Electroencephalography and clinical Neurophysiology, 87 (1993) 46–53

EEG 92190

A neurophysiologic correlate of visual short-term memory in humans

H. Begleiter, B. Porjesz and W. Wang

Neurodynamics Laboratory, Department of Psychiatry, State University of New York, Health Science Center at Brooklyn, Brooklyn, NY 11203 (USA)

(Accepted for publication: 13 February 1993)

Summary Neurophysiological investigations in non-human primates and neuropsychological studies in patients with lesions indicate that the inferotemporal cortex is critically involved in visual object recognition. We have recorded event-related potentials from 31 electrodes in a group of healthy normal individuals performing a modified delayed matching to sample task. We have identified a visual memory potential (VMP) which indexes visual short-term memory in humans. This component of the event-related brain potential occurs as early as 170 msec, is maximal at 240 msec, and is generally located in the temporal region. Both the temporal and spatial characteristics of the VMP in humans are in keeping with single cell studies in monkeys.

Key words: Memory; Visual memory potential; Short-term memory; Event-related potential; Inferotemporal cortex; Visual object recognition

It is now well established that the inferotemporal cortex (IT) participates in the sensory analysis of visual features (Gross et al. 1967). A large body of data indicates that in monkeys IT neurons have discrete receptive fields which respond solely to visual stimuli (Gross et al. 1972; Desimone and Gross 1979). The response properties of IT neurons are quite heterogeneous. Indeed, many IT neurons do respond to shape, color or texture (Desimone et al. 1985). In the non-human primate, Klüver and Bucy (1938) first observed that the complete removal of both temporal lobes resulted in a well delineated syndrome, known as the Kluver-Bucy syndrome, which included a failure to recognize visual stimuli.

There is recent neurophysiological evidence in monkeys that neuronal activity in the IT is related to memory processes. This evidence has been obtained in a delayed matching to sample task in which a sample stimulus is followed by a test stimulus after a delay. If the test stimulus matches the sample, the monkey makes one response; if the test stimulus does not match the sample stimulus, a different response must be made (Mikami and Kubota 1980; Furster and Jervey 1982). With the use of this paradigm, Baylis and Rolls (1987) reported that IT neurons are involved in short-term visual memory.

Other investigators have demonstrated that lesions in the IT are sufficient to produce visual memory deficits (Iwai and Mishkin 1968; Cowey and Gross 1970). The delayed non-matching to sample task has been used successfully to study experimentally induced memory deficits in monkeys (Mishkin and Delacour 1975; Mishkin 1978; Zola-Morgan and Squire 1985) as well as amnestic conditions in humans (Aggleton et al. 1988; Squire et al. 1988).

The inferotemporal cortex is not only involved in the analysis and processing of visual patterns, but it also plays a critical role in visual object recognition. Damage to the IT region of the human brain results in significant deficits in visual object recognition. Patients with associative agnosia cannot recognize visual stimuli despite intact visual perception (see Farah 1990 for review). Neurophysiologic and lesion studies in the non-human primate indicate that the IT is involved in visual memory. While lesion studies in humans are compatible with the findings in monkeys, it should be noted that neurophysiologic data in humans are currently lacking.

Event-related potentials (ERP) are ideally suited to study brain processes which require high temporal resolution. We have examined human ERPs obtained to sample and test stimuli as well as matching and non-matching test stimuli in a delayed matching to sample

Correspondence to: H. Begleiter, Neurodynamics Laboratory, Department of Psychiatry, State University of New York, Health Science Center at Brooklyn, Brooklyn, NY 11203 (USA).

paradigm. Moreover, in an attempt to assess the effects of stimulus complexity on memory processes, we examined the effects of simple and complex visual stimuli. With the use of spline-Laplacian techniques, we studied the topographic distribution of ERP components associated with short-term memory.

