this mechanism (see also Zipser *et al.*, 1996). We investigated this possibility in humans using intracranial ERPs, which allow recording directly from the cortical surface of the electrical events associated with a perceptual or cognitive process. Although scalp ERPs provide valuable details about the time course of perceptual and cognitive processing, this technique has poor spatial resolution. Functional MRI has excellent spatial resolution but poor temporal resolution and is an indirect measure of neural changes. Recording ERPs from the cortical surface and deep structures of patients with intractable epilepsy provides the spatiotemporal resolution necessary to make inferences about the neural events involved in perceptual and cognitive processes (Halgren *et al.*, 1980; Nobre *et al.*, 1994) and the temporal resolution and sensitivity needed to make statements about processing level and order (Allison *et al.*, 1999). Here we summarize the results of the first intracranial ERP study of top-down contextual modulation of neural activity in human visual cortex.

Context and attention

We used the contextual cueing paradigm to study top-down, memory-based attentional guidance (Chun and Jiang, 1998). Subjects were required to look for a target in a visual search display (Fig. 1). Visual search is a commonly used spatial attention manipulation. Previous investigators have used visual search to study spatial attention as measured by scalp ERPs (Luck and Hillyard, 1994*a, b*). In contextual cueing, the distractor items, or the ‘context’, are arranged to form spatial configurations that are repeated over time (Old condition). Subjects find targets more quickly when their location is associated with a repeated spatial context, compared with targets located in novel contexts (New condition), even though they are unaware of the repeated context. Thus, contextual cueing refers to the guidance of attention by implicit memory traces of context information.

The mechanisms of contextual cueing are unknown. Although an intact hippocampus and medial temporal lobe

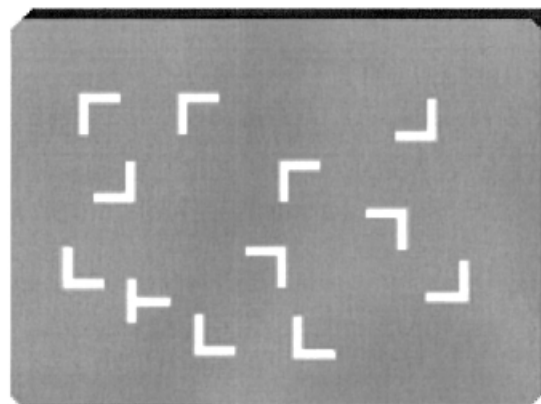


Fig. 1 A sample spatial configuration used in contextual cueing search tasks. In the actual experiment, the elements were coloured and the background was grey. In the repeated condition (‘Old’), many different spatial configurations were repeated over time. In the unrepeated condition (‘New’), the spatial configurations were random in each block, although the target appeared in the same set locations in every block.

system appears to be important for storing spatial context information (Chun and Phelps, 1999), the process of memory-based, top-down attentional deployment is likely to be performed by other areas in the brain. The question is whether such contextual guidance of attention occurs in early visual areas such as V1 and V2 or in later stages of visual processing. Although search tasks are not as direct as cueing tasks for measuring the deployment of attention, Luck and Hillyard have established that scalp ERP signs of attentional enhancement to targets are the same in search and cueing tasks (Luck and Hillyard, 1994*a*). Hence, by measuring both the timing and location of intracranial ERPs, inferences can be made about the mechanism of contextual modulation of attention. First, we examine whether memory-based context information influences activity in V1 and V2. Secondly, if modulation is observed, what is its time course? If contextual guidance modulates neural activity at early stages of cortical processing, a temporally early potential, peaking at ~100 ms in V1 and V2 (Allison *et al.*, 1999), should be affected. However, attentional guidance that modulates activity after 100 ms in these areas would suggest that top-down processing operates by re-entrant feedback from higher cortical areas to early visual areas.

Method

Subjects

Eighteen patients (15 right-handed, average age 29 years) with medically intractable epilepsy, who were being evaluated for possible resection surgery (Spencer *et al.*, 1982), served as subjects. All were patients of the Yale-New Haven Hospital Epilepsy Surgery Program. Prior to resection surgery, electrodes were implanted to localize the seizure focus. The protocol used was approved by the Human Investigations Committee of the Yale University School of Medicine.

Informed consent was obtained. Subjects volunteered to participate and understood the experimental nature of the task. Five patients who did not show a contextual cueing benefit and one patient who had severe EEG artefacts were excluded from the analysis.

