

# Visual Perceptual Learning in Human Object Recognition Areas: A Repetition Priming Study Using High-Density Electrical Mapping

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It is often the case that only partial or degraded views of an object are available to an observer, and yet in many of these cases, object recognition is accomplished with surprising ease. The perceptual filling-in or “closure” that makes this possible has been linked to a group of object recognition areas in the human brain, the lateral occipital (LO) complex, and has been shown to have a specific electrophysiological correlate, the  $N_{cl}$  component of the event related potential. Perceptual closure presumably occurs because repeated and varied exposure to different classes of objects has caused the brain to undergo “perceptual learning,” which promotes a robust mnemonic representation, accessible under partial information circumstances. The present study examined the impact of perceptual learning on closure-related brain processes. Fragmented pictures of common objects were presented, such that information content was incrementally increased until just enough information was present to permit closure and object recognition. Periodic repetition of a subset of these picture sequences was used to induce repetition priming due to perceptual learning. This priming has an electrophysiological signature that is putatively generated in the LO complex, but significantly precedes the electrophysiological correlate of closure. The temporal progression of priming- and closure-related activity in the LO complex supports the view that sensory processing entails multiple reentrant stages of activity within processing modules of the visual hierarchy. That the earliest priming-related activity occurs over LO complex, sug-

gests that the sensory trace itself may reside in these object recognition areas. © 2001 Academic Press

## INTRODUCTION

A striking feature of the human visual system is its ability to recognize objects from degraded or incomplete views (e.g., Snodgrass and Feenan, 1990). The term “perceptual closure” has been used to describe the apparent filling-in of missing information that enables object-recognition under such partial viewing conditions (e.g., Bartlett, 1916; Foley *et al.*, 1997). A recent electrophysiological study showed that perceptual closure processes are linked to differential activation of the lateral occipital (LO) complex (Doniger *et al.*, 2000), a system of areas implicated in object recognition in humans (e.g., Malach *et al.*, 1995; Kanwisher *et al.*, 1997; Grill-Spector *et al.*, 1999; Haxby *et al.*, 1999), and considered analogous or even homologous with inferotemporal (IT) cortices in macaque monkeys (e.g., Sary *et al.*, 1993; Ito *et al.*, 1995; Vogels, 1999). In our previous study (Doniger *et al.*, 2000), high-density electrical mapping revealed a robust event-related potential component that appeared to track the neural processes related to perceptual closure (termed  $N_{cl}$  for negativity associated with closure). This component was seen as a relative negativity over bilateral occipitotemporal scalp (onset ~230 ms, peak latency at ~290 ms) and was maximal when just enough visual information was present for subjects to finally identify fragmented images.

Object recognition under incomplete viewing conditions is presumably possible because previous exposure to the object and like objects of its class, under a variety of viewing conditions (e.g., viewing angles, sizes, lighting conditions), has resulted in perceptual learning such that the appropriate mnemonic representation can be accessed despite the impoverished information. In fact, it has been shown that only brief

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exposure to a complete or unambiguous object is required for perceptual learning to result in repetition priming, enabling recognition of a previously ambiguous version of the same object (Tovee *et al.*, 1996; Dolan *et al.*, 1997).

This study uses high-density electrical mapping to examine the effect of repetition priming due to perceptual learning on closure-related activity over the LO complex. Our paradigm involved presenting sequences of fragmented pictures such that incrementally more complete versions of an object are presented until just enough information is present for subjects to “close” the picture and recognize the object (e.g., Snodgrass and Corwin, 1988; Doniger *et al.*, 2000). Priming due to perceptual learning was induced by the repetition of a picture sequence following its initial presentation, with one or two novel picture sequences intervening. As expected, perceptual learning enabled recognition to occur at a significantly more fragmented level when picture sequences were repeated as compared to when initially presented. For example, the stimuli shown in Fig. 1c were uninterpretable to most of our subjects when initially presented, but became interpretable following perception of the complete versions of the stimuli (shown in Fig. 7). Moreover, two successive enhancements in electrical activity over LO were found for highly fragmented images that were unrecognizable when initially presented, but became recognizable when repeated due to perceptual learning. The later enhancement is consistent with our prior finding of a component of the evoked potential ( $N_{cl}$ ) that is most pronounced when closure is possible and object recognition is achieved (Doniger *et al.*, 2000). We propose that the earlier enhancement is an electrical signature of priming due to perceptual learning, reflecting access to a sensory trace laid down when the object was initially recognized. The temporal progression from priming- to closure-related activity over LO supports the view that sensory perceptual processing entails multiple reentrant stages of activity within modules of the visual hierarchy (e.g., Schroeder *et al.*, 1998). That the earliest priming-related activity occurs over the human LO complex, suggests that the sensory trace itself resides in these object-recognition areas.

## MATERIALS AND METHODS

### *Subjects*

Ten (3 female), neurologically normal, paid volunteers, aged 20–30 (mean = 23.6) participated. All subjects provided written informed consent, and the procedures were approved by the Institutional Review Board of the Nathan Kline Institute. All subjects reported normal or corrected-to-normal vision. Nine of the 10 were right-handed.