Methods

Twenty-five healthy right-handed male volunteers (mean age = 20.3) participated in this study. Each individual was fitted with a 31-lead electrode cap (ECI, Electrocap International). We used the entire 10–20 montage and also recorded from an additional 12 sites as follows: AF3, AF4, FC5, FC6, FC1, FC2, CP1, CP2, CP5, CP6, PO3, and PO4 (Standard Electrode Position Nomenclature, American Electroencephalographic Society 1990). All scalp electrodes were referred to Cz. The selection of this reference electrode is based on best results obtained during pilot studies, and our interest to study topographic distribution using the Laplacian operator. Moreover, it has been suggested that the vector of electrode position as well as the absolute position may be critical in observing certain physiological phenomena (Rudell and Fox 1992). Subjects were grounded with a forehead electrode and all impedances were kept below 5 kΩ. Vertical eye movements were monitored with electrodes placed directly above and below the right eye, and horizontal eye movements were monitored with electrodes placed at the outer canthi of the two eyes. Trials with excessive eye movements (> 75 μV) were eliminated from the final average. The electrical activity recorded at each electrode was fed to a set of amplifiers (Sensorium 2000) with a 10,000 gain and a bandpass of 0.1–100 Hz. The amplified activity was sampled at a rate of 256 Hz during an epoch of 100 msec preceding, and 1 sec following each stimulus presentation.

The subject was seated in a reclining chair located in a sound-attenuated RF shielded room (IAC, Industrial Acoustics) and fixated a point in the center of a computer display located 1 m away from his eyes. A modified delayed matching to sample task was used in which two visual stimuli were presented in succession with a 1.5 sec fixed inter-stimulus interval. A trial consisted of a rectangular frame which was presented on the computer display 500 msec before the appearance of the first visual pattern (S1), and remained on the screen for another 900 msec after the presentation of the second visual pattern (S2). The visual frame was presented to indicate the beginning and end of a trial. The inter-trial interval was 4.5 sec. The visual stimuli subtended a visual angle between 3° and 6° and lasted 100 msec. The simple visual stimuli consisted of a few line elements, and the complex stimuli were comprised of a greater number of elements (Fig. 1). These stimuli were selected to be difficult to name, that is lacking simple verbal descriptors. Consequently the mnemonic processes involved were not likely to be semantically mediated.

The presentation of trials with simple and complex stimuli was randomized as were trials with matches and non-matches. A total of 70 simple and 70 complex visual patterns were randomly presented as training stimuli (S1). No S1 stimulus was repeated as S1. On half of the trials the test stimuli (S2) were identical to S1; on the other half of the trials the S2 stimuli were distinctly different from S1. The simple S1 stimuli were always followed by simple matching or non-matching S2 stimuli, while the complex S1 stimuli were followed by complex matching or non-matching S2 stimuli.

On each trial, after the presentation of S2, the subject was asked to press a microswitch in one hand if S2 matched S1, and to press a microswitch in his other hand if S2 differed from S1. The designation of the hand indicating match or non-match was alternated across subjects. It is important to note that reaction time was not stressed but that accuracy and speed were equally emphasized.

The ERPs were averaged for 6 cases: simple S1, complex S1, simple matching S2, simple non-matching S2, complex matching S2, and complex non-matching S2. This experiment yielded an ERP consisting of 5 different peaks most clearly discernible at the more posterior electrodes (see Fig. 2): peak 1 (30–65 msec), peak 2 (90–105 msec), peak 3 (150–175 msec), peak 4 (185–250 msec), and peak 5 (300–360 msec). In addition, a slow negative going wave between 180 and 800 msec was present to all S2 stimuli. In this experiment, a downward deflection indicates greater negativity at the most posterior electrodes with respect to the vertex (Cz) electrode. Amplitudes and latencies were initially measured at electrode P8 where maximal amplitudes were obtained. Measurements at other electrodes were based on the latency of each component obtained at P8.

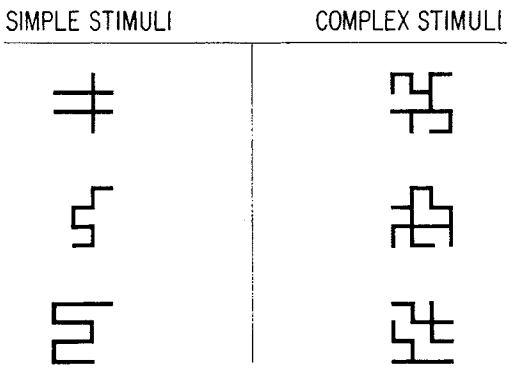

Fig. 1. Sample of simple and complex stimuli used in the delayed matching and non-matching to sample task.

