

Activation Timecourse of Ventral Visual Stream Object-recognition Areas: High Density Electrical Mapping of Perceptual Closure Processes

Glen M. Doniger

New York University and Nathan Kline Institute for Psychiatric Research

John J. Foxe, Micah M. Murray, and Beth A. Higgins

Albert Einstein College of Medicine and Nathan Kline Institute for Psychiatric Research

Joan Gay Snodgrass

New York University

Charles E. Schroeder and Daniel C. Javitt

Nathan Kline Institute for Psychiatric Research and New York University School of Medicine

Abstract

■ Object recognition is achieved even in circumstances when only partial information is available to the observer. Perceptual closure processes are essential in enabling such recognitions to occur. We presented successively less fragmented images while recording high-density event-related potentials (ERPs), which permitted us to monitor brain activity during the perceptual closure processes leading up to object recognition. We reveal a

bilateral ERP component (N_{cl}) that tracks these processes (onsets ~ 230 msec, maximal at ~ 290 msec). Scalp-current density mapping of the N_{cl} revealed bilateral occipito-temporal scalp foci, which are consistent with generators in the human ventral visual stream, and specifically the lateral-occipital or LO complex as defined by hemodynamic studies of object recognition. ■

INTRODUCTION

The human brain is capable of identifying objects despite only partial visual information due to such factors as poor lighting and partial occlusion. The term “perceptual closure” has been used to refer to the operation of completion processes that enable these identifications (Foley, Foley, Durso, & Smith, 1997; Bartlett, 1916). Fragmented line drawings have been extensively used to study the completion processes of perceptual closure (Snodgrass & Feenan, 1990). In fact, fragmented images have been shown to prime test items better than their complete counterparts, implying that more intensive processing is required for perceptual closure than for simple object recognition (Snodgrass & Feenan, 1990; Snodgrass & Kinjo, 1998). Further, moderately fragmented images are remembered as having been presented in their complete form (Foley et al., 1997), suggesting that the activation of completion processes brings about object recognition. This study uses the presentation of fragmented images

in conjunction with high-density electrical mapping to detail the spatio-temporal activation pattern of perceptual closure processes.

There has been no neuroimaging investigation of perceptual closure processes to date. However, hemodynamic studies of the closely related processes of object recognition (Haxby et al., 1999; Grill-Spector, Kushnir, Edelman, Itzhak, & Malach, 1998; Grill-Spector, Kushnir, Hendler, et al., 1998; Kanwisher, Woods, Iacoboni, & Mazziotta, 1997; Kohler, Kapur, Moscovitch, Winocur, & Houle, 1995; Malach et al., 1995) localize these processes in the ventral visual stream in a system of areas that have been termed the lateral-occipital or LO-complex (Malach et al., 1995). Additionally, lateral extrastriate regions have been implicated in the perception of illusory contours (ffytche & Zeki, 1996; Hirsch et al., 1995), which may reflect similar mechanisms to those invoked during perceptual closure processes. The characteristics of the human LO-complex appear highly similar to those of monkey infer-

otemporal (IT) cortex, which is known to play a role in object recognition (Gross, Rocha-Miranda, & Bender, 1972). Compellingly, both monkey IT neurons (Sary, Vogels, & Orban, 1993) and human LO (Grill-Spector, Kushnir, Edelman, et al., 1998) show cue-invariant object recognition such that the neural representation of objects and shapes remains constant regardless of whether the objects are defined by luminance, texture or motion cues. Additionally, many IT neurons show both size and position invariance by continuing to show selectivity for an optimal shape despite large changes in position and up to 64-fold changes in size (Logothetis, Pauls, & Poggio, 1995; Ito, Tamura, Fujita, & Tanaka, 1995; Sary et al., 1993; Schwartz, Desimone, Albright, & Gross, 1983). IT cells also display invariance in the presence of foreground occlusion (Kovacs, Vogels, & Orban, 1995). The implication is that monkey IT and human LO-complex are higher-order integration areas that can abstract object identity from highly variable stimulus conditions—a necessary property for an area subserving perceptual closure processes.