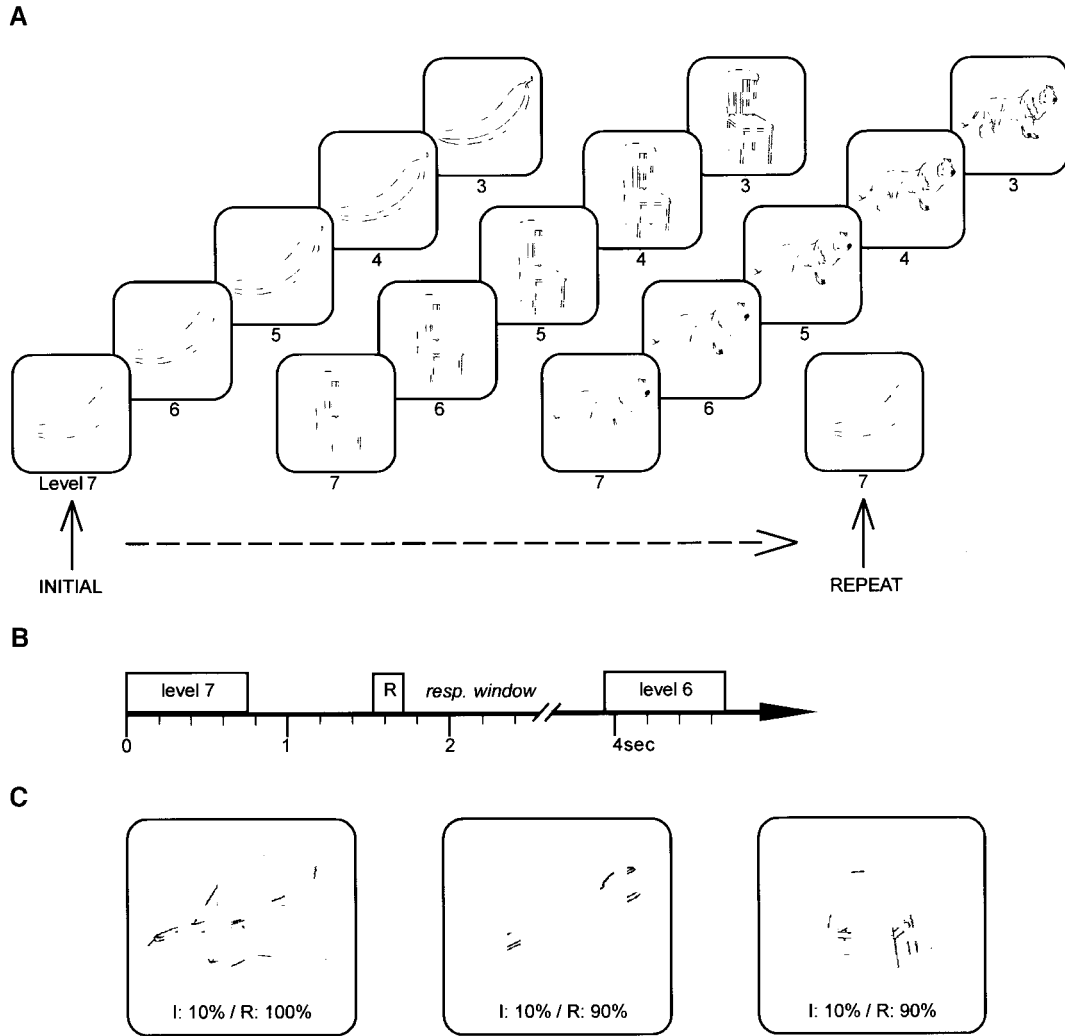
### *Stimuli and Task*

Subjects were presented with 400 line drawings (black on a gray background) of natural and man-made objects; 260 from the Snodgrass and Vanderwart (1980) normed set; the rest from Cycowicz *et al.* (1997). Images were  $256 \times 256$  pixel bitmaps, divided into  $16 \times 16$  segments. Segments containing black pixels were randomly and cumulatively deleted to produce seven incrementally fragmented versions of each picture (Snodgrass and Corwin, 1988). Level 1 refers to the complete picture and Level 7 to the most fragmented version, where the proportion of deleted segments for any level equals  $[1 - 0.7^{(\text{level}-1)}]$ . Stimuli were presented on a computer monitor located 143 cm from the subject. Images subtended an average of  $4.8^\circ$  ( $\pm 1.4^\circ$ ) of visual angle in the vertical plane and  $4.4^\circ$  ( $\pm 1.2^\circ$ ) in the horizontal plane.

Images were presented in accordance with the ascending method of limits (AML) (Fig. 1), from least complete (Level 7) to most complete (Level 1). After the presentation of each fragmented image a “Y|N” cue appeared, prompting a forced-choice response. Subjects pressed one button for a “No” response, indicating that they could not “close” and more information was needed or a second button for a “Yes” response, indicating that they could “close” and name the previous fragmented image. Following “No” responses, subjects were presented with the next most complete image of the same picture and were again cued for a forced-choice decision. Following “Yes” responses, the picture sequence was terminated and subjects were required to verbally name the picture. The experimenter then gave a verbal “Go” cue, indicating that the subject should press either button to initiate the next sequence of fragmented images.

