Stimulation of Frontal Cortex and Delayed Alternation Performance in the Monkey

Abstract. Unilateral or bilateral stimulation of the region surrounding the sulcus principalis of the cortex of the monkey interferes with delayed alternation performance. It is without effect on auditory discrimination performance. Bilateral stimulation is more disrupting than unilateral stimulation. The impairment is limited in time to the period of stimulation and is fully reversible.

That delayed response and delayed alternation performance of monkeys are severely impaired by surgical lesions of the lateral frontal cortex has been firmly established during the past 20 years (*1*). The present report is concerned with the effect of electrical stimulation of regions of the frontal lobes on delayed alternation and discrimination performance. Traditionally, electrical stimulation of the cerebrum has been used as an evoking stimulus, producing such phenomena as "motor maps," "sham rage," and "ergotropic" and "trophotropic" responses. More recently it has been used as a rewarding or punishing stimulus (*2*). Less frequently have its effects on the efficiency of on-going behavior been observed, at least in a systematic fashion; this is especially true where no obvious motor or reward effects are apparent. Such a use of stimulation was adopted by Rosvold and Delgado (*3*), who showed that stimulation of the caudate nucleus impaired delayed alternation behavior. But there have been, as yet, no reports of the effects of stimulation of the frontal cortex on this type of behavior. The results of the study reported here suggest that the technique might be rather more powerful than surgical lesion for the analysis of cortical function.

The electrodes were designed to permit the fine silver ball contacts (0.8 mm in diameter) to rest upon the cortex near the banks of sulcus principalis and sulcus arcuatus. Each electrode contained 13 points, implanted in each hemisphere according to the technique of Delgado (*4*). The positions of the contacts in one animal, as determined by post-mortem examination, are shown in Fig. 1. Stimulation was applied between the points that are joined by lines. Principalis points are joined by lines ventrally adjacent to the points; arcuatus points, by lines dorsally adjacent. In our study only principalis points *or* arcuatus points were stimulated—never both simulaneously. The stimulus was a unidirectional square wave (duration, 0.2 msec; frequency, 100 cy/sec), generated by a Grass stimulator. During any stimulation condition, pulses were delivered repeatedly for periods of 1 second, with 3 seconds of nonstimulation between presentations. This pattern of stimulation was begun at the beginning of the first trial of a stimulation session and continued without interruption until the end of the last trial; hence, the animal was stimulated both during a trial and between trials. The voltages for each animal for each mode of stimulation (to principalis and to arcuatus) were selected prior to the commencement of formal testing so as to be 1 or 2 volts below the threshold for overt motor responses.

Prior to implantation, three young macaque monkeys (each weighing about 3 kg) were trained to perform delayed alternation, auditory discrimination, and visual discrimination tasks (*5*). All testing was carried out in a Wisconsin general testing apparatus. For the delayed-alternation task the animal was presented with two covered food wells. On successive trials (between trials an opaque screen was lowered for 7 seconds) the animal was required to lift the cover that he had *not* lifted on the prior trial. In the auditory problem the two stimuli to be discriminated consisted of a white noise and a pure tone of 1000 cycles, each interrupted briefly three times per second and each approximately 70 db above the room noise level. The animal was required to lift a food-well cover when the white noise was presented and to refrain from lifting the cover when the tone was presented. Correct responses to either stimulus were rewarded. In both the delay and the auditory tasks, correction trials were run. All animals learned the tasks sufficiently well to satisfy a criterion of 90 correct responses in 100 successive trials (exclusive of correction trials).

After implantation, various orders of testing were employed which cannot be described in detail here. It should be mentioned that the stimulation testing for delayed alternation was carried out intermittently over a period of more than 2 months, during which time the effect was quite stable. Typically, the animal was given 30 control trials without stimulation, then 30 trials with stimulation, followed by another 30 control trials, although the last step was not always taken. Within each session, stimulation and nonstimulation periods followed each other without any time gap between.