This study used high-density event-related potential (ERP) recordings to examine the activity over occipito-temporal cortex related to perceptual closure processes and to detail the timecourse of this activity. We employed the ascending method of limits (AML) procedure, in which the amount of visual information was incrementally increased with each subsequent image presentation until “closure” was achieved (Snodgrass & Feenan, 1990). That is, initially, a highly fragmented version of a picture was followed in turn by less and less fragmented versions of the same picture until the point at which just enough detail was present to allow for object recognition. This technique permitted the analysis of brain activity during both object recognition and the completion processes at preceding levels. We wished to determine whether these processes changed in an all-or-none or a graded manner, as indexed by latency and amplitude changes. We provide the first strong evidence that perceptual closure is subserved by bilateral ventral occipito-temporal areas, consistent with the LO complex as defined by hemodynamic data. We elucidate the timing of onset and peak activity for perceptual closure processes. Specifically, we provide the first evidence for a graded increase in LO activity with progressively more complete stimuli and an abrupt increment in activity at the point of perceptual closure.

RESULTS

Subjects correctly identified pictures 85% of the time. The modal level of identification (ID) was Level 3 (mean proportion identified at Level 3 was .24), consistent with prior work (Snodgrass & Corwin, 1988). Both correct and incorrect identifications were considered valid in our analyses.

Inspection of group averaged visual evoked potentials (VEPs) for the level ID and for the three preceding levels revealed the traditional series of ERP components, including the P1, N1, and P2. These components were maximal at occipital sites and neither P1 nor N1 showed amplitude or latency differences between levels. In contrast, a large difference in waveform morphology became apparent during the peak of the P2. Onsetting at ~230 msec and peaking at ~290 msec, a prominent negative deflection was evident between the responses to successive levels (i.e., 3-prior to 2-prior, 2-prior to 1-prior, and 1-prior to ID), apparently building as the point of closure approached (Figure 1a). Since this relative negative deflection appears to track perceptual closure processes, we termed it the N_{cl} (for negativity associated with closure).

The difference was largest over lateral occipito-temporal sites bilaterally. We tested for significant differences between the levels ID, 1-prior, 2-prior, and 3-prior by a repeated measures analysis of variance. P1, N1, and N_{cl} components were included in this analysis. Peak latencies were determined at the electrode site of maximal amplitude from group averaged waveforms that collapsed all levels (component P1 at electrode P5; N1 at PO6; N_{cl} at T5). Area measures (Figure 1b) were taken from a 20-msec window centered at the peak latency for each component for each of the eight subjects (P1 = 110 msec; N1 = 164 msec; N_{cl} = 290 msec). A repeated measures ANOVA (3 components \times 4 levels) revealed a significant within subjects, component \times level interaction ($F(6,42)=14.71, p < .001$, Greenhouse–Geisser $\epsilon = .31$). Follow-up planned comparisons (two-tailed t tests) tested for significant N_{cl} amplitude differences between successive levels at the left hemisphere site T5 by comparing level ID with 1-prior ($t_7 = 8.49, p < .0001$); 1-prior with 2-prior ($t_7 = 4.75, p = .002$); and 2-prior with 3-prior ($t_7 = 3.0, p = .02$). The same result was found at T6, the equivalent right hemisphere site [ID vs. 1-prior ($t_7 = 7.44, p = .0001$), 1-prior vs. 2-prior ($t_7 = 4.56, p = .003$), 2-prior vs. 3-prior ($t_7 = 3.13, p = .016$)]. Similar comparisons between successive levels revealed no significant differences for either the P1 or N1 components.

The significant progression of N_{cl} amplitude between successively less fragmented levels is not related to the amount of sensory stimulation (less fragmented levels contain more sensory stimulation). We discount this possibility in two ways. Firstly, the absence of significant amplitude changes between successive levels for either the P1 or N1 component argues strongly that the N_{cl} effect is not related to the amount of sensory stimulation (see Figure 1b). Secondly, the use of a large number of images (>350) in our study allowed us to perform a within-level analysis (Figure 2). That is, equivalent numbers of ID and Non-ID sweeps at a given level of fragmentation were averaged for each subject. In this case, both ID and Non-ID contain the