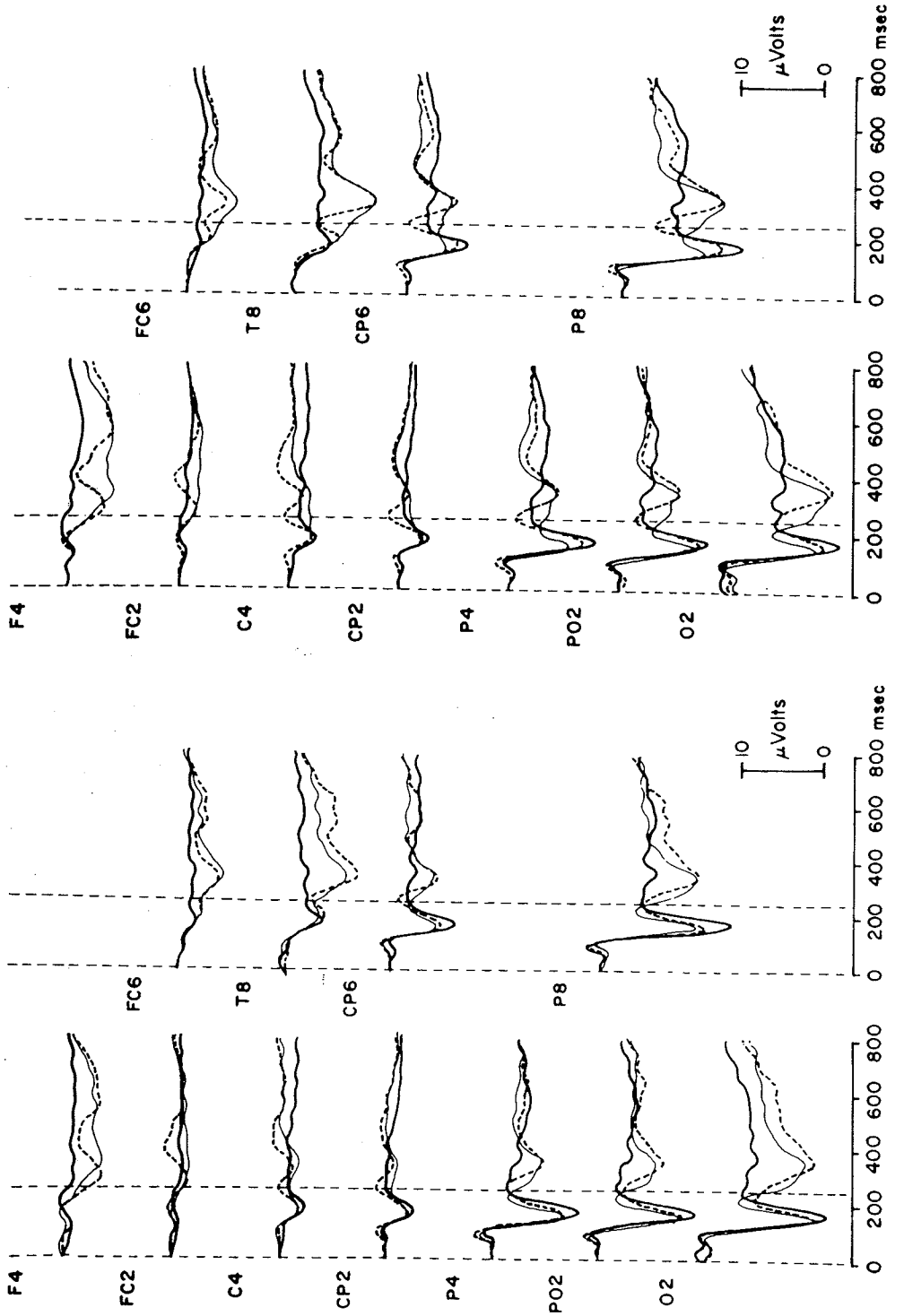

Fig. 2. Grand mean of ERPs obtained in all subjects. Peak-to-peak voltage is approximately 10 μV. The right figure illustrates the ERPs to simple stimuli presented as S1 and S2 when the subjects perceived them as same or different from S1, while the left figure illustrates this for the complex stimuli. A downward deflection indicates greater negativity for the posterior electrodes with respect to the vertex electrode.

The topographic analysis of the neurophysiologic data were based on the entire ERP data set using a spline-Laplacian transformation (Perrin et al. 1987; Gevins et al. 1991; Nunez and Pilgreen 1991; Law et al. 1993). The surface Laplacian is an estimate of the local current density through the skull into the scalp. It is a spatial filter that emphasizes local sources over distant sources. The Laplacian is a model-free and reference-independent technique which improves spatial resolution. Positive values of the current source density indicate local current flow out of the skull, whereas negative values indicate current flow into the skull.

