Active touch exploration of extrapersonal space elicits specific electrogenesis in the right cerebral hemisphere of intact right-handed man

John E. Desmedt

Brain Research Unit, University of Brussels, 115 Boulevard de Waterloo, B1000 Brussels, Belgium

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ABSTRACT Language and analytic processing are currently thought to be represented in the left hemisphere, whereas spatial and holistic processing would involve primarily the right hemisphere in man. An experimental paradigm for engaging the nonlanguage hemisphere (generally the right) is described. This involves active touch exploration with the index finger to identify the orientation of a ridge with respect to the subject's body. The task is compatible with the electronic averaging of transient event-related cerebral potentials recorded from the intact scalp. A consistent positive electrogensis of 1–5 μV and about 0.5–1.5 sec in duration was recorded over the nonlanguage hemisphere, regardless of whether the left or the right index finger performed the tactile scanning. The lateralized specific electrogensis did not extend to the midline, and it is to be differentiated from the decision P300 component.

These findings provide a new procedure for analyzing, in intact man, measurable focal potentials associated with unique processor subsystems during cognitive behavior. The method will make it possible to investigate the dynamic distributions of processing tasks between the two hemispheres in normal man in whom the commissural integration is normal, thereby adding to the data collected on patients with unilateral brain lesions or with surgical transection of the corpus callosum.

The two cerebral hemispheres appear to be functionally equivalent in nonhuman primates but present in man a differential specialization such that, for example, language disturbances frequently follow unilateral lesions to the left (but not to the right) hemisphere in right-handed individuals. Because speech is such a salient feature of human culture, this fact led to the view of an absolute superiority of the left hemisphere. This concept of cerebral dominance now appears to be misleading and recent data increasingly document the apparently major role of the right, nonlanguage, hemisphere for several nonverbal cognitive functions, such as the perception of melodies, orientation in extrapersonal space, and the ability to generate a concept of the whole from fragmentary spatial information about objects. Much of the evidence has been provided by clinical observations of patients with unilateral cerebral disease (1–5) and by studies of patients with a complete surgical section of the interhemispheric connections carried out for the treatment of intractable epileptic seizures (6, 7). For example, because the afferent pathways for somatic sensation are anatomically crossed, the sensory signals from one hand only reach the hemisphere on the other side in a split-brain patient in whom the discrimination of tactile shapes is found to be performed much better for the left hand (connected to the right hemisphere) than for the right hand (8, 9).

This type of data is giving new vigor to the analysis of higher cerebral functions in man, while also disclosing the complexities of the problems thus raised. Furthermore, in patients with unilateral cortical lesions or with a callosal transection, the interaction between the two hemispheres is partially or totally eliminated. While providing essential information about the intrinsic capabilities of the left or the right hemisphere, the abilities remaining in these patients do not elucidate how the two corresponding modes of cognitive processing (verbal analytic versus spatial holistic) (cf. 6, 7, 10) blend, integrate, and/or compete with each other during the normal operations of an intact brain.

An essential step in an attempt to resolve these questions is to study neurologically intact individuals by noninvasive technics during appropriate behavioral tasks. Limited results have been obtained by psychological methods in which different concurrent inputs are presented to the right or left hand (or ear, or visual field) and the relative accuracy of perception is evaluated. This approach assumes that the arrival of sensory signals in the receiving areas of one hemisphere, which is involved in the higher perceptual processing relevant to a given task, should result in a performance superior to the one recorded when the same stimuli are first projected to the receiving areas of the opposite hemisphere. These psychological experiments have produced data, with statistical differences in the expected direction, for either verbal or nonverbal material, but the effects were quite small (5). This approach does not appear to provide a versatile method for resolving pending questions.