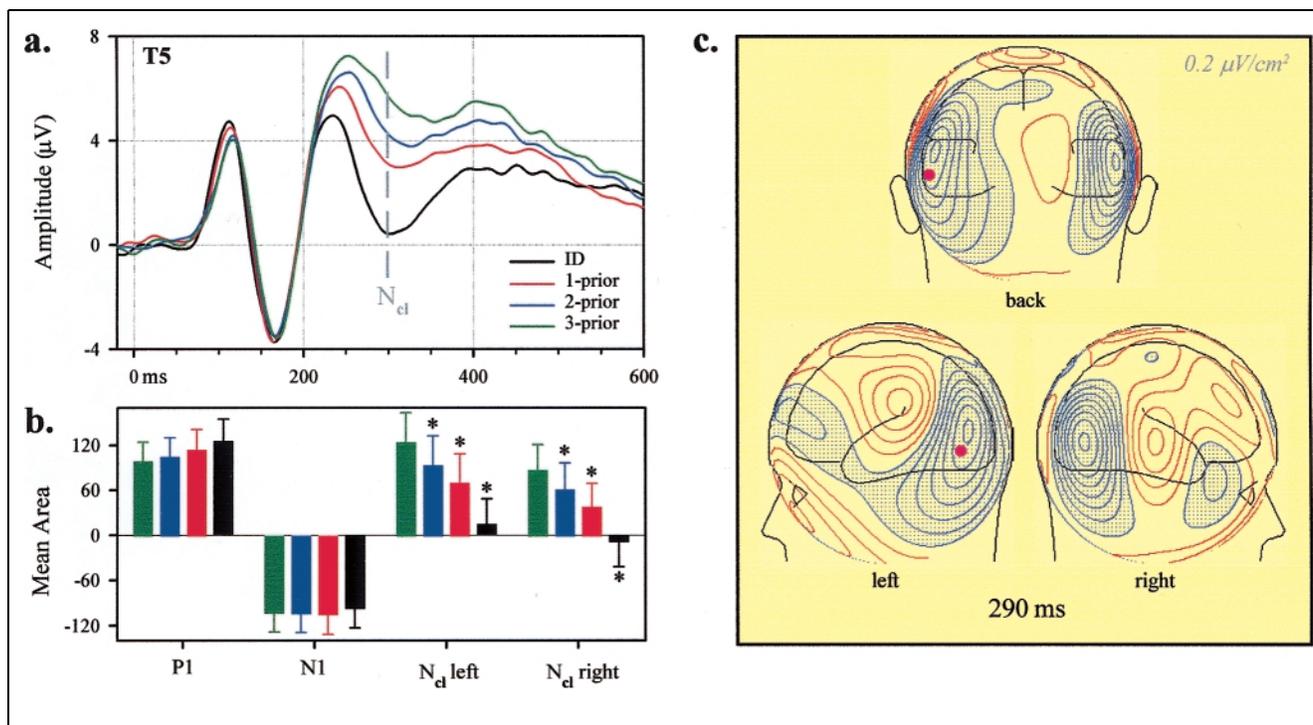


Figure 1. Results. (a) Group averaged ($N = 8$) voltage waveforms at the left hemisphere occipito-temporal electrode displaying maximal N_{cl} amplitude (T5), at the level of object identification (ID; black trace) and at three prior levels (1-prior, red; 2-prior, blue; 3-prior, green). (b) Mean amplitude area measures (standard errors indicated) for three components (P1, N1, and N_{cl}) at levels ID, 1-prior, 2-prior and 3-prior. Significant differences between levels ($* p < .03$) were seen only for the N_{cl} at both left (T5) and right (T6) hemisphere electrode sites. (c) Scalp current density (SCD) topographic maps of the difference waveform between level ID and 1-prior at 290 msec post-stimulus onset. Red isocontour lines ($.2 \mu\text{V}/\text{cm}^2$) indicate positive values and blue, negative. A magenta disk indicates the location of electrode T5 shown in panel (a). Prominent bilateral negative foci over occipito-temporal scalp are evident.

same amount of sensory stimulation. N_{cl} (area measured as above at 300 msec peak) was present to the within-level ID versus Non-ID ($p = .04$ at T5; $p = .03$ at T6) in the absence of either a P1 ($p = .47$ at P5) or an N1 ($p = .11$ at PO6) difference and despite the relatively low signal-to-noise ratio inherent in this comparison (~ 75 sweeps per subject per condition versus ~ 250 sweeps in the between-level analysis above).

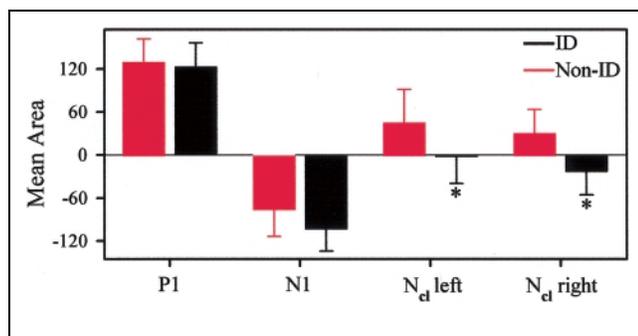


Figure 2. Within level analysis. Mean area measured (standard errors indicated) for Identifications (ID; black bars) versus Non-Identifications (Non-ID; red bars), matched for amount of sensory stimulation. No difference is seen for either the P1 or N1 component, but N_{cl} is present in both the left and right hemispheres ($*p < .03$).