Electrode placement and localization

Under general anaesthesia, strips or grids of electrodes were placed subdurally on the lateral and ventral surface of the brain. The exposed surface of each stainless steel electrode was 2.2 mm in diameter; inter-electrode spacing was 10 mm. Electrodes were maximally sensitive to field potentials generated within the 3.8 mm² area in contact with the brain, but were less sensitive to activity generated in surface cortex more than a few millimetres distant from the electrode. Depth probes were inserted from the lateral temporal lobe and were targeted to the hippocampus and other medial temporal lobe structures (McCarthy *et al.*, 1991); each electrode was a cylinder 1 mm in diameter, 2 mm long, spaced 9 mm apart. Each patient had electrodes placed on portions of the occipital, temporal, parietal and frontal lobes. Procedures used to determine electrode locations are described in detail elsewhere (Allison *et al.*, 1999). Briefly, this was performed by localizing electrodes in T₁-weighted three-dimensional MRIs obtained the day following implantation. Locations were translated into the standardized coordinate system of Talairach and Tournoux (Talairach and Tournoux, 1988). Standardized Talairach space was used to characterize electrode locations along the *y*-axis. However, the use of Talairach space in the *x*-axis would lead to incorrect anatomical characterization due to individual anatomical variation in the configuration of gyri and sulci. Thus in the medial–lateral dimension, we used major landmarks for localization. Coronal images allowed identification of electrode sites in V1 (cuneate and superior lingual gyri), V2 (inferior lingual gyrus) and extrastriate areas (fusiform, inferior occipital and inferior temporal gyri).

ERPs

Recordings were made simultaneously from 64 electrodes per patient. ERP recordings were obtained concurrently with clinical EEG and behavioural video recordings, and were time-locked to stimulus onset. ERP recordings were not obtained immediately before or after seizures, and the EEG was normal at recording sites of interest. An experimenter sat at the patient's bedside to monitor general fixation and alertness. Patients were free to scan the display. Possible EEG contamination by the EOG is not a problem in intracranial compared with scalp recordings due to the order of magnitude larger ERPs recorded intracranially. Bandpass was 0.1–100 Hz (–3 dB points), gain was 10 000 and digitization rate was 250 Hz. Recordings were referential to a surface electrode at the mastoid, and were obtained 3–7 days post-implant.

ERP waveforms for each condition and set were stored for later averaging.

Task

The experiment began with instructions followed by a practice block of 12 trials to familiarize patients with the task. They were not informed that the spatial configurations of the stimuli would be repeated on some trials, nor were they told to attend to the global array. They were simply instructed to search for a rotated 'T' target among the rotated 'L' distractors (Fig. 1). A target was present in every trial. Patients were instructed to respond as quickly and as accurately as possible. Each trial began with a small fixation cross in the centre of the screen. The display appeared 200 ms later. After finding the target, they indicated the direction of the target, either left or right, by pressing a corresponding button, which cleared the screen for the next trial. No feedback was given. A mandatory break of 8 s was given at the end of each 32 trials. At the end of the break, the task resumed by itself.

The search display contained an equal number of red, blue, green and yellow items, 12 in total, which appeared within an invisible grid of 8 × 6 locations (Fig. 1). The background was grey. The base of the 'T' target pointed either left or right. The L shapes were presented randomly in one of four orientations (0, 90, 180 or 270°). The visual search array subtended ~37 × 28° of visual angle. The size of the stimuli was ~2 × 2°. The position of each item was jittered within the rectangular array to prevent colinearities with other stimuli. The jittered position for each item was held constant throughout the experiment for Old arrays. Patients viewed the stimuli on a 17-inch colour computer monitor placed 60 cm from the eyes. The experiment was conducted on a PC computer using in-house software.

The two main variables were configuration (Old versus New) and set (1–4). The search task consisted of 24 blocks of 16 trials. Blocks were grouped into four sets, increasing the statistical power. Each block contained eight Old trials and eight New trials. The Old block of stimuli consisted of eight randomly generated configurations which were repeated throughout the entire experiment, once per set. The direction of the target rotation was chosen randomly, but it always appeared in the same location, with the same colour, within a particular configuration. The New configurations were generated randomly. The probability of chance repetition was extremely low, given the large number of unique configurations (17.4 billion) that could be generated from a sampling of 11 out of 47 locations (excluding the target location). The target consistently appeared in eight locations, in the same colour, throughout the experiment, as in the Old condition. This ruled out the possibility that the results were due to sensitivity to position frequency of the target. Thus target colour and location were preserved in both the Old and New conditions. Distractor locations in each configuration were sampled randomly from all possible locations. Target identity was randomized across trials to eliminate stimulus–

response learning. The eccentricity or spatial location of the targets was chosen randomly and assigned to the two configuration conditions.