In a smaller sample of subjects (N = 15) we assessed the potential effect of the inter-stimulus interval (ISI) between S1 and S2. Specifically, we increased the ISI from 1.5 sec to 4 sec. In addition, we also tested the effect of stimulus probability by changing the ratio from 50–50, S2-same/S2-different, to 25% S2-same, 75% S2-different, and 75% S2-same, 25% S2-different.

Results

Subjects responded accurately on 97.8% of the trials for simple stimuli and 94.7% for the complex stimuli. Response times were significantly shorter for simple matching stimuli (587.07 msec) than for simple non-matching stimuli (633.67 msec); similarly, response times for complex matching stimuli (624.32 msec) were significantly shorter than to complex non-matching stimuli (658.85 msec). In addition reaction times to complex stimuli were significantly longer than to simple stimuli for all conditions (see Table I).

Statistical analyses of ERP data were only conducted on artifact-free trials with correct behavioral responses. We carried out a number of MANOVAs separately for each component using the amplitude and latency at each of the 31 scalp electrode array as a dependent vector, namely comparing S1 to S2 for simple and complex stimuli, as well as comparing matching and non-matching responses to S2. Amplitudes and latencies obtained to both simple and complex sample (S1) stimuli were not statistically different. A number of MANOVAs assessing differences between conditions resulted in statistically significant findings. For the simple stimuli only, significantly smaller amplitudes ($P < 0.04$) of peak 4 (240 msec) were obtained to matching stimuli (S2) compared to physically identical sample stimuli (S1), and significantly larger amplitudes ($P < 0.05$) of peak 4 were obtained for the non-matching S2 stimuli compared to the sample stimuli. For both the simple and complex stimuli, significantly smaller amplitudes of the peak 4 component were obtained to the matching S2 compared to the non-matching S2 ($P < 0.008$ for simple, and $P < 0.05$ for complex stimuli).

In addition to the aforementioned analyses, we also assessed the contributions of various regions. This was accomplished by dividing the 31 electrode locations into 4 different regions as follows: frontal – Fz, F4, F3, AF1, AF2, FP1, FP2, FC1, FC2; parietal – Pz, P3, P4, CP1, CP2, C3, C4; temporal – P7, P8, T7, T8, CP5, CP6, F7, F8, FC5, FC6; occipital – O1, O2, PO1, PO2. MANOVA was applied for each component, in which the amplitudes or latencies recorded at the electrode sites for each region were entered as a dependent vector for comparisons among different conditions. The amplitudes of peak 3 (N170) and peak 4 (P240) were significantly smaller ($P < 0.03$) for the simple matching stimuli (S2) compared to the physically identical sample stimuli (S1) in the temporal region only. The amplitude of peak 4 (240) was significantly larger ($P < 0.002$) for the non-matching test stimuli compared to the sample stimuli in the parietal region.

The amplitudes of the peak 4 component to the simple matching stimuli (S2) were significantly smaller than those of the non-matching stimuli (S2) at the parietal ($P < 0.0001$), and temporal ($P < 0.005$) regions. Similarly, the amplitude of the peak 4 component was significantly smaller for the complex matching stimuli compared to the complex non-matching stimuli at the parietal ($P < 0.0001$), and temporal ($P < 0.05$) regions.

The latency of the peak 4 component was significantly shorter for the simple matching stimuli compared to the non-matching stimuli. This was only significant ($P < 0.02$) at the parietal region.

We selected the more significant amplitude effect for recognition (peak 4 240 msec) to assess its topographic distribution, using a spherical surface spline interpolation on the entire electrode montage, and

TABLE I

Reaction time for simple and complex stimuli (same and different).

Simple stimulus matching		Complex stimulus matching
	$F = 23.88$ $P < 0.0001$	
Same Mean = 587.07 S.D. = 113.73		Same Mean = 633.67 S.D. = 120.68
$F = 11.09$ $P < 0.0028$		$F = 5.22$ $P < 0.0314$
Simple stimulus non-matching		**Complex stimulus non-matching**
	$F = 28.16$ $P < 0.0001$	
Different Mean = 624.32 S.D. = 97.85		Different Mean = 658.85 S.D. = 94.73

computed the spatial derivatives of the spherical spline functions to obtain current density distributions (Perrin et al. 1987). The current density distributions delineate the scalp locations where the current emerges (sources) from the brain or enters (sinks) from the scalp into the brain. In contrast to the dipole localization method, the current density distribution or Laplacian is independent of any volume conduction model of the head. The spline method uses data obtained at all electrodes to estimate Laplacians at all locations within the electrode montage. The current density map for the peak 4 component obtained to S2 yielded a temporal current field (see Fig. 3) located primarily in the right temporal region.