The experiment consisted of 40 blocks, each block containing 10 different picture sequences, of which 7 were presented only once and 3 were presented twice (i.e., 13 picture sequences per block). Repeated picture sequences consisted of the identical fragmented images as when initially presented. The positions of the to-be-repeated picture sequences were randomly selected. The number of picture sequences intervening between initial and repeated presentations was either one or two, determined at random. Subjects were encouraged to take breaks between blocks whenever they deemed it necessary to maintain high concentration and prevent fatigue.

The timing of presentations (Fig. 1) was such that each image appeared for 750 ms, followed by a blank screen for 800 ms. Then a “Y|N” response prompt appeared for 200 ms, followed by a blank screen for 2200 ms. Subjects’ response window extended for 2300 ms from the onset of the “Y|N” prompt. Use of the response prompt was motivated by the desire to diminish the impact of motor responses on the sensory ERP to the pictures.

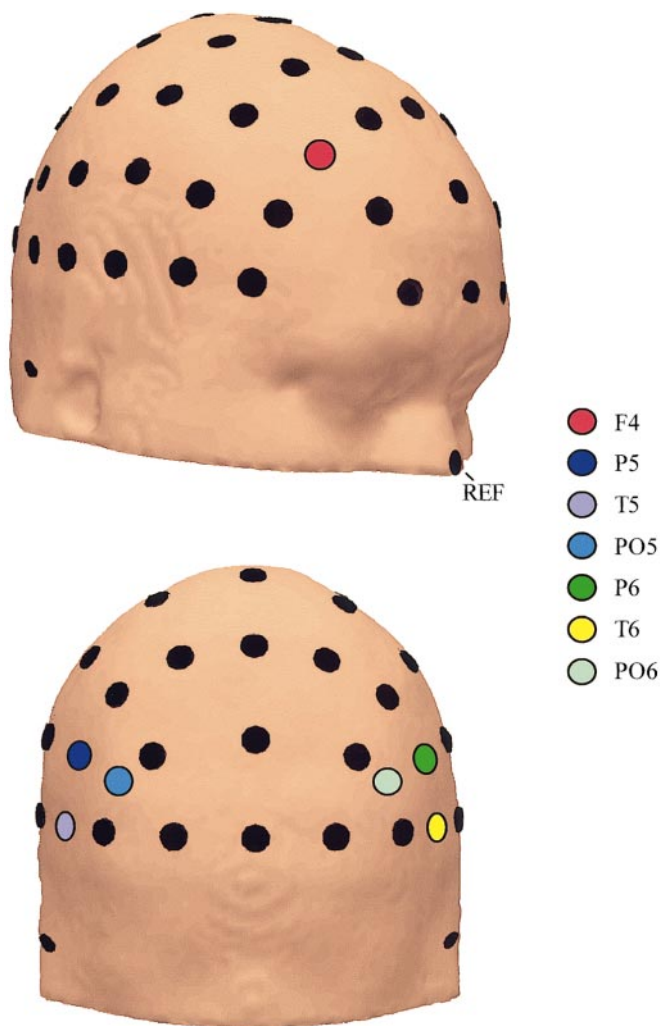


**FIG. 1.** Stimulus configuration. (a) A series of four picture sequences from a typical block. Images are presented at successively less fragmented levels until identification is possible. The fourth picture sequence is a repeat of the first, but identification occurs at a more fragmented level (Level 7), demonstrating the behavioral repetition priming effect. "Repeat" refers to an image at the level of identification on the repeat picture sequence; "Initial" refers to the same image prior to identification on the initial presentation of the sequence. (b) The most fragmented image (Level 7) onset at 0 ms (duration 750 ms), followed by a "Y|N" response prompt (R; duration 200 ms) at 1550 ms. An "N" response resulted in presentation of the next level image, 2.2 s after the response prompt. A "Y" response terminated the sequence for the subject's verbal response. (c) Sample highly fragmented images (Level 6). For 10% of subjects, these images contained sufficient visual information to permit object recognition when initially presented. After perception of the complete picture (see Fig. 7), 100% of subjects were able to recognize the image on the left, and 90% could identify the remaining two images.

### Measurements and Analyses

High-density event-related potentials (ERP) were acquired from 64 scalp electrodes referenced to nose (band-filtered from 0.05 to 100 Hz; digitized at 500 Hz; impedances < 5 k $\Omega$ ). The basic layout is an extension of the modified "International extended 10-20 system" (American EEG Society, 1991) and can be seen in Fig. 2. Note that sites where analyses were conducted are highlighted. Trials with blinks and large eye movements were rejected off-line on the basis of horizontal (HEOG) and vertical (VEOG) electro-oculogram (artifact rejection window of  $\pm 60 \mu\text{V}$ ). No systematic differences in HEOG or VEOG were seen across condi-

tions. An artifact criteria of  $\pm 60 \mu\text{V}$  ( $N = 8$ ) or  $\pm 70 \mu\text{V}$  ( $N = 2$ ) was used at all other electrode sites to reject trials with excessive EMG or other noise transients. Average rejection rates were 25.9% ( $\pm 11.3$ ) with a high of 48% for one subject and a low of 14% for the least noisy subject. Accepted trials were epoched ( $-100$  ms prestimulus to 700 ms poststimulus) and then averaged separately for each condition: ID, the level of fragmentation at which object recognition was achieved during the first presentation of a picture sequence; 1-prior, the level of fragmentation immediately preceding this ID level; Initial, the initial presentation of a highly fragmented image that was not identified,



**FIG. 2.** Electrode array. Positions of the 64 scalp sites from which event-related potentials (ERP) were recorded are represented on a three-dimensional reconstruction from anatomic MRI (front and back view). Sites used in analyses are highlighted.

but would subsequently be identified at this level when repeated; Repeat, the level of fragmentation at which object recognition was achieved for the repeat presentation for which priming was demonstrated relative to Initial (note that Repeat includes the identical highly fragmented images as in Initial).