Analysis

Response times (RTs) of >10 s or <200 ms were discarded. Fewer than 1% of the trials were omitted by this trimming procedure. ERPs from correct trials were averaged into four sets. Each subject's ERPs from the set data were analysed separately and later combined in a within-subject analysis. ERP amplitude was calculated from baseline to peak, where baseline was the mean voltage in the 100 ms period preceding stimulus onset. Latency was calculated from stimulus onset at time 0 to peak.

Visual inspection showed that the primary difference between Old and New conditions occurred at ~ 200 ms. Thus peak amplitudes of short-latency ERPs that showed differentiation by condition were submitted to a t test between Old and New conditions. We defined this potential as any negative deflection showing modulation occurring between 150 and 250 ms. All electrode sites were inspected including sites in parietal and frontal regions. All differentiated ERPs were included in the analysis, regardless of the direction of change, i.e. whether the Old condition ERP amplitude was larger or smaller than the New condition amplitude. Data from adjacent electrode sites were not included to avoid the problem of correlated activity. Because each electrode strip contained 10 electrodes on average, thereby covering a large cortical area, multiple sites on one strip were included in the analysis as long as they were not adjacent. To ensure unbiased analysis of the data, ERPs recorded in set 4 were checked against those in set 3 to ensure that changes were consistent over time. Inconsistent results were assumed to be artefactual and were eliminated.

P100 and N100 sites were defined as any sharp positive (e.g. P100) or negative (e.g. N100) deflection peaking at 80–120 ms in V1 or V2. To assess possible contextual cueing-related changes in long-latency ERPs following P100 and N210, the area under the curve (AUC) was calculated (Allison *et al.*, 1999) within a latency range of 200–400 ms, which captured most of this activity; measurements were pooled for sets 3 and 4 and submitted to t tests comparing condition.

Results

Behavioural performance

The contextual cueing effect is defined as an RT benefit in the Old condition compared with the New condition. Overall accuracy was 85%. Accuracy did not differ by condition, set, or their interaction (all F values <1).

The mean RTs for all correct trials within a set were computed separately for each condition, and were submitted to a repeated-measures ANOVA (analysis of variance) with configuration (Old versus New) and set (1–4) as factors.

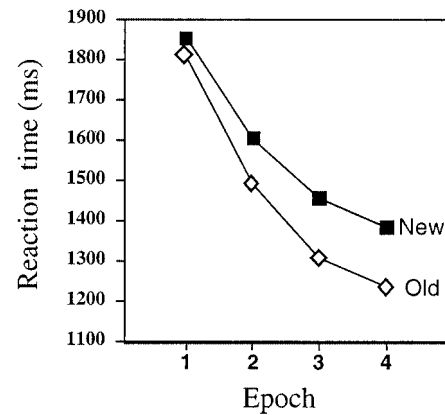


Fig. 2 Reaction times as a function of set for each condition to show the contextual cueing effect. Significant contextual cueing (RT benefit in the Old condition compared with the New condition) began at set 2.

Overall search RT decreased over time [$F(3,33) = 9.615$, $P < 0.0001$] due to skill learning. A second learning component, particular to learning of the repeated configurations in the Old condition (the contextual cueing effect), was also found [$F(1,11) = 47.998$, $P < 0.0001$] (Fig. 2). The overall interaction was not significant, but a comparison across all blocks showed a significant interaction [$F(23,253) = 2.139$, $P < 0.002$], suggesting that performance was similar at the beginning of the experiment, but that learning of contexts rapidly ensued. There was no difference between conditions at set 1 [$t(11) = 1.17$, n.s.] but differences were found at sets 2–4 (all P s < 0.01). By set 4, the cueing benefit was 149 ms.

ERPs

The ERP that consistently differentiated the New and Old conditions in sets 3 and 4 was a negative potential peaking at ~ 208 ms (termed N210) and defined as a sharp negativity with a peak latency between 150 and 250 ms. A representative recording is shown in Fig. 3A. This ERP did not show any statistically significant differentiation by condition early in the experiment, at set 1, suggesting that the enhanced N210 in set 4 was indeed driven by contextual cueing and attentional training.