An alternative approach for acquiring pertinent data in intact man would become available if the electrical signs of focal processing in either hemisphere could be recorded during perceptual behaviors likely to require their special capabilities. It is well known that discrete sensory stimulation evokes in the human brain electrical responses of only a few microvolts, which can be recorded by electrodes on the scalp and then extracted from background noise by electronic averaging. In subjects performing a selective attention task about simple stimuli, the sensory signals, which resolve the subject's uncertainty and thereby allow him to make a definite perceptual decision, will elicit a large positive component (P300) of about 300-msec peak latency; this component is related not to the physical characteristics of the sensory stimuli but to cerebral processing functions (11–15). The P300 is maximal over the parietal scalp (14) but is distributed equally on both sides of the brain (15). This is not surprising, because the electrical stimulation of nerves or skin and the other stimuli used in previous studies do not provide a behaviorally meaningful input that would require any special processing in, say, the right hemi-

Abbreviation: P300, a positive component of about 300-msec peak latency related to cerebral processing functions.
sphère. On the other hand, current attempts to engage the left hemisphere by presenting language material, such as syllables, have achieved variable success, and significant data are only beginning to emerge (16). One difficulty is that sensory features discrete in time must be presented to elicit phasic cerebral event-related potentials and such stimuli may fail to capture the subject's interest and become trivial after the many repetitions required for accumulating sufficient response samples in the average record.

The present paper describes unexpectedly clear results along this line for nonverbal material that was thought likely to engage the right hemisphere capabilities for spatial exploration. The paradigm uses tactile scanning, which is a natural process for acquiring at fingertips a pattern of skin stimulations, whereby the texture, size, and shape of an object can be perceived (17). Special instrumentation has been designed to make the active touch input fairly reproducible but still interesting for the subject and to confine it to a brief and identifiable period, which can provide an accurate time reference for the coherent electronic averaging of the concomitant event-related potentials.

MATERIALS AND METHODS

After preliminary trials with earlier prototypes, 10 experiments were carried out with six adult subjects (scientific staff, medical students, and the author) who were highly motivated to perform the task correctly. The subjects could relax to minimize interferences from eyeblinks and muscle potentials and they did not have excess background α waves in the electroencephalogram. These subjects were definitely right-handed as tested by the Edinburgh inventory (18). In two subjects (one illustrated by Fig. 1), cerebral blood flow measurements confirmed that language was represented in the left hemisphere. In addition, a left-handed girl was investigated, in whom the language was shown by cerebral blood flow measurements to be located in the right hemisphere (cf. 19). The subjects sat comfortably in a reclining armchair in a sound-proofed, air-conditioned, copper-shielded room.

The active touch device included a vertical Plexiglas rod terminated on its flat top by a circular ridge, 10 mm in diameter, protruding by 0.5 mm. The ridge was interrupted by one gap of 1.5 mm. The rod was mounted on the shaft of a step motor interfaced to the electronic program, which changed the gap orientation to one of four positions at 90° (forward, backward, to the left, or to the right with respect to the subject) between successive trials of any run. The sequence of gap orientation was randomized. The hand of the subject rested on a stand with the index finger lifted by an electromagnetic device. To initiate any trial of a run, the fingertip was dropped onto the ridge and the subject then quickly identified the gap orientation with respect to his body by active touch. He did not have to report or memorize the orientation and was told to refrain from spelling it out for himself and to avoid the use of any language label. Three seconds later, the index finger was automatically lifted from the ridge in preparation for the next trial. There was no warning signal. The intervals between trials varied at random from 7 to 15 sec. The equipment operated quietly and provided no cues to the subject about occurrence of the next trial. Alternate runs of about 30 trials were carried out, either with the ridge as described or with a smooth Plexiglass surface replacing the ridge on the rod, which the subject explored similarly without obtaining any spatial information.