The average number of accepted sweeps per condition was: 304.4 ( $\pm$  32.3) for ID; 300.1 ( $\pm$  35.4) for 1-prior; 73.6 ( $\pm$  15.8) for Initial; and 73.5 ( $\pm$  16.2) for Repeat. Baseline was defined as the mean voltage over  $-100$  to  $20$  ms. Scalp current density (SCD) topographic maps (second spatial derivative of the potential) were computed from spherical spline interpolation of the surface voltage recordings (see Perrin *et al.*, 1989), defining a quantity proportional to the magnitude of current-flow radial to the surface of the scalp. SCD reduces the high degree of spatial overlap of the ERPs that would otherwise be observed in the scalp voltage data due to volume conduction, and eliminates

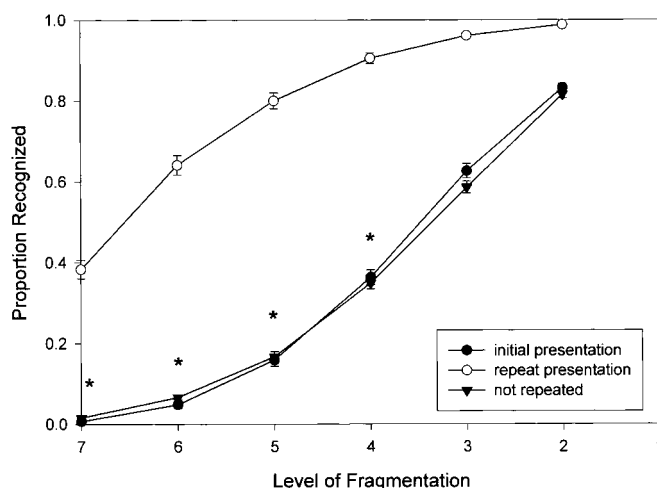
the effect of the reference electrode. Hence, SCD produces scalp topography maps that emphasize local changes in ERP amplitude and are relatively insensitive to contributions from remote generators.