Over the patient group, there were 48 N210 sites; for statistical purposes, we excluded 13 sites on adjacent electrodes, which may have had correlated activity, leaving 35 sites in 12 patients. Contextual cueing (Old versus New) evoked a significantly larger N210 ($P < 0.0001$). N210s averaged across all patients (one site per patient with the largest condition-dependent amplitude difference, regardless of direction of change) are shown in Fig. 3B. Contextual cueing did not affect peak latency (average latency = 208.5 ± 34 ms in the New condition, 208.9 ± 30 ms in the Old condition) nor were there significant peak latency differences between anatomical regions.

The most prevalent N210 sites were in V2 (43%), although

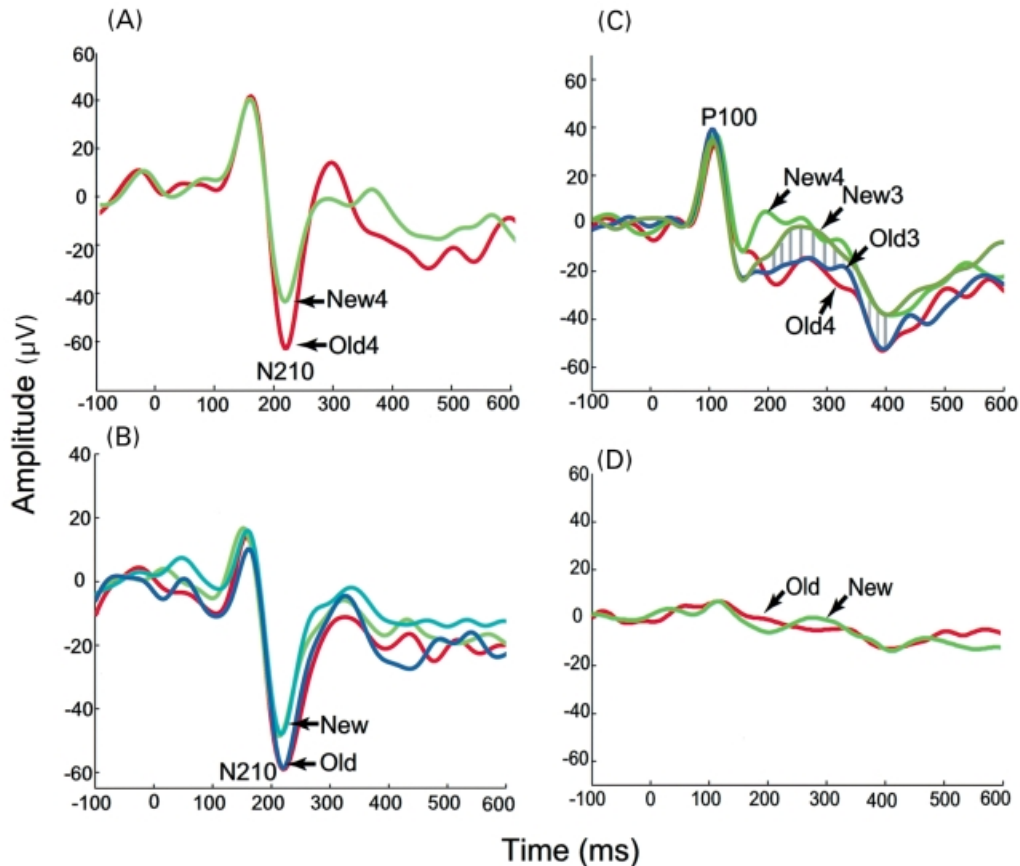


Fig. 3 (A) ERPs from one patient showing the typical effect of an enhanced N210 in the Old condition in set 4. Stimulus onset is at time 0. (B) Averaged ERPs from 12 sites (one site per patient) showing the typical effect of an enhanced N210 in the Old condition. Waveforms are from the Old condition, sets 3 and 4 (purple and red), and from the New condition, sets 3 and 4 (dark and light green). (C) Averaged ERPs from the four sites generating P100s. Waveforms are from the Old condition, sets 3 and 4 (purple and red), and from the New condition, sets 3 and 4 (dark and light green). The striped area denotes the minimum area of New–Old divergence. (D) Averaged ERPs from 12 sites within or adjacent to the hippocampus. Waveforms are from set 4 of the Old condition (red) and from the new condition (light green).