To estimate the location of neural generators contributing to the N_{cl} effect, SCD topographic maps were generated from the difference wave between the ERP to ID and 1-prior. At the peak of the N_{cl} , these maps show a bilateral occipito-temporal negativity (Figure 1c).

We tested for the point of onset of this negative deflection with a series of paired one-tailed t tests between level ID and level 1-prior at electrode sites T5 and T6. The t tests were conducted at latencies preceding the N_{cl} peak to establish the earliest timepoint that conformed to a .05 alpha criterion. This point was only accepted as the earliest divergence if at least 11 subsequent consecutive time-points (>20 msec at 500 Hz digitization rate) met the .05 criterion (see Rugg, Doyle, & Wells, 1995 for a similar strategy). The criterion was met at 232 msec for both T5 and T6. It should be noted that this measure is sensitive to signal-to-noise ratio and onset latency is likely overestimated.

DISCUSSION

High-density electrical mapping revealed a bilateral occipito-temporal negative potential (N_{cl}), which tracked perceptual closure processes. The occipito-temporal topography of N_{cl} foci strongly suggests that areas of the LO-complex as defined by hemodynamic studies of object recognition generate this surface potential (Grill-

Spector, Kushnir, Edelman, et al., 1998; Grill-Spector, Kushnir, Hendler, et al., 1998; Malach et al., 1995; Moscovitch, Kapur, Kohler, & Houle, 1995). We demonstrate that occipito-temporal N_{cl} amplitude builds over a number of pre-identification steps rather than being an all-or-none phenomenon at the point of closure. Hence, in the current study, activation of the occipito-temporal areas is not limited to the point of object recognition, but also indexes perceptual closure processes that precede recognition. This pre-recognition activity may reflect extraction of object “primitives” (Malach et al., 1995), consistent with theories that posit recognition by components (Biederman, 1987; Marr & Nishihara, 1978). In support, neurons in monkey IT, which show selectivity for complex objects, also show selective but attenuated responses to highly simplified versions of the same objects (Kobatake & Tanaka, 1994). Object recognition can be conceived of as a segmentation of retinal input into an arrangement of simplified geometric components. The pre-recognition climb in N_{cl} amplitude may represent extraction of successively more of such components until enough are present to give rise to closure.

The present findings elucidate the timing of perceptual closure processes. We find bilateral N_{cl} activations that onset at approximately 232 msec and have a peak latency of approximately 290 msec. This peak latency is in agreement with a recent magneto-encephalographic (MEG) study of object recognition (Vanni, Revonsuo, Saarinen, & Hari, 1996). These MEG activations, like N_{cl} , were localized to bilateral sources in LO. The onset of N_{cl} at ~232 msec is relatively late in visual processing. Based on findings in monkey, we can estimate the timing of response onset in human LO. In awake monkeys, V1 is active by 25–30 msec (Givre, Schroeder, & Arezzo, 1994; Maunsell & Gibson, 1992) and IT is active on average by 50 msec (Schroeder, Mehta, & Givre, 1998). Applying a 3/5 rule in order to draw a correspondence between monkey and human component latencies (Schroeder et al., 1995; Schroeder et al., 1998) and allowing for differences in stimulus qualities, a conservative estimate of onset is 45–50 msec in human V1 and 80–100 msec in LO. The projected V1 onset latency is confirmed by empirical findings (Clark, Fan, & Hillyard, 1995). Given that LO is projected to be active by no later than 100 msec, it appears that the initial input to ventral visual areas does not produce closure in the partial information situations of the present study. Rather, the extended timeframe of the N_{cl} likely reflects the substantial additional processing necessary for closure processes, possibly involving recursive feedback–feedforward mechanisms (Mumford, 1992; Pollen, 1999). Consistent with this, onset latencies in monkey IT were later when objects were occluded as opposed to complete (Kovacs et al., 1995). Higher-order ventral stream areas have extensive feedback projections to earlier visual areas (Felleman & Van Essen, 1991), and

there is evidence that the later sustained activity in early areas, including V1, is modulated by higher areas (Lamme, Super, & Spekreijse, 1998; Payne, Lomber, Villa, & Bullier, 1996; Lamme, 1995). We propose that perceptual closure processes are subserved by such feedback–feedforward recursive mechanisms and that this is reflected by the late onset of divergent activity at 232 msec.