## RESULTS

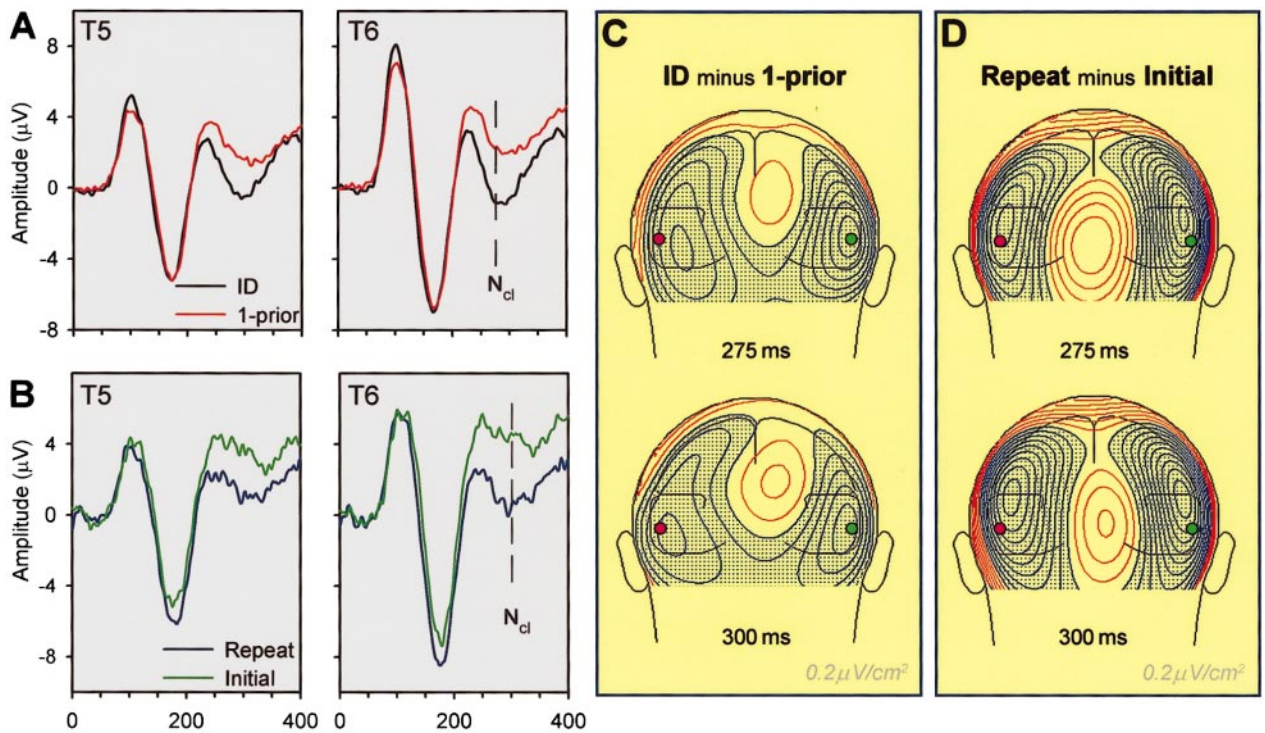
### Behavioral Results

Subjects correctly identified pictures 88% of the time, with a modal level of identification (ID) for all initially presented picture sequences of Level 3 (mean proportion identified at Level 3 was 0.24), replicating the findings of Doniger *et al.* (2000). Modal level of identification for repeat picture sequences (Repeat) was Level 7 (mean proportion identified at Level 7 was 0.41). The modal level of identification for the initial presentations of this subset of picture sequences (Initial) was Level 3 (mean proportion identified at Level 3 was 0.27). Thus, subjects were often able to recognize objects at their most fragmented level when these images had been previously presented. Subjects demonstrated a substantial improvement (on the order of four levels of fragmentation) in their ability to achieve object recognition from initial to repeat presentations of the same picture sequences. Similarly, in examining the cumulative proportion of pictures recognized by a given level (Fig. 3), a significantly greater proportion of pictures were recognized for repeat relative to initial presentations for all but the two most complete levels. There was no difference in the proportion recognizable curves between initial presentations of pictures that were subsequently repeated and presentations of pictures that were not repeated.

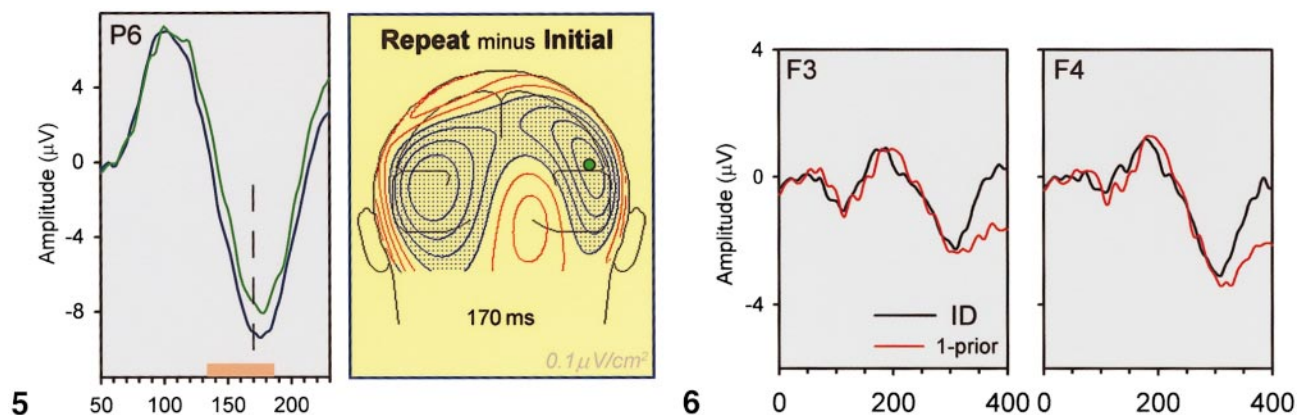
Cumulative Proportion Recognizable



**FIG. 3.** Behavioral perceptual learning effect. Cumulative performance curve versus level of fragmentation for initial and repeat presentations of the same picture sequences.



**FIG. 4.** Results. (a) Group averaged ( $N = 10$ ) voltage waveforms at left (T5) and right (T6) hemisphere occipitotemporal electrodes of maximal  $N_{cl}$  amplitude, at the level of object identification (“ID”; black trace) and at the level prior to identification (“1-prior,” red trace). (b) Group averaged ( $N = 10$ ) voltage waveforms at T5 and T6, for repeated images at the level of object identification (“Repeat”; blue trace) and for the identical fragmented images when presented initially but not identifiable (“Initial”; green trace). (c) Scalp current density (SCD) topographic maps (back views) of the difference waveform between level “ID” and “1-prior” at 275 ms (“ID”/“1-prior” peak) and 300 ms (“Repeat”/“Initial” peak) poststimulus onset. Red isocontour lines ( $0.2 \mu\text{V}/\text{cm}^2$ ) indicate positive values and blue, negative. A magenta disk indicates the location of electrode T5 and a green disk the position of electrode T6. Bilateral negative foci, characteristic of  $N_{cl}$ , are evident over occipitotemporal scalp. (d) SCD topographic maps of the difference waveform between “Repeat” and “Initial” presentations at 275 ms and 300 ms poststimulus onset. Bilateral negative foci of the  $N_{cl}$  effect are again evident over occipitotemporal scalp.



**FIG. 5.**  $N_1$  effect. Group averaged ( $N = 10$ ) voltage waveforms at the right hemisphere site of maximal  $N_1$  amplitude (P6), for “Repeat” (blue trace) and “Initial” (green trace) presentations. An orange bar indicates a significant difference between conditions ( $P < 0.05$ ) for the marked time-points. SCD topographic map (back view) of the difference waveform between “Repeat” and “Initial” presentations at 170 ms poststimulus onset. Red isocontour lines ( $0.1 \mu\text{V}/\text{cm}^2$ ) indicate positive values and blue, negative. Bilateral negative foci are evident over occipitotemporal scalp.