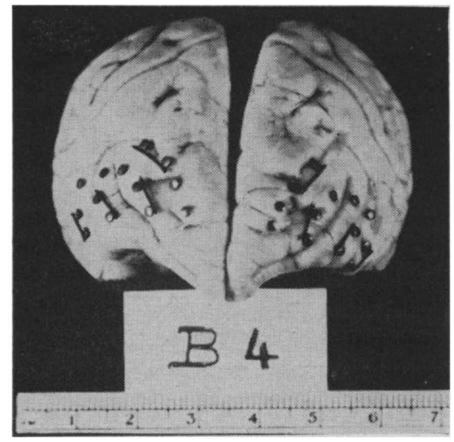

Fig. 1. Position of electrode contacts as determined by post-mortem examination. It should be noted that the markers in the photograph are about 2.5 times the size of the actual contacts, which were 0.8 mm in diameter. Lines ventrally adjacent to pairs of contacts connect arcuatus stimulation points; lines dorsally adjacent connect principalis stimulation points.

In Table 1 are listed the results of stimulation of sulcus principalis and sulcus arcuatus upon delayed alternation and auditory discrimination. It will be seen that there is a very clear effect of bilateral principalis stimulation upon delayed alternation ($P < .0005$). In fact, the behavior is not significantly better than chance. Unilateral stimula-

Table 1. Ratios of correct to total trials.

Animal	Delayed alternation					Auditory discrimination		
	Before stimulation		During stimulation		After stimulation	Before stimulation	During stimulation	After stimulation
				Bilateral principalis				
B–2	104/120	*	57/120	*	52/60	77/90	71/90	28/30
B–3	81/90	*	44/90	*	30/30	80/90	77/90	22/30
B–4	85/90	*	54/90	†	27/30	84/90	84/90	26/30
Av. percent	90.4	*	51.9	*	92.2	90.0	85.9	84.4
				Unilateral principalis				
B–2	178/180	*	118/180	*	86/90			
B–3	212/230	*	153/250	*	117/140			
B–4	144/150	*	100/150	†	29/30			
Av. percent	95.8	*	64.5	*	92.0			
				Bilateral arcuatus				
B–2	81/90		81/90		29/30	75/90	78/90	29/30
B–3	78/90		84/90		29/30	77/90	77/90	26/30
B–4	80/90		75/90		29/30	84/90	86/90	29/30
Av. percent	88.6		88.9		96.7	87.7	89.3	93.3

*$.0005 > P$ (one-tailed chi-square); †$.005 > P > .0005$.

tion also has a clear but less marked effect ($P < .0005$). Neither arcuatus nor principalis stimulation affected auditory discrimination, a point clearly relevant to results from experiments with surgical lesions (*6*).

A few points bear emphasizing. Arcuatus stimulation is without effect on delayed alternation; this finding reinforces a view derived from experiments with surgical lesions that the focus for the deficit is to be found near sulcus principalis. However, the division is not made as sharply with surgical lesions. Second, the poststimulation control period for delayed alternation yields scores as good as those of the prestimulation period. Hence, it appears that the deficit literally can be turned on and off at the discretion of the experimenter. Finally, it should be stressed again that no overt motor responses to stimulation were evident, nor could one detect any change in the animals' motivation or willingness to be tested. Indeed, with the parameters of stimulation employed, the only reliable behavioral indication that the stimulation was having any effect whatsoever was the inability of the animals to perform delayed alternation tasks.

It appears, therefore, that electrical stimulation can reproduce some of the effects of surgical lesions in the frontal region. It also has certain clear advantages over lesions that commend its wider use for the analysis of cortical function. The deficit appears to be fully reversible, and hence each animal can be used as its own control. Indeed, there would seem to be no obstacle to obtaining "double dissociation" within a single organism. Furthermore, electrical stimulation appears to permit a somewhat finer fractionation than is possible with surgical lesions. Finally, certain types of questions, such as those involved in separating the effects on short-term storage from the effects on long-term storage, cannot be unequivocally answered with surgical lesions because these questions are of the form: Is behavior acquired during a "lesion" state altered in a subsequent "nonlesion" state? (*7*).

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References and Notes

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7. We are pleased to acknowledge the assistance of S. Hopkins and R. Hutchison. This research was supported in part by the Air Research and Development Command, U.S. Air Force.
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Glacial Retreat in the North Bay Area, Ontario

Abstract. Geological and palynological studies in Ontario and Quebec, supported by radiocarbon dates, suggest that the opening of the North Bay outlet and the initiation of the Stanley-Chippewa stages in the Huron and Michigan basins took place 10,000 to 11,000 years ago.