It is important to note that our data do not preclude the involvement of earlier or later visual areas in completion processes. For example, V2 cells have been shown to be sensitive to illusory contours (von der Heydt, Peterhans, & Baumgartner, 1984) and to display cue-invariant boundary detection (Leventhal, Wang, Schmolesky, & Zhou, 1998). Additionally, contextual modulations of cells as low in the hierarchical structure as V1 have also been shown in figure-ground segregation studies (Lee, Mumford, Romero, & Lamme, 1998; Zipser, Lamme, & Schiller, 1996). Involvement of these mechanisms in perceptual closure processes is likely, as constructing boundaries from partial information and segregation of foreground from background facilitate the perception of complete objects. However, the operation of these early mechanisms may be equivalent across images at various levels of fragmentation. Therefore, the equivalent amplitudes that we record for P1 and N1 across levels in the current study do not rule out earlier involvement in perceptual closure processes.

The incremental increase in N_{cl} is marked by a disproportionately large increase in the final step—identification itself. This final step represents the culmination of perceptual closure processes in object recognition and likely represents the added processing that identification itself appropriates. This added processing at the point of closure may be related to the passage of information to semantic processing areas and frontal executive areas.

While there is evidence of hemispheric asymmetry in perceptual closure (Lewis & Kemptner, 1987) and object recognition (Atchley & Atchley, 1998), it is clear on both theoretical (Farah, 1991) and empirical grounds (Haxby et al., 1999; Grill-Spector, Kushnir, Edelman, et al., 1998; Grill-Spector, Kushnir, Hendler et al., 1998; Vanni et al., 1996; Kohler et al., 1995; Malach et al., 1995; Farah, 1991) that there is bilateral involvement of LO in these processes. Our data strongly support bilateral LO involvement in perceptual closure and object recognition. Furthermore, the closure-related activation (N_{cl}) undergoes equivalent incremental amplitude increases with equivalent timing across hemispheres. Thus, while the hemispheres may have different roles in these processes, their spatio-temporal activation patterns are extremely similar.

A number of previous electrophysiologic investigations have shown negative potentials during discrimination tasks that have lateral occipital topographies and

relatively similar latencies to the N_{cl} (e.g., Simson, Ritter, & Vaughan, 1985; Ritter, Simson, Vaughan, & Macht, 1982; Ritter, Simson, & Vaughan, 1983; Ritter, Simson, & Vaughan, 1988). For example, presentation of letter stimuli during a form-discrimination task resulted in an enhanced lateral-occipital negativity at a latency of 310 msec compared to when the same letters served in a simple reaction time task (Lovrich, Simson, Vaughan, & Ritter, 1986). This negative component (termed the N_a) was interpreted as reflecting enhanced pattern analysis of stimuli, likely involving similar object recognition areas to those producing the N_{cl} during perceptual closure processes.

In conclusion, our data support a critical role for areas of the occipito-temporal cortex of both hemispheres in perceptual closure processes. We recorded a component of the ERP with an onset latency of approximately 232 msec and a peak latency of approximately 290 msec (N_{cl}) that appears to originate in the LO-complex and tracks perceptual closure processes. N_{cl} activity builds incrementally over a number of pre-closure levels, dissociating the N_{cl} from object recognition. However, the activity underlying N_{cl} is likely to be necessary for subsequent object recognition.

METHODS

Subjects

Nine (two female), neurologically normal, paid volunteers, aged 18–29 (mean = 23.7, \pm 3.9) participated. All subjects provided written informed consent, and the procedures were approved by the Institutional Review Board of the Nathan Kline Institute for Psychiatric Research. All subjects reported English as their first language, had normal or corrected-to-normal vision, and were right-handed. One subject reported marked difficulty with the task, and his accuracy performance was more than two standard deviations from the group mean. His data were excluded from further analyses.

Stimuli and Task

Subjects were presented with between 350 and 380 line drawings (black on a gray background) of animate and inanimate objects; 260 from the Snodgrass and Vanderwart (1980) normed set; the rest from Cycowicz, Friedman, Rothstein, and Snodgrass (1997). Images were stored as 256×256 pixel bitmaps and divided into 16×16 segments. Segments containing black pixels were randomly and cumulatively deleted in order to produce eight incrementally fragmented versions of each picture (Snodgrass & Corwin, 1988). Level 1 refers to the complete picture and Level 8 to the most fragmented version, where the proportion of deleted segments for any level equals $[1 - .7^{(\text{level}-1)}]$. Stimuli were presented on a computer monitor located 143 cm from the subject (seven of eight) and 109 cm from one subject. Images

subtended an average of 4.8° ($\pm 1.4^\circ$) of visual angle in the vertical plane and 4.4° ($\pm 1.2^\circ$) in the horizontal plane.