**FIG. 6.** Frontal scalp sites. Group averaged ( $N = 10$ ) voltage waveforms at left (F3) and right (F4) frontal sites, at the level of object identification (“ID”; black trace) and at the level prior to identification (“1-prior,” red trace). Early stimulus-driven componentry is evident, but there is no between-condition difference until after 300 ms, following peak  $N_{cl}$  activity.

### Electrophysiological Results

Group averaged visual evoked potentials (VEPs) for the level ID and for the level prior to identification (1-prior) replicated our findings (Doniger *et al.*, 2000) of a robust negative deflection in the 230 to 330 ms latency range related to perceptual closure processes that we have previously termed the  $N_{cl}$  (see Fig. 4a). A difference in N1 amplitude was evident bilaterally between group averaged VEPs for Repeat and Initial, but absent from the ID/1-prior comparison (Figs. 4a and 4b). As in our prior work, the large divergence that characterizes the  $N_{cl}$  arose just following the peak of the P2 component.

A pair of ANOVAs (2 conditions X 2 hemispheres X 3 electrode locations) tested for significant differences in  $N_{cl}$  amplitude between ID and 1-prior and between Repeat and Initial. As SCD maps (Figs. 4c and 4d) interpolated from all electrode sites confirmed that the topographic distribution of  $N_{cl}$  was consistent with our prior study, the following pairs of sites were tested: P5/P6, T5/T6, and PO5/PO6. Area measures were taken from a 20 ms window centered at peak  $N_{cl}$  latency for each comparison (ID/1-prior = 275 ms; Repeat/Initial = 300 ms). The ID/1-prior ANOVA revealed a significant main effect of condition ( $F(1,9) = 29.06$ ,  $p < 0.0001$ ) and a significant condition X hemisphere interaction ( $F(1,9) = 5.94$ ,  $p < 0.04$ ), reflecting greater amplitude at ID over the right hemisphere. The ANOVA that tested for  $N_{cl}$  enhancement between Initial and Repeat presentations of the same fragmented image also produced a significant main effect of condition ( $F(1,9) = 40.96$ ,  $p < 0.0001$ ) and a significant condition X hemisphere interaction ( $F(1,9) = 6.85$ ,  $p < 0.03$ ).

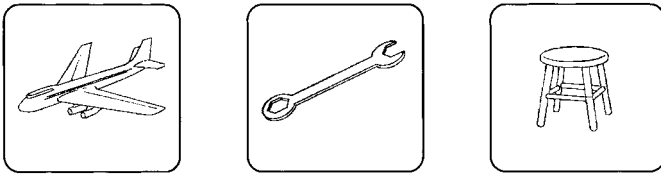
$N_{cl}$  foci for the Repeat/Initial comparison have higher amplitude than those for the ID/1-prior comparison. Recall that subjects typically achieved object recognition after five levels of fragmentation had been presented. Further, consistent with our prior work, recall that presentation of successively more complete levels was accompanied by an incremental increase in  $N_{cl}$  amplitude (Doniger *et al.*, 2000). Also recall that for repeat picture sequence presentations, subjects identified objects most often at their most fragmented level. Hence, images in the Initial condition were presented approximately four levels of fragmentation prior to object recognition, whereas the identical images in the Repeat condition were presented at object recognition. This likely accounts for the greater amplitude of  $N_{cl}$  foci in the Repeat/Initial comparison (Fig. 4c) relative to the ID/1-prior comparison (Fig. 4d).

We tested for point of  $N_{cl}$  onset with a series of paired two-tailed  $t$  tests between ID and 1-prior at the three representative pairs of electrode sites used in the above analyses (P5/P6, T5/T6, and PO5/PO6). Tests were conducted at latencies preceding the  $N_{cl}$  peak to mark the earliest timepoint that conformed to a 0.05 criterion. Onset latencies across the three left and across the three right hemisphere electrode sites were averaged

to provide a best estimate of  $N_{cl}$  onset in a given hemisphere. A point was only accepted as the earliest divergence if at least 11 subsequent consecutive time-points ( $>20$  ms at 500 Hz digitization rate) met the 0.05 criterion (see Guthrie and Buchwald, 1991). The criterion was met at 236 ms for the right hemisphere and 241 ms for the left. These onset latencies are consistent with those of our previous study where  $N_{cl}$  was found to onset at 232 ms in both hemispheres (Doniger *et al.*, 2000). As  $N_{cl}$  onsets just after the peak of the P2 component, the question arises whether P2 and  $N_{cl}$  are both modulated by perceptual closure processes. In this regard, we found peak P2 amplitude to be at 229 ms at electrode site P3. That maximal P2 amplitude preceded  $N_{cl}$  onset and that it peaks at a more medial electrode site suggests that P2 generators are distinct from those that give rise to  $N_{cl}$ . We found no significant modulation of the P2 component at any scalp site.