Table 1 Anatomical locations of N210s, their frequency in percentages, average Talairach (Talairach and Tournoux, 1988) y coordinates and mean peak latency

N210 location	% of N210s	Talairach y	Mean latency \pm SD (ms)
V1	19	-77	212 \pm 22
V2	43	-73	211 \pm 51
IOG	09	-85	202 \pm 22
ITG	04	-64	194 \pm 8
FG	25	-51	234 \pm 24

IOG = inferior occipital gyrus; ITG = inferior temporal gyrus, FG = fusiform gyrus.

sites in V1 and in extrastriate cortex were also found (Table 1). All 48 sites that exhibited N210s are shown in views of the inferior and mesial surfaces of the brain (Fig. 4A–C). Although most of the patients had numerous electrodes in frontal, lateral temporal and parietal regions, there were no

N210s or any other contextual cueing-related changes in ERPs at these sites.

To assess whether earlier ERPs were modified by contextual cueing, we searched for sites that generated N100 or P100 ERPs, which reflect initial activation of human V1 and V2 and are sensitive to low-level stimulus attributes such as luminance (Allison *et al.*, 1999). There were four P100 sites (Fig. 3C) and four N100 sites. There were no significant task-related effects on amplitude or latency for P100 or N100. However, a slow negative ERP following P100 was larger in the Old compared with the New condition (Fig. 3C); AUC measurements showed that Old amplitudes were significantly larger ($P < 0.03$) than New amplitudes in the 200–400 ms latency range (Fig. 3C, striped area). No significant AUC difference for the late negative ERP was found at N100 sites.

In six patients, a total of nine depth probes were placed to sample EEG activity in the hippocampus and adjacent temporal lobe structures. Post-operative MRIs showed that

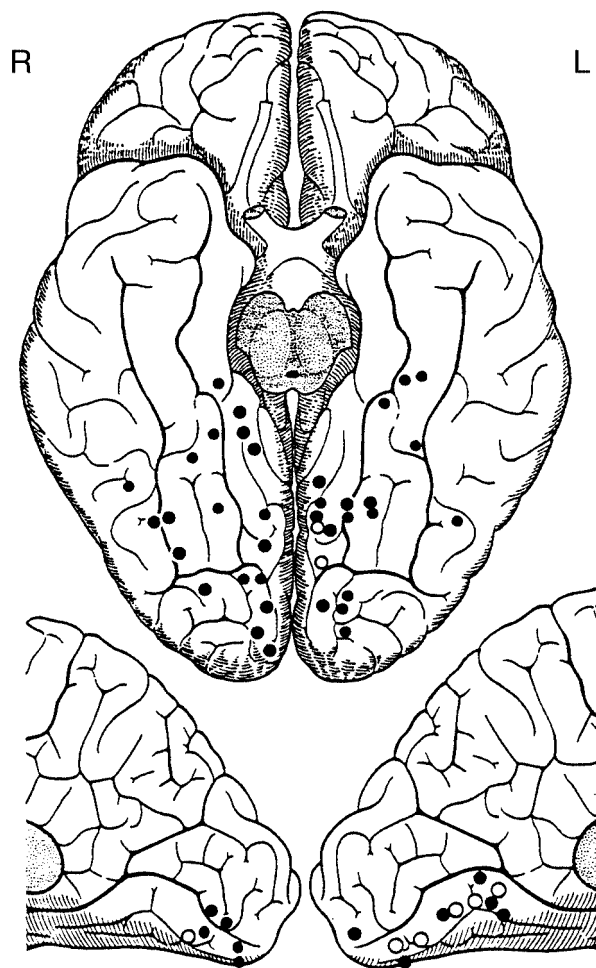


Fig. 4 Locations of N210 (solid circles) and P100/N100 (open circles) sites on views of the inferior surface of the brain, and right and left mesial surfaces posterior to the splenium of the corpus callosum.

in all cases the end of the probe penetrated the hippocampus. None of these sites recorded N210s or other ERPs (Fig. 3D).