Images were presented in accordance with the AML (Figure 3a), from least complete (Level 8) 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, the subjects were presented with the next most complete image of the same picture and would again be cued for a forced-choice decision. Following “Yes” responses, the picture sequence was terminated and the 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 entire experiment consisted of at least 35 blocks, each block containing 10 picture sequences. Subjects were encouraged to take breaks between blocks whenever they deemed it necessary to maintain high concentration and prevent fatigue.

The timing of presentations (Figure 3b) was such that each image appeared for 750 msec, followed by a blank screen for 800 msec. Then, a “Y|N” response prompt appeared for 200 msec, followed by a blank screen for 2200 msec. Subjects’ response window extended for 2300 msec from the onset of the “Y|N” prompt. Use of

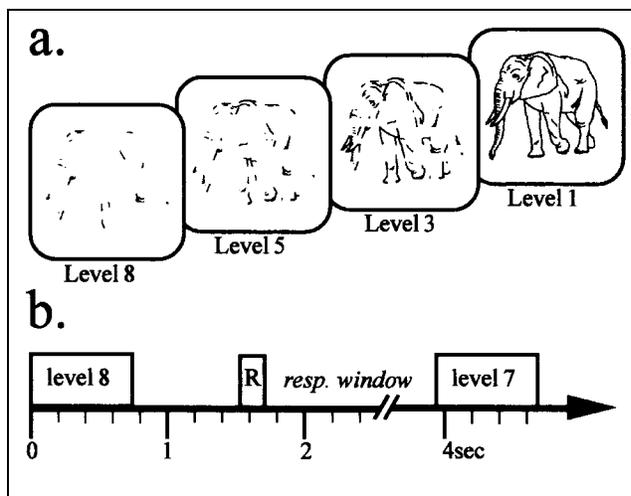


Figure 3. Stimulus configuration. (a) Images displayed from least complete to most complete (four of eight levels shown). (b) The most fragmented image (level 8) onset at 0 msec (duration 750 msec), followed by a “Y|N” response prompt (R; duration 200 msec) at 1550 msec. An “N” response resulted in the presentation of the next level image, 2.2 sec after the response prompt. A “Y” response terminated the sequence for the subject’s verbal response.

the response prompt was motivated by the desire to diminish the impact of motor responses on the sensory ERP to the pictures.

Measurements and Analyses

High-density ERPs were acquired from 64 scalp electrodes referenced to nose (band-filtered from .05 to 100 Hz; digitized at 500 Hz; impedances <5 k Ω). Trials with blinks and large eye movements were rejected offline on the basis of horizontal (HEOG) and vertical (VEOG) electro-oculogram. No systematic differences in HEOG or VEOG were seen in the responses to different fragmentation levels. Scalp current density (SCD) maps (second spatial derivative of the potential) were computed from spherical spline interpolation of the surface voltage recordings (Perrin, Pernier, Bertrand, & Echallier, 1989). This technique eliminates the influence of the reference electrode and emphasizes local contributions to the surface map, providing good visualization of approximate locations of intracranial generators. VEP averages were made for identification level and the three preceding levels for each subject, referred to hereafter as "ID," "1-prior," "2-prior," and "3-prior."

Acknowledgments

Sincere appreciation for critical comments on multiple drafts go to Drs. Dirk Heslenfeld, Anna Roe, Seppo Ahlfors, Michael Worden, Herbert G. Vaughan Jr. and Matthew Hoptman. We also thank Dr. Haftan Eckhold, Jin Fan, Tirza Doniger, Alice Glinert and Robert Lindsley for technical support. Work supported by grants from the NIMH (MH1143 to JJJ, MH49334 and MH01439 to DCJ) and the McDonnell-Pew foundation.

Reprint requests should be sent to John J. Foxe, Cognitive Neurophysiology Laboratory, Nathan Kline Institute for Psychiatric Research, Program in Cognitive Neuroscience and Schizophrenia, 140 Old Orangeburg Road, Orangeburg, NY 10962, USA. Tel.: +1-914-398-6538; fax: +1-914-398-6545; e-mail: foxey@balrog.aecom.yu.edu.

REFERENCES

Atchley, R. A., & Atchley, P. (1998). Hemispheric specialization in the detection of subjective objects. *Neuropsychologia*, *36*, 1373–1386.

Bartlett, F. C. (1916). An experimental study of some problems of perceiving and imagining. *British Journal of Psychology*, *8*, 222–266.

Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review*, *94*, 115–147.