Another pair of ANOVAs (2 conditions X 2 hemispheres X 3 electrode locations) was conducted to examine differences in N1 amplitude in the ID/1-prior and Repeat/Initial comparisons. Area measures were taken from a 10-ms window (electrodes: P5/P6, T5/T6, and PO5/PO6) centered at the peak latency for N1 in each comparison (ID/1-prior = 165 ms; Repeat/Initial = 175 ms). The Repeat/Initial ANOVA yielded a significant main effect of condition ( $F(1,9) = 6.66$ ,  $P < 0.04$ ), which was absent from the ID/1-prior ANOVA ( $F(1,9) = 0.08$ ,  $P = 0.78$ ). Further, post-hoc analyses revealed that the magnitude of the difference between conditions for the Repeat/Initial comparison was significantly greater than that for the ID/1-prior comparison ( $F(1,9) = 5.48$ ,  $P < 0.05$ ). Both the Repeat/Initial and ID/1-prior ANOVAs yielded significant main effects of hemisphere (Repeat/Initial:  $F(1,9) = 10.46$ ,  $P < 0.02$ ; ID/1-prior:  $F(1,9) = 5.78$ ,  $P < 0.05$ ). No other significant effects were seen. Follow-up planned comparisons (2-tailed  $t$  tests) showed the N1 effect to be highly robust at the scalp site of maximal effect (site P6) ( $t_9 = 3.80$ ,  $P < 0.005$ ). The location of neural generators contributing to the N1 effect was estimated with an SCD map generated from the difference wave between the ERP to Repeat and Initial (Fig. 5). At the peak of this N1 difference, bilateral occipitotemporal foci, similar to those of the subsequent  $N_{cl}$ , were apparent.

In order to support our hypothesis that the N1 repetition effect results from priming-related identification, we conducted a control analysis in which we examined N1 amplitude for Level 7 images that remained unidentifiable when repeated ( $\sim 59\%$  of Level 7 presentations were not identified upon repeat presentation). Nonidentified images at Level 7 on the repeat presentation of the picture sequence (RNID) were compared to the same nonidentified images on the initial picture sequence presentation (INID). The RNID/INID ANOVA (2 conditions X 2 hemispheres X 3 electrode locations) showed no significant modulation



**FIG. 7.** Complete versions of the images shown in Fig. 1c.

of N1 ( $F(1,9) = 1.26$ ,  $P = 0.29$ ). There were no other significant main effects or interactions.

We tested for point of N1 onset with a series of paired two-tailed  $t$  tests between Initial and Repeat at the electrode sites used in the above analyses. The site of maximal N1 difference was at site P6, which showed an onset conforming to the 11 point criterion at 132 ms. None of the differences at left-hemisphere sites conformed to this criterion.

We also investigated whether conditional effects were seen over frontal sites that either preceded or were contemporaneous with the effects over lateral occipital sites. Multiple 2-tailed paired  $t$  test comparisons in the period from 0 to 300 ms yielded no significant differences over any frontal scalp sites (see Fig. 6). Late differences after 300 ms and after the peak of  $N_{cl}$  were observed and will be the subject of future investigations. Note that early stimulus-driven componentry is evident over these frontal scalp sites (Fig. 6) but is not modulated by perceptual closure processes.

## DISCUSSION

The current findings elucidate the brain mechanisms that subserve visual perceptual learning in humans. We define an electrophysiological correlate of repetition priming due to perceptual learning over LO complex that precedes closure processes over the same region. Localization of priming effects to the LO complex is consistent with findings from hemodynamic imaging studies in humans (e.g., Dolan *et al.*, 1997; James *et al.*, 1999; Badgaiyan *et al.*, 1999; Buckner *et al.*, 2000; Henson *et al.*, 2000) and single-unit studies in the corresponding region (area IT) of macaque visual cortex (e.g., Tovee *et al.*, 1996). Brain operations related to repetition priming in the present study appear to differ from those related to perceptual closure, in that, priming produces enhancement of both the N1 and  $N_{cl}$  components of the ERP, while closure effects are confined to the latter component. That  $N_{cl}$ -enhancement is observed to the same highly fragmented image after perceptual learning has occurred indicates that  $N_{cl}$  is largely dissociable from the physical parameters of the visual stimulation itself, but rather, indexes perceptual closure and object recognition processes (see also Doniger *et al.*, 2000).

Recognition of a highly impoverished stimulus due to perceptual learning requires access to a representation or sensory trace laid down when "closure" was previ-

ously achieved. A central question in repetition priming studies is the neural locus of this trace. Candidate regions include posterior object recognition areas (e.g., Lueschow *et al.*, 1994; Desimone, 1996; Gibson and Maunsell, 1997; Chelazzi *et al.*, 1998; but see Miller *et al.*, 1993), perirhinal cortex (see Sakai and Miyashita, 1991; Murray and Bussey, 1999), and prefrontal working memory areas (e.g., Miller *et al.*, 1993; Levy and Goldman-Rakic, 1999; Jiang *et al.*, 2000), all of which show delay activity during explicit memory tasks. It is important to point out that these studies showing memory-related delay activity employ distinctly different paradigms to the one used in the current study. In particular, the delay periods are usually far shorter than the period between the Initial and Repeat presentation in our study and do not involve the interim presentation of many other stimuli. Nonetheless, these studies implicate the above mentioned areas as likely candidates for maintenance of a perceptual trace. While not disputing the obvious possibility that maintenance of such a trace is shared between inferotemporal and prefrontal areas, our finding that the earliest priming-related differentiation is an N1-enhancement over LO suggests that these object recognition areas may play a predominant role in trace maintenance. That we do not find such early differences over frontal scalp is consistent with the idea that the memory processes associated with priming may not involve a working memory component, normally associated with frontal areas (see Fig. 6).