Two considerations suggest that the patients' epilepsy did not affect the ERPs recorded in this study: (i) in a larger sample of similar recordings, there were no N200 latency or amplitude differences between the normal and abnormal hemispheres (Allison *et al.*, 1999); and (ii) all learning-related N210s and late negative ERPs were recorded from posterior temporal and occipital sites, whereas the epileptogenic foci were in anterior temporal and frontal regions. In three of the six patients with hippocampal depth probes, the anterior temporal lobe was determined to be the site of the epileptogenic focus; it is possible that ERPs in this region were affected in these patients.

Discussion

Contextual cueing of attention

It is commonly assumed that ERPs of increasing latency reflect activity in successive stages of a neural system. However, the major finding of this study is that contextual

cueing modifies later ERPs generated in anatomically early areas including V1, the initial site of visual cortical processing. The modification consisted of an enhancement of N210 (Fig. 3A and B), and an enhancement of a slow negative ERP at P100 sites, from 200 to 400 ms (Fig. 3C, striped area), 100–300 ms after the onset of initial activation of visual cortex (Fig. 3C). The 'attentional amplification' (Posner and Dehaene, 1994) of N210 also occurred in several regions of extrastriate cortex (Fig. 4A–C). If these changes were due to modifications of early, bottom-up perceptual processes, modification of P100 and N100 (reflecting a portion of the initial activation of V1 and V2; Allison *et al.*, 1999) would be expected. However, these ERPs were unaffected. In addition, a bottom-up effect independent of context would have to rely on low-level differences in Old and New displays, which seems highly unlikely since they were identical in all low-level features. The relatively late timing of these changes suggests that the mechanism of attentional guidance operates by an interaction between early and late visual areas. Re-entrant or feedback processes from higher areas may modulate processes in initial visual areas. Other groups have drawn similar conclusions based on the timing and location of word processing (Nobre *et al.*, 1998), context encoding (e.g. Zipser *et al.*, 1996; Gilbert, 1998), the allocation of spatial attention (Luck and Hillyard, 1994; Aine *et al.*, 1995; Gratton, 1997; Vidyasagar, 1998; Martinez *et al.*, 1999) and intermodal selective attention (Mehta *et al.*, 2000a, b; Foxe and Simpson, 2001). In an intracranial ERP study of attention to colours and words (Nobre *et al.*, 1998), attention strongly modulated long-latency, but not short-latency, ERPs. The authors concluded that the modulation was due to top-down influences from downstream regions involved in word processing. However, in contrast to the present results, attention had the effect of reducing the amplitude of a long-latency negative ERP. The reason for this difference in attentional modulation is unknown but may be due to mechanisms specific to word processing.

In a recent study of spatial attention, modulation of V1 was detected by functional MRI, but evidence for delayed modulation was not present in scalp-recorded ERPs (Martinez *et al.*, 1999). However, a follow-up study by the same group found some evidence for a late attentional affect in or around V1 (Martinez *et al.*, 2001). The authors noted that 'such a delayed attention effect . . . could have escaped detection if the striate cortex source were weak enough to be masked by the stronger sources that were concurrently active in extrastriate cortex.' Intracranial ERPs avoid this limitation by allowing direct recording from striate cortex, and demonstrate that a 'delayed attention effect' is present in V1.

The results reported herein are also consistent with cognitive models which propose that context may influence visual processing within the first few hundred milliseconds of processing (Biederman *et al.*, 1982). Although the ERP evidence clearly shows that learned context did not affect the initial volley of visual information into the cortex, the 200 ms latency of modulatory effects and their early

anatomical foci support the hypothesis that top-down context information is affecting early perceptual processes. Understanding how such early contextual modulation influences the recognition of objects in scenes is an important issue for future research (Henderson and Hollingworth, 1999).

Sources of top-down modulation

We hypothesize that visual areas receive memory-based feedback from medial temporal lobe structures important for storing spatial context information (Chun and Phelps, 1999). Half of the patients in the present study had depth probes targeted to the hippocampus. These electrodes recorded either no ERPs (Fig. 3D) or small ERPs (0–20 μ V) that were not modulated by contextual cueing. Except for large ERPs to infrequent target-related stimuli (McCarthy *et al.*, 1989), most recordings from the human hippocampus have not demonstrated learning-related ERP changes (Nobre and McCarthy, 1995; Puce *et al.*, 1999). Hence, the present results were not helpful in evaluating possible feedback effects from medial temporal lobe structures, and we do not interpret the null effect here as evidence against possible hippocampal involvement in contextual cueing tasks.