The results obtained in additional experiments in which we changed the ISI between S1 and S2, or the probability of occurrence of same-S2 and different-S2 did not yield statistically significant differences from the aforementioned results.

Discussion

In the present experiment we examined whether or not the memory of a sample visual stimulus influences the neurophysiological response to subsequent test stimuli. If the physical characteristics of the visual stimuli were the sole determinants of neural responses, then for identical stimuli, the ERPs to S2 would be expected to be the same as those to S1. The results indicate that identical sample and test stimuli yield significantly different neurophysiological characteristics. Indeed, the data show that event-related brain potentials are different to a test stimulus depending on whether or not it matches an immediately preceding sample stimulus. The ERPs to matching stimuli were significantly reduced compared to the ERPs to non-matching stimuli. This response reduction is not caused solely by the temporal contiguity between sample and test stimuli, but is specific for matching stimuli com-

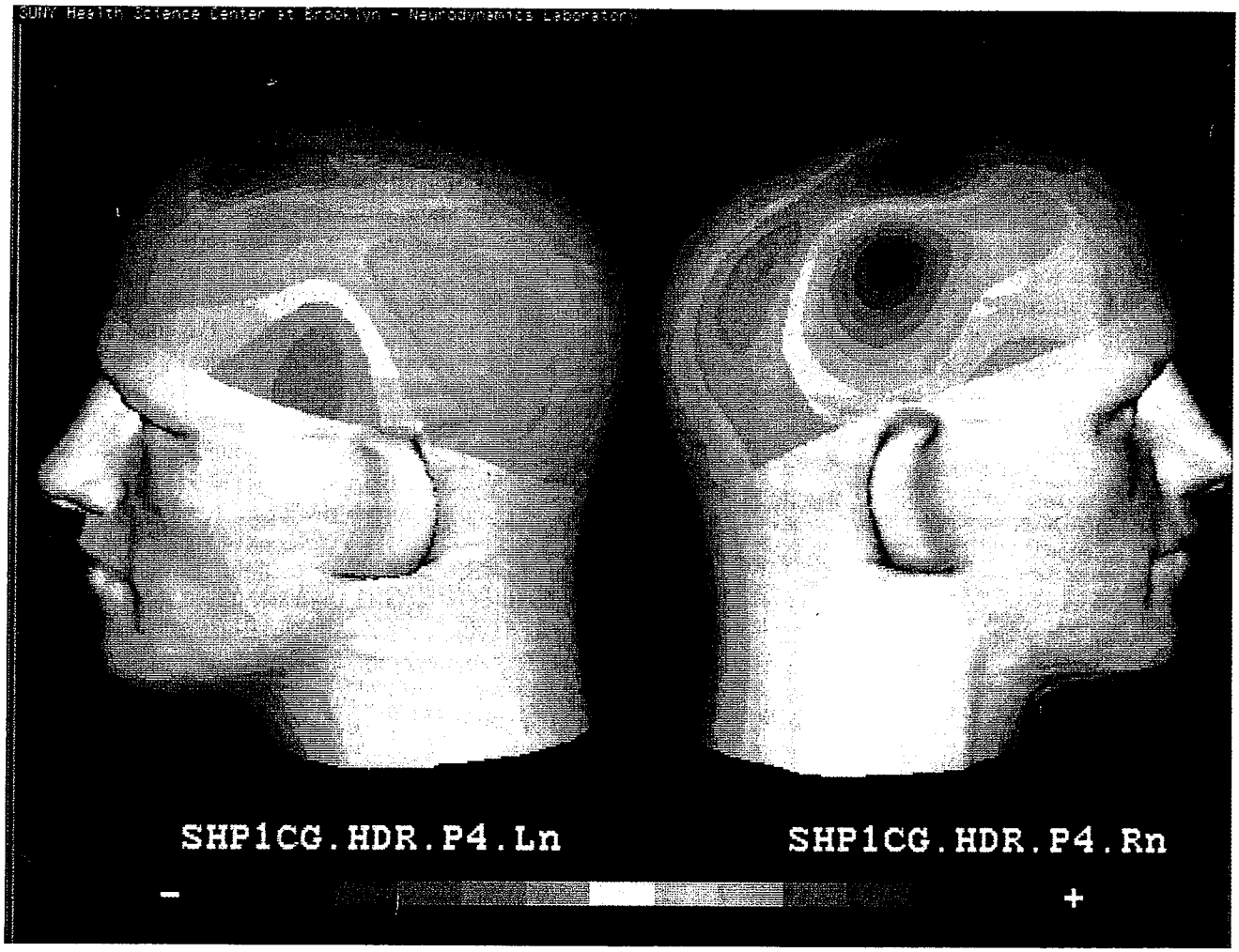

Fig. 3. Scalp current density of the ERP component (peak 4 240 msec) involved in short-term memory. The current density map discloses a strong positive source in the right temporal region.

pared to non-matching stimuli, and appears to be independent of the inter-stimulus interval. Moreover, this finding does not appear to be influenced by stimulus probability. It is hypothesized that in the current experiment it is the similarity between sample and test stimuli which results in a significant reduction of the physiological response.

The decrement in ERP responses to previously observed stimuli was most striking at peak 4, approximately 240 msec after the simple matching stimuli. While we did not find significant differences in the peak 4 component between sample and matching complex stimuli, significant differences were noted between complex matching and complex non-matching stimuli. To the extent that complex sample stimuli are more difficult to encode than simple stimuli, this may result in excessive difficulty in working memory. It has been demonstrated that the degree of memory impairment increases with stimulus load. The differentiation in the peak 4 component between sample and matching stimuli is particularly strong to simple or easily encoded stimuli and may possibly reflect a visual memory potential (VMP).

Because accuracy was stressed as much as speed, subjects performed the required tasks with very few errors. The reaction times obtained to matching stimuli are significantly shorter than those obtained to non-matching stimuli. These findings are in agreement with repetition effects on reaction time which are well established (Bentin and Moscovitch 1988; Rugg et al. 1988). The significantly longer reaction times to complex stimuli compared to simple stimuli reflect the effect of differential stimulus complexity resulting in increased information processing for the more complex stimuli. This increase in reaction time to complex stimuli parallels the smaller peak 4 amplitude results obtained to those stimuli.