Clark, V. P., Fan, S., & Hillyard, S. A. (1995). Identification of early visual evoked potential generators by retinotopic and topographic analyses. *Human Brain Mapping*, *2*, 170–187.

Cycowicz, Y. M., Friedman, D., Rothstein, M., & Snodgrass, J. G. (1997). Picture naming by young children: Norms for name agreement, familiarity, and visual complexity. *Journal of Experimental Child Psychology*, *65*, 171–237.

Farah, M. J. (1991). Patterns of co-occurrence among associative agnosias: Implications for visual object representation. *Cognitive Neuropsychology*, *8*, 1–19.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, *1*, 1–47.

ffytche, D. H., & Zeki, S. (1996). Brain activity related to the perception of illusory contours. *Neuroimage*, *3*, 104–108.

Foley, M. A., Foley, H. J., Durso, F. T., & Smith, N. K. (1997). Investigations of closure processes: What source-monitoring judgments suggest about what is "closing." *Memory and Cognition*, *25*, 140–155.

Givre, S. J., Schroeder, C. E., & Arezzo, J. C. (1994). Contribution of extrastriate area V4 to the surface-recorded flash VEP in the awake macaque. *Vision Research*, *34*, 415–428.

Grill-Spector, K., Kushnir, T., Edelman, S., Itzhak, Y., & Malach, R. (1998). Cue-invariant activation in object-related areas of the human occipital lobe. *Neuron*, *21*, 191–202.

Grill-Spector, K., Kushnir, T., Hendler, T., Edelman, S., Itzhak, Y., & Malach, R. (1998). A sequence of object-processing stages revealed by fMRI in the human occipital lobe. *Human Brain Mapping*, *6*, 316–328.

Gross, C. G., Rocha-Miranda, C. E., & Bender, D. B. (1972). Visual properties of neurons in inferotemporal cortex of the Macaque. *Journal of Neurophysiology*, *35*, 96–111.

Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*, *22*, 189–199.

Hirsch, J., DeLapaz, R. L., Relkin, N. R., Victor, J., Kim, K., Li, T., Borden, P., Rubin, N., & Shapley, R. (1995). Illusory contours activate specific regions in human visual cortex: Evidence from functional magnetic resonance imaging. *Proceedings of the National Academy of Sciences, U.S.A.*, *92*, 6469–6473.

Ito, M., Tamura, H., Fujita, I., & Tanaka, K. (1995). Size and position invariance of neuronal responses in monkey inferotemporal cortex. *Journal of Neurophysiology*, *73*, 218–226.

Kanwisher, N., Woods, R. P., Iacoboni, M., & Mazziotta, J. C. (1997). A locus in human extrastriate cortex for visual shape analysis. *Journal of Cognitive Neuroscience*, *9*, 133–142.

Kobatake, E., & Tanaka, K. (1994). Neuronal selectivities to complex object features in the ventral visual pathway of the macaque cerebral cortex. *Journal of Neurophysiology*, *71*, 856–867.

Kohler, S., Kapur, S., Moscovitch, M., Winocur, G., & Houle, S. (1995). Dissociation of pathways for object and spatial vision: A PET study in humans. *Cognitive Neuroscience and Neurophysiology*, *6*, 1865–1868.

Kovacs, G., Vogels, R., & Orban, G. A. (1995). Selectivity of macaque inferior temporal neurons for partially occluded shapes. *Journal of Neuroscience*, *15*, 1984–1997.

Lamme, V. A. F. (1995). The neurophysiology of figure-ground segregation in primary visual cortex. *Journal of Neuroscience*, *15*, 1605–1615.

Lamme, V. A. F., Super, H., & Spekreijse, H. (1998). Feedforward, horizontal, and feedback processing in the visual cortex. *Current Opinion in Neurobiology*, *8*, 529–535.

Lee, T. S., Mumford, D., Romero, R., & Lamme, V. A. F. (1998). The role of the primary visual cortex in higher level vision. *Vision Research*, *38*, 2429–2454.

Leventhal, A. G., Wang, Y., Schmolesky, M. T., & Zhou, Y. (1998). Neural correlates of boundary perception. *Visual Neuroscience*, *15*, 1107–1118.

Lewis, R. S., & Kamptner, L. N. (1987). Sex differences in spatial tasks performance of patients with and without unilateral cerebral lesions. *Brain and Cognition*, *6*, 142–152.