Mehta and colleagues (Mehta *et al.*, 2000a, b) recorded from visual cortex while monkeys performed an attention task. They found early attentional modulation in area V4 and late modulation in area V1, suggesting that V4 might be a source of feedback to V1. While this is a plausible source of feedback insofar as V1 is concerned, we also found modulation of N210 and later activity in regions of anterior extrastriate cortex (Fig. 4) and in the posterior fusiform gyrus in which the possible human homologue of monkey area V4 is primarily located (Clarke and Miklossy, 1990; Allison *et al.*, 1993; Sereno *et al.*, 1995; De Yoe *et al.*, 1996). The source of feedback to these regions of extrastriate cortex is unknown, but might arise from the human homologues of areas TEO and TE, which send feedback projections to earlier visual areas including V4 (Rockland and Drash, 1996).

Contextual cueing differs from repetition priming

Although our task involved repetition of configurations, contextual cueing can be distinguished behaviourally from repetition priming (Chun and Jiang, 1998). First, Chun and Jiang showed that the specific form of the items making up the Old configurations can be changed midway through the experiment with no detrimental affect on contextual learning. Thus contextual cueing is independent of the surface features of the array, which is atypical of low-level repetition priming. Secondly, Chun and Jiang showed that repeated configurations did not benefit search performance when the contexts and target locations were decorrelated. Rather, subjects learned associations between configurations and embedded target locations.

Several intracranial ERP studies also suggest that the N210 effect found in this study is not due to repetition priming

(reviewed by Guillem *et al.*, 1999) or semantic priming (reviewed by Schacter and Buckner, 1998). In a habituation study, the first repetition of the stimulus significantly decreased N200 amplitude to face stimuli (Puce *et al.*, 1999), while semantic priming had no significant effect on word-related (Nobre *et al.*, 1994) or face-related (Puce *et al.*, 1999) N200 amplitude. Repetition and semantic priming also significantly reduced the amplitude of N400 and N700 ERPs (Nobre and McCarthy, 1995; Guillem *et al.*, 1999; Puce *et al.*, 1999) recorded from the temporal lobe. Thus repetition and semantic priming decrease or have no effect on the amplitude of negative ERPs, results opposite to the enhancement of negative ERPs seen in this study.

Relationship to N2pc

Several studies have identified a scalp-recorded ERP component in visual search tasks that may be related to attentional filtering. This ERP is called the 'N2pc' (e.g. Luck and Hillyard, 1994b). It consists of a negative deflection that occurs 200–300 ms following target onset. N2pc is localized to the occipital region and is evoked by targets or difficult non-targets embedded in an array of distractor items that need to be filtered in order to discriminate the target correctly. N2pc is a slow negative-going shift without a discrete peak; it is not clear whether N210, the late negative ERP or both are the cortical surface-recorded counterparts of N2pc. It is possible that all three ERPs reflect a common underlying mechanism, providing additional evidence for our conclusion above that contextual modification of N210 and the late negative ERP reflect an attentional rather than a priming effect.

Physiological mechanisms of top-down modulation

The neural mechanisms responsible for the postulated feedback processes are unknown, but physiological and anatomical data allow an informed guess. Surface-negative ERPs are thought to reflect excitation of the apical dendrites of pyramidal cells (Schlag, 1973; Wood and Allison, 1981). Anatomical studies demonstrate that feedback projections are primarily to superficial (layer I) or deep (layers V–VI) cortex (Rockland, 1997). The superficial projection, which is mainly to the apical dendrites of pyramidal cells, would be expected to influence dendritic ERPs such as N210. In rat V1, input to layer I (Cauller and Connors, 1994), including feedback projections to layer I (Shao and Burkhalter, 1996; Nowak *et al.*, 1997), evokes long-duration depolarizing potentials. ERPs, multi-unit activity and current source density in several areas of visual cortex have been analysed while monkeys performed a visual attention task (Mehta *et al.*, 2000a, b). Attentional modulation of neuronal activity in V1 was found to be due to depolarizing current sinks in superficial layers (I and II), in agreement with our inference in humans. The modulation in V1 occurred at 200–400 ms, similar to the modulation we observed in V1 at P100 sites (Fig. 3C, striped

area). Taken together, the human, rat and monkey recordings provide strong evidence for late attentional and contextual excitatory modulation of anatomically early areas of visual cortex, and provide a plausible neurophysiological explanation of its mechanism of action.

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