In the current study we used a modified delayed matching to sample task in which the subject was asked to press a button for matching and another for non-matching stimuli. The task imposes a general demand on the subject's attention, starting with the encoding of the sample stimulus, the maintenance of the memory of the sample stimulus during the delay interval, and a subsequent retrieval and comparison of the sample and test stimuli. The results suggest that event-related potentials index neural processes involved in short-term memory for visual shapes. Our findings indicate that ERPs recorded to matching and non-matching stimuli may reflect cognitive processes involved with acquisition and encoding of stimuli as well as retrieval and comparison of stimuli. Indeed, for the simple stimuli, the responses to matching and non-matching test stimuli differed significantly from those obtained to sample stimuli. Moreover, for both simple and complex stimuli, the responses to matching stimuli were significantly smaller than those obtained to non-matching stimuli. Therefore the neural processes involved in working memory may be indexed not just by the response to the matching stimuli, but also by the response to non-matching stimuli. The ERPs to S2 appear to reflect neural information about the memory of preceding stimuli. It may well be the similarity between the present stimulus and the memory trace for that stimulus which results in a significant reduction of the ERP. However, the degree of reduction cannot be taken to reflect solely the process of retrieval, but instead, involves a number of different processes including encoding of the original stimulus, maintenance of the memory trace, and retrieval and comparison of stimuli.

It should be noted that while a number of ERP investigations have specifically studied mnemonic processes, all have focused on late ERP components (Neville et al. 1986; Kutas 1988; Rugg and Nagy 1989; Friedman 1990; Paller and Kutas 1992). The findings of our present study indicate that neural correlates of visual short-term memory (VMP) start as early as 170 msec and become most pronounced at about 240 msec.

Our present results are quite consistent with single cell recordings in inferior temporal cortex of monkeys where decrements in neuronal responses to matching stimuli have also been reported (Mikami and Kubota 1980; Riches et al. 1991). Recently, Miller et al. (1991) recorded from the inferior temporal cortex of rhesus monkeys during a delayed matching to sample procedure. They observed that the neuronal response to matching stimuli was significantly attenuated compared to non-matching stimuli. Moreover, the neuronal response to novel stimuli decreased as the stimuli became increasingly familiar to the animals. Our findings are in agreement with the results from animal experiments.