Another key finding of the current study is that while both hemispheres are activated during perceptual closure processes (also Doniger *et al.*, 2000), right hemisphere activation is of significantly greater amplitude than left. A prominent hypothesis holds that the right hemisphere is more involved in the processing of global form, while the left hemisphere is more involved in analytic local processing (see e.g., Robertson *et al.*, 1988; Atchley and Atchley, 1998; Corballis *et al.*, 1999). In this vein, the greater right-hemisphere activation in this study might reflect a relatively greater contribution of global processing to perceiving a complete object from fragmentary evidence. This view is supported by both electrophysiological and hemodynamic studies where selective attention to global versus local features of a stimulus array was manipulated (e.g., Heinze *et al.*, 1998; Fink *et al.*, 1997), and by neuropsychological studies of perceptual closure and amodal completion (e.g., Wasserstein *et al.*, 1984). Critically, despite the asymmetry in activation amplitudes across hemispheres, we find that  $N_{cl}$  onsets at the same time in both the right and left hemispheres, suggesting that both hemispheres access object identity information in parallel.

The N1 effect is  $\sim 100$  ms earlier than  $N_{cl}$ , yet has a very similar scalp-topography. This suggests that the N1 effect and  $N_{cl}$  may reflect successive stages of differential activation in areas of the LO complex. This

progression of events can be interpreted within a theoretical framework that posits a distinction between “perceptual” and “conceptual” modes of object recognition (see Tulving and Schacter, 1990; Schacter, 1992). That is, the “perceptual mode” would describe repetition priming due to perceptual learning, where object recognition is facilitated by a presemantic (sensory) trace laid down by recent sensory exposure to an item, and is rapid and effortless. In contrast, the “conceptual mode” would describe object recognition during initial picture sequence presentations, as sensory information is actively compared with semantic/episodic memory representations. Within this theoretical framework, the N1 may represent structural analysis of the object (i.e., perceptual mode) that is enhanced for Repeat versus Initial presentations, reflecting access to the sensory trace laid down when closure was first achieved. In turn, the later  $N_{cl}$  component (~290 ms) might be biased towards semantic processing (i.e., conceptual or memory mode). Indeed  $N_{cl}$  appears only when effort is required to decipher incomplete images, whereas when complete and easily-identified objects are presented, only N1 is modulated. N1 activity in the vicinity of LO has been found in studies of face-, object-, and word-recognition (e.g., Allison *et al.*, 1999; Roission *et al.*, 2000; Bentin *et al.*, 1999). Moreover, it has been suggested that this activity reflects the structural encoding of object components and may be particularly sensitive to the presence of particular object components (Eimer, 1998; Bentin *et al.*, 1996). Finally, it should be noted that structural processing, as reflected by N1, might facilitate the subsequent conceptual processing reflected by  $N_{cl}$ . Hence, the N1/ $N_{cl}$  sequence may constitute evidence for an important object-processing system within LO.

It is important to note that while we interpret the N1- and  $N_{cl}$ -enhancements as reflecting successive stages of object-processing within the LO complex based on their very similar scalp topographies (Figs. 4c, 4d, and 5), this is not to imply that only a single generator is responsible for both effects. In fact, while the SCD topographic maps provide compelling evidence for generators in inferotemporal cortices, it is also evident that both modulations (N1 and  $N_{cl}$ ) represent contributions from more than a single intracranial generator. It is likely that the LO complex comprises a number of distinct functional units (e.g., Ishai *et al.*, 1999), which may play differential roles in priming-related versus closure-related processes. Indeed, intracranial recordings in humans have shown at least two distinct areas of the occipitotemporal cortex that contribute to object recognition (Allison *et al.*, 1999). Additionally, our effects are likely to also represent some contribution from lower-tier extrastriate regions as the complex operations of perceptual closure likely involve recursive feedback-feedforward mechanisms between areas at different levels of the cortical hierarchy (e.g., Pollen, 1999; see Doniger *et al.*, 2000, for a more de-

tailed treatment). Future studies combining the high spatial resolution of hemodynamic imaging with the fine temporal resolution that can only be provided by high-density electrical mapping, should allow for further dissociation of these functional units and elucidation of their temporal relations (e.g., Simpson *et al.*, 1995; Martinez *et al.*, 1999).

In conclusion, the current study extends previous work in finding a sequence of electrical events that indexes repetition priming due to visual perceptual learning in humans and in detailing the timecourse of these events. We provide evidence for a neural correlate of repetition priming as evidenced by enhancement of the N1 component of the ERP followed by closure-related  $N_{cl}$ -enhancement. The N1/ $N_{cl}$  sequence may reflect successive stages of object processing in regions of the LO complex, with N1-enhancement reflecting more perceptual structural analysis of the fragmented images and  $N_{cl}$  reflecting more conceptual effortful analysis. Within this framework, our data underscore the importance of considering the temporal dimensions of the visual processing hierarchy (e.g., Nowak and Bullier, 1997; Schroeder *et al.*, 1998).

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