Deglaciation of the vicinity of North Bay, Ontario, opened a discharge channel to the east by the way of Mattawa and Ottawa river valleys, initiating the low-water Stanley and Chippewa stages in the Huron and Michigan basins. This event provides an ideal starting point for a chronology of deglaciation of the region north of the Great Lakes.

Opening of the North Bay outlet is generally judged to have taken place about 6000 years before the present (B.P.) (*1*, Table 22), but new radiocarbon dates suggest that this event may have occurred 4000 to 5000 years earlier. The dates may be divided into two categories: (i) minimum dates for deglaciation of localities in the vicinity of North Bay, which may be used directly as minimum dates for the opening of the North Bay outlet; (ii) minimum dates for events recorded in deposits of the glacial Lake Barlow-Ojibway (Fig. 1) of northern Ontario and Quebec, and James Bay Lowland. To these dates must be added estimates, based on varve counts and extrapolations, of the number of years required for the ice margin to retreat from North Bay to the localities concerned.

The Champlain Sea reached its highest limits at Ottawa some 10,000 to 11,000 years ago (*2*), and the post-Champlain Sea peat in the St. Lawrence Lowlands has been dated at about 9500 years (*3*). Terasmae (*2, 3*) has suggested that the Champlain Sea episode is in part contemporaneous with the Valders substage. Recent studies indicate that the ice had retreated north of Pembroke and Deep River, latitude about 46° north, during the Champlain Sea episode. This reasoning suggests an age of about 10,000 years for the opening of the North Bay outlet.

Lee (*4*) established a minimum age of 9130 ± 350 years (sample W-345) for the archeological site at Sheguiandah on Manitoulin Island. This date on a bog bottom sample (elevation about 720 feet) is a minimum date for post-Lake Algonquin time in the Huron basin. A pollen diagram for the Sheguiandah bog (*4*) correlates well with two other radiocarbon dated pollen sequences from High Hill bog and Little Current bog, Manitoulin Island. An age of 9560 ± 110 years (sample GRO-1926) for the bog bottom sample from the High Hill bog (elevation about 860 feet) is a minimum age for early post-Lake Algonquin time. The Little Current bog (elevation about 1010 feet) is above the highest postulated level of Lake Algonquin (*1*) and provides a pollen sequence beginning shortly after deglaciation of that locality. A sample of the basal organic deposit in this bog was dated at 9450 ± 350 years (sample I GSC-3), but the pollen sequence begins in the underlying silty clay, indicating that deglaciation of the site took place some time earlier.

A sample of basal peat and a pollen profile were collected from a bog in the Fossmill channel, the earliest proposed outlet at North Bay. This sample was dated at 6090 ± 85 years B.P. (sample GRO-1924). However, the palynological evidence shows that mixed hardwood forest (including hickory and walnut) grew near this site at the time, and hence the ice retreat from Fossmill must have occurred much earlier.

Palynological studies about 10 miles north of North Bay, made by Ignatius (*5*) and by Terasmae have shown that lacustrine deposits and peat began to accumulate there about 9500 years ago.

Clay varves number 1163 to 2027 of Antevs' Timiskaming series (*6*), deposited in glacial Lake Barlow-Ojibway, have been remeasured at 12 localities (*7*) scattered through a north-south distance of 50 miles and an east-west distance of 56 miles. Varve diagrams prepared from these measurements show good agreement with one another and with diagrams prepared by Antevs (*6, 7*), especially for "normal" varves. Agreement is less satisfactory for those parts of the diagrams which represent thick proximal varves, or thin ultradistal varves. The restudy confirms Antevs' counting of the varves and his calculations of the rate of retreat of the ice sheet northward across the basin of glacial Lake Barlow-Ojibway.

The rate of ice retreat, from 454 feet (*8*, p. 143) to 926 feet per varve cycle (*7*, p. 160) is compatible with interpretation of the varves as annual deposits, but not with interpretation of them as diurnal deposits. Terasmae has found that pollen is markedly more abundant in the silt layers than in the clay layers of the same varves. Distribution of the pollen is best explained by assuming that the silt is a summer layer, the clay a winter layer, and the