Logothetis, N. K., Pauls, J., & Poggio, T. (1995). Shape repre-

- sensation in the inferior temporal cortex of monkeys. *Current Opinion in Biology*, 5, 552–563.
- Lovrich, D., Simson, R., Vaughan, H. G., Jr., & Ritter, W. (1986). Topography of visual event-related potentials during geometric and phonetic discriminations. *Electroencephalography and Clinical Neurophysiology*, 65, 1–12.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., & Tootell, R. B. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, 92, 8135–8139.
- Marr, D., & Nishihara, H. K. (1978). Representation and recognition of the spatial organization of three-dimensional shapes. *Proceedings of the Royal Society of London-Series B: Biological Sciences*, 200, 269–294.
- Maunsell, J. H., & Gibson, J. R. (1992). Visual response latencies in striate cortex of the macaque monkey. *Journal of Neurophysiology*, 68, 1332–1344.
- Moscovitch, C., Kapur, S., Kohler, S., & Houle, S. (1995). Distinct neural correlates of visual long-term memory for spatial location and object identity: A positron emission tomography study in humans. *Proceedings of the National Academy of Sciences, U.S.A.*, 92, 3721–3725.
- Mumford, D. (1992). On the computational architecture of the neocortex: II. The role of cortico-cortical loops. *Biological Cybernetics*, 66, 241–251.
- Payne, B. R., Lomber, S. G., Villa, A. E., & Bullier, J. (1996). Reversible deactivation of cerebral network components. *Trends in Neuroscience*, 19, 535–542.
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, 72, 184–187.
- Pollen, D. A. (1999). On the neural correlates of visual perception. *Cerebral Cortex*, 9, 4–19.
- Ritter, W., Simson, R., & Vaughan, H. G., Jr. (1983). Event-related potential correlates of two stages of information processing in physical and semantic discrimination tasks. *Psychophysiology*, 20, 168–179.
- Ritter, W., Simson, R., & Vaughan, H. G., Jr. (1988). Effects of the amount of stimulus information processed on negative event-related potentials. *Electroencephalography and Clinical Neurophysiology*, 69, 244–258.
- Ritter, W., Simson, R., Vaughan, H. G., Jr., & Macht, M. (1982). Manipulation of event-related potential manifestations of information processing stages. *Science*, 218, 909–911.
- Rugg, M. D., Doyle, M. C., & Wells, T. (1995). Word and nonword repetition within-and across-modality: An event-related potential study. *Journal of Cognitive Neuroscience*, 7, 209–227.
- Sary, G., Vogels, R., & Orban, G. A. (1993). Cue-invariant shape selectivity of macaque inferior temporal neurons. *Science*, 260, 995–997.
- Schroeder, C. E., Mehta, A. D., & Givre, S. J. (1998). A spatio-temporal profile of visual system activation revealed by current source density analysis in the awake macaque. *Cerebral Cortex*, 8, 575–592.
- Schroeder, C. E., Steinschneider, M., Javitt, D. C., Tenke, C. E., Givre, S. J., Mehta, A. D., Simpson, G. V., Arezzo, J. C., & Vaughan, H. G., Jr. (1995). Localization of ERP generators and identification of underlying neural process. *Electroencephalography and Clinical Neurophysiology: Supplement*, 44, 55–75.
- Schwartz, E. L., Desimone, R., Albright, T. D., & Gross, C. G. (1983). Shape recognition and inferior temporal neurons. *Proceedings of the National Academy of Sciences, U.S.A.*, 80, 5776–5778.
- Simson, R., Ritter, W., & Vaughan, H. G., Jr. (1985). Effects of expectation on negative potentials during visual processing. *Electroencephalography and Clinical Neurophysiology*, 62, 25–31.
- Snodgrass, J. G., & Corwin, J. (1988). Perceptual identification thresholds for 150 fragmented pictures from the Snodgrass and Vanderwart picture set. *Perceptual Motor Skills*, 67, 3–36.
- Snodgrass, J. G., & Feenan, K. (1990). Priming effects in picture fragment completion: Support for the perceptual closure hypothesis. *Journal of Experimental Psychology: General*, 119, 276–296.
- Snodgrass, J. G., & Kinjo, H. (1998). On the generality of the perceptual closure effect. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 24, 645–658.
- Snodgrass, J. G., & Vanderwart, M. (1980). A standardized set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Learning and Memory*, 6, 174–215.
- Vanni, S., Revonsuo, A., Saarinen, J., & Hari, R. (1996). Visual awareness of objects correlates with activity of right occipital cortex. *NeuroReport*, 8, 183–186.
- von der Heydt, R., Peterhans, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science*, 224, 1260–1262.
- Zipser, K., Lamme, V. A. F., & Schiller, P. H. (1996). Contextual modulation in primary visual cortex. *Journal of Neuroscience*, 16, 7376–7389.