The decrement in ERP voltage obtained to previously seen stimuli is in keeping with neural network models of memory (McClelland and Rumelhart 1986). In this model, the memory trace of a specific spatiotemporal pattern is represented by changes in the set of synaptic weights which results in a more efficient neuronal processing of previously experienced stimuli. This efficiency is manifested by a decrease in the number of neural elements necessary to process familiar stimuli. Our data support the hypothesis proposed by Miller et al. (1991) who suggested that neurons may behave as adaptive memory filters that selectively process novel information.

The results of current density mapping for peak 4 indicate a strong current field in the temporal region (Fig. 3) possibly reflecting the involvement of this region in processing shape stimuli. Moreover, our current density map indicates a stronger field in the right hemisphere compared to the left. While the current source density technique cannot provide a high level of

spatial resolution, it is nevertheless remarkable that the active fields are quite compatible with the localization of visual short-term memory in temporal cortex of monkeys.

This is entirely consistent with single cell recordings in the inferior temporal cortex of monkeys which are known to encode information about shape and color of stimuli (Gross et al. 1972; Desimone et al. 1984; Baylis and Rolls 1987; for review see Desimone and Ungerleider 1989). Clinical evidence and recent PET findings in humans (Corbetta et al. 1991) indicate that the temporal region in humans is critically involved in object recognition (Farah 1990).

Recent evidence from amnestic patients as well as animal studies suggest that short-term memory may be established in neocortical areas dedicated to the analysis and processing of specific information while long-term memory is dependent on the complex interaction between structures in the medial temporal lobe and the neocortex (Squire and Zola-Morgan 1991). While the nature of memory consolidation is not fully elucidated, retrieval of memory appears contingent on the integrity of distributed neocortical representations. Neurophysiologic correlates of memory such as the VMP should provide a productive approach to the study of normal mnemonic processes as well as amnestic conditions in humans.

We thank Arthur Stimus for his most valuable assistance.

This work was supported by N.I.H. Grants AA-02686 and AA-05524.

References

Aggleton, J.P., Nicol, R.M., Huston, A.E. and Fairbairn, A.F. (1988) The performance of amnesic subjects on tests of experimental amnesia in animals: delayed matching-to-sample and concurrent learning. Neuropsychologia, 26: 265–272.

Baylis, G.C. and Rolls, E.T. (1987) Responses of neurons in the inferior temporal cortex in short-term and serial recognition memory tasks. Exp. Brain Res., 65: 614–622.

Bentin, S. and Moscovitch, M. (1988) The time course of repetition effects for words and unfamiliar faces. J. Exp. Psychol.: Gen., 117: 148–160.

Corbetta, M., Miezin, F.M., Dobmeyer, S., Shulman, G.L. and Petersen, S.F. (1991) Selective and divided attention during visual discriminations of shape, color and speed: functional anatomy by positron emission topography. J Neurosci., 1: 2383–2402.

Cowey, A. and Gross, C.G. (1970) Effects of foveal prestriate and inferotemporal lesions on visual discriminations by rhesus monkeys. Exp. Brain Res., 11: 128–144.

Desimone, R. and Gross, C.G. (1979) Visual areas in the temporal cortex of the macaque. Brain Res., 178: 363–380.

Desimone, R. and Ungerleider, L.G. (1989) Neural mechanisms of visual processing in monkeys. In: G. Boller and J. Grafman (Eds.), Handbook of Neuropsychology, Vol. 2. Elsevier, New York, pp. 267–269.

Desimone, R., Albright, T.D., Gross, C.G. and Bruce, C. (1984) Stimulus selective properties of inferior temporal neurons in the macaque. J. Neurosci., 4: 2051–2062.

Desimone, R., Schein, S.J. and Albright, T.D. (1985) Form, color, and motion analysis in prestriate cortex of the macaque. In: S.J. Schein and T.D. Albright (Eds.), Pattern Recognition Mechanisms. Springer, Berlin, pp. 1665–1678.

Farah, M.J. (1990) Visual Agnosia. MIT Press, Cambridge, MA.

Friedman, D. (1990) Cognitive event-related potential (ERP) components during continuous recognition memory for pictures. Psychophysiology, 27: 136–148.

Furster, J.M. and Jervey, J.P. (1982) Neuronal firing in the inferotemporal cortex of the monkey in a visual memory task. J. Neurosci., 2: 361–375.