Brain potentials were recorded by sterile stainless steel needles (0.2 mm diameter) inserted into the scalp and connected to differential amplifiers of 10-MΩ input impedance. The system band pass extended from 3 kHz to 0.05 Hz (3 sec time constant), which avoided distortion of the potentials (20). The data were stored on frequency modulation tape, edited off-line to exclude each trial with amplifier blocking or artifacts, and then averaged on a Nicolet 1074 digital computer (4096 words of nine bits). Standard scalp derivatives were from the parietal leads on both sides (3 cm behind the C3 and C4 of the international 10–20 system) (cf. 21) and midline vertex (Cz), all referred to the earlobe on the same side. The averaged potentials were written on an X–Y plotter. Details are available elsewhere (20).

RESULTS

Fig. 1 presents a typical experiment on a right-handed subject palpating the ridge gap with the right index finger. A large positive electrogenesis was recorded for about 1.5 sec over the right parietal cortex compared to the left (Fig. 1B). The early deflections (up to about 0.25 sec) were related to afferent stimulation by contact when the finger was dropped on the ridge. Several crucial controls are presented. The electro-oculogram averaged over the same trials was flat, indicating absence of eye movement artifacts, which could have contaminated the brain potentials (cf. 20) (Fig. 1A). Comparison of event-related potentials during active touch of either the ridge gap (thicker trace) or a smooth surface showed no significant difference at the left hemisphere (Fig. 1C) but large positivity for the ridge gap at the right hemisphere (Fig. 1E). When the same samples of brain potentials were averaged in the add-subtract mode (Fig. 1D and F), whereby each successive sample is in turn added or subtracted by the computer to eliminate the response temporally related to the sensory event (22), the remaining contribution of nonresponse background was obtained and this also was flat and similar for ridge or smooth surface palpation. This add-subtract check showed that changes in the background electroencephalogram could not explain the phenomenon thus recorded in Fig. 1E. In addition, when the same subject performed the same active touch task with the left index finger instead of the right, a similar positivity was recorded over the right hemisphere. The phenomenon was thus associated with the nonlanguage hemisphere, not with the hand used in active touch, and it must be distinguished from the (contralateral) motor potentials (23, 24) related to movements of the exploring finger. The parietal positivity was consistently recorded on the right side in these experiments; it ranged from 1 to 5 μV peak voltage and lasted 0.5–1.5 sec.

By contrast, the left-handed subject with language represented in the right hemisphere consistently presented a prolonged positive electrogenesis over the left parietal cortex, regardless of whether the active touch was performed by the left or right index finger.

Fig. 2 presents records in which data for three experiments with the right index and two experiments with the left index on three right-handed subjects were pooled. The record from the midline vertex (Cz) was superimposed on the two parietal records. The prolonged positivity was again recorded on the right side. The left side presented only a smaller positivity with respect to the midline. In these experiments, a photic dot display with four possible orientations at 90° from each other was presented 1.5 sec after finger contact on the ridge and the subject was asked at that time to judge the relative orientations for the dots and for the gap in the ridge. This perceptual decision elicited a large P300, which had the same peak voltage and wave form at the two parietal derivations. The scalp topography clearly dissociated the symmetrical decision P300 from the more localized positive electrogenesis which was lateralized.
DISCUSSION

The cerebral hemispheres of man include neuron assemblies with special capabilities for handling complex information but the lateralization is not absolute and integration of the hemispheric subsystems is required to produce a smooth, efficient course of behavior. Furthermore, if the class of information considered (language, music, spatial orientation, etc.) influences the preferential routing of signals between hemispheres, the segregation is unlikely to be rigid and an additional criterion based on the kinds of processing required (analytical versus holistic) may affect the distribution of processing tasks. For example, whereas melody perception would be lateralized to the right when treated holistically (as in musically naive persons), it would also partially involve the left hemisphere in sophisticated listeners who analyze the music into sets of relationships between its components (cf. 10). These interactions and the dynamic balance of assignments between hemispheres should be studied in intact man, in whom commissural integration is possible. The cerebral event-related potentials would