Gevins, A.S., Le, J., Brickett, P., Reuter, B. and Desmond, J. (1991) Seeing through the skull: advanced EEGs using MRI to accurately measure cortical activity from the scalp. Brain Topogr., 4: 125–131.

Gross, C.G., Schiller, P.H. and Wells, C. (1967) Single-unit activity in temporal association cortex of the monkey. J. Neurophysiol., 30: 833–843.

Gross, C.G., Rocha-Miranda, C.E. and Bender, D.B. (1972) Visual properties of neurons in inferotemporal cortex of the macaque. J. Neurophysiol., 35: 96–111.

Iwai, E. and Mishkin, E. (1968) Two visual foci in the temporal lobes of monkeys. In: N. Yoshii and N.A. Buchwald (Eds.), Neurophysiological Basis of Learning and Behavior. Osaka University Press, Osaka, pp. 23–33.

Klüver, H. and Bucy, P.C. (1938) "Psychic blindness" and other symptoms following bilateral temporal lobectomy in rhesus monkeys. Am. J. Physiol., 119: 352–353.

Kutas, M. (1988) Review of event related potential studies of memory. In: M. Gazzaniga (Ed.), Perspectives in Memory Research. MIT Press, Cambridge, MA, pp. 181–218.

Law, S.D., Nunez, P.L. and Wijesinghe, R. High resolution EEG using spline generated surface Laplacians with applications to spherical and ellipsoidal surfaces. IEEE Trans. Biomed. Eng., 1993, in press.

McClelland, J. and Rumelhart, D. (1986) Parallel Distributed Processing, Vols. 1 and 2. MIT Press, Cambridge, MA.

Mikami, A. and Kubota, K. (1980) Inferotemporal neuron activities and color discrimination with delay. Brain Res., 182: 65–78.

Miller, E.K., Li, L. and Desimone, R. (1991) A verbal mechanism for working and recognition memory in inferior temporal cortex. Neurosci. Abst., 2: 1377–1379.

Mishkin, M. (1978) Memory in monkeys severely impaired by combined but not by separate removal of amygdala and hippocampus. Nature, 273: 297–300.

Mishkin, M. and Delacour, J. (1975) An analysis of short-term visual memory in the monkey. J. Exp. Psychol., 1: 326–334.

Neville, H., Kutas, M., Chesney, G. and Schmidt, A.L. (1986) Event-related potentials during initial encoding and recognition of congruous and incongruous words. J. Mem. Lang., 25: 75–92.

Nunez, P.L. and Pilgreen, K.L. (1991) The spline-Lapacian in clinical neurophysiology: a method to improve EEG resolution. J. Clin. Neurophysiol., 8: 397–413.

Paller, K.A. and Kutas, M. (1992) Brain potentials during memory retrieval provide neurophysiological support for the distinction between conscious recollection and priming. J. Cogn. Neurosci., 4: 375–390.

Perrin, F., Bertrand, O. and Pernier, J. (1987) Scalp current density mapping: value and estimation from potential data. IEEE Trans. Biomed. Eng., 34: 283–287.

Riches, I.P., Wilson, F.A.W. and Brown, M.W. (1991) The effects of visual stimulation and memory on neurons of the hippocampal formation and the neighboring parahippocampal gyrus and inferior temporal cortex of the primate. J. Neurosci., 11: 1763–1779.

Rudell, A.P. and Fox, S.E. (1991) The propagation potential: an axonal response with implications for scalp-recorded EEG. Biophys. J., 60: 556–567.

Rugg, M.D. and Nagy, M.E. (1989) Event-related potentials and recognition memory for words. Electroenceph. clin. Neurophysiol., 72: 395–406.

Rugg, M.D., Furda, J. and Lorist, M. (1988) The effects of task on the modulation of event-related potentials by word repetition. Psychophysiology, 25: 55–63.

Squire, L.A. and Zola-Morgan, S. (1991) The medial temporal lobe memory system. Science, 253: 1380–1385.

Squire, L.R., Zola-Morgan, S. and Chen, K.S. (1988) Human amnesia and animal models of amnesia: performance of amnesic patients on tests designed for the monkey. Behav. Neurosci., 102: 210–221.

Zola-Morgan, S. and Squire, L. (1985) Medial temporal lesions in monkeys impair memory on a variety of tasks sensitive to human amnesia. Behav. Neurosci., 99: 22–34.