FIG. 1. Active touch by the right index finger in a right-handed subject with language located in the left hemisphere. The finger is dropped onto the Plexiglass ridge at the time indicated by the arrow. The traces represent the averages of 101 trial samples. (A) Electro-oculogram control over the same trials. (B) Palpation of the ridge; superimposed traces simultaneously recorded from the right (thicker trace) and the left parietal cortex. The vertical hatching indicates the extent of the positive electrogenesis on the right side. (C and D) Traces recorded over the left parietal cortex in two different sets of runs involving active touch of either the ridge (thicker traces) or a smooth Plexiglas surface (thinner traces). (D) Presents, as a control for nonresponse background activity, the add-subtract averaging of the same trial samples as in C. (E and F) Traces recorded over the right cortex in the same two sets of runs, thus involving active touch of either the ridge (thicker traces) or a smooth surface. F is the add-subtract average control of E. (G) Calibrating step function (2.5 μV). Negativity of the active electrode records upward. The reference electrode is at the midline vertex, which minimizes interferences from muscle potentials and from α waves of the electroencephalogram. Similar features were recorded with earlobe references in this experiment.

FIG. 2. Pooled data of five experiments on three subjects, with active touch by either the right or the left index finger. The active electrodes at the right and left parietal cortices (thicker traces) were referred to the earlobe on the same side. The midline vertex (Cz) electrode (thinner trace) was referred to the left earlobe. First arrow, index finger is dropped onto the ridge for active touch. Second arrow, photic dot display is presented and the subject judges the relative orientations of the ridge gap and of the dots.
acquire a considerable pertinence for adding to the available clinical and psychological evidence, if appropriate experimental designs could engender unique processor subsystems and elicit measurable focal electrogensis from them. The extraction of the (small) transient brain potentials by electronic averaging requires (i) the presentation of large numbers of similar target stimuli and (ii) the use of rather brief stimuli occurring at a definite point in time. This represents a challenge for the analysis of cognitive functions because, for example, the repeated presentation of simple isolated stimuli like syllables (ba, pa, etc.) is unlikely to engage the language processor as consistently as conversation. Some recent experiments on selective attention successfully involved special cognitive subsystems by presenting simple stimuli at high rate in forced paced tasks, thus imposing a constraint on the subject's use of his processing resources (15, 25, 26).

The present experiments successfully resolved several difficulties and succeeded in engaging the spatial orientation processor by a natural active touch task carried out leisurely at intervals of about 10 sec. The active touch behavior occurred at a well-defined point in time, thus allowing coherent averaging of transient brain potentials. The subjects found themselves quite interested in relating the ridge gap to their own body orientation. At this stage, they were asked not to use verbal labels so as to minimize intervention of the language processor. Introspection suggests that closure of the orientation problem is achieved in about 1 sec. The active touch paradigm elicited a consistent and prolonged positive electrogensis over the right parietal cortex in right-handed subjects and over the left parietal cortex in one left-handed subject with language represented on the right side, regardless of whether the right or left hand performed the tactile scanning. The positivity is not recorded at the midline vertex and its topographical features on the scalp clearly differentiate it from the well-known P300 decision component (Fig. 2). The P300, which presumably indexes the completion of a perceptual decision and the clearance of the information channel, is symmetrical and widely distributed over the posterior scalp. By contrast, the active touch-specific electrogensis appears to be related to more focalized and discrete lateral generators, which do not extend to the midline under the conditions of these experiments. It should be pointed out that the experiments of Fig. 2 serve to illustrate these different topographies in the same paradigm. However, this should not be taken to imply that the double stimulation of Fig. 2 would be required for bringing out the active touch phenomenon. The latter can in deed be elicited with no sensory stimulation either before or after the tactile scanning and it does not depend on expectancy effects or on motor responding.

The finding that the prolonged positive electrogensis is roughly concomitant with the processing of the active touch behavior and that it is consistently located in the nonlanguage hemisphere, whichever hand is used for acquiring the tactile cues, is probably the strongest evidence to date for the view that transient event-related potentials can indeed index the detailed operations of specific cerebral processor functions.