ACTA NEUROBIOL. EXP. 1972, 32: 193-209

Lecture delivered at Symposium "The frontal granular cortex and behavior"
held in Jabłonna near Warszawa
August 1971

CORTICAL STEADY POTENTIAL SHIFTS AND ANODAL POLARIZATION DURING DELAYED RESPONSE PERFORMANCE

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Abstract. Two experiments are described in which monkeys with chronically implanted non-polarizable electrodes in prefrontal, precentral, and occipital cortex were trained on delayed response (DR) tasks for food rewards. In the first experiment, involving recordings of cortical steady potentials (SPs), variations in DR task parameters enabled us to delineate three surface negative SP shifts during the DR trial: (i) before cue presentation, (ii) following the response when reward is eaten, and (iii) at the start of the delay period. The first two shifts are interpreted as indicative of diffuse neuronal processes related to "expectancy" and "reinforcement", respectively, since similar shifts were recorded from other cortical areas. The third shift, recorded only from prefrontal cortex, is interpreted as a correlate of short-term spatial memory formation. Its magnitude was unaffected by variation in duration of either the cue or the delay period, but was significantly correlated with the level of correct performance (*r*'s from 0.74 to 0.90 for four monkeys).

In the second experiment, surface anodal polarization was applied to prefrontal cortex in three monkeys during acquisition sessions of 4-sec or 8-sec DR. In all monkeys higher acquisition rates were obtained under polarization than under comparable non-polarization conditions. The most dramatic facilitation was obtained with 40 μa current applied throughout several successive sessions. These findings support the concept of excitability changes of prefrontal neurons during DR performance.

The aim of our investigations has been the determination of relationships between brains functions and behavior in animals with intact brains. Among the experimental techniques which we have employed are the recording of changes in transcortical steady potentials (SPs) during the monkey's performance of complex tasks, such as delayed response (DR). With this method it has been possible to delineate the involvement of each of several cortical structures during specific periods of the trial and, moreover, to observe the effects of variations in parameters of the behavioral task on the characteristics of the cortical potentials. Thus, we have described (Stamm and Rosen 1969) the occurrence of a surface negative SP shift from the monkey's prefrontal cortex during DR performance. The shift, which was of several seconds duration and reached maximum amplitude of 25–50 μv at the beginning of the delay period, was considered as a reflection of cortical processes involved in the formation of spatial short-term memory. This interpretation is supported by the findings obtained with electrical stimulation experiments (Stamm 1969, Stamm and Rosen 1969). In these studies stimulation across the monkey's principal sulcus was found to substantially disrupt correct DR performance only when it was applied for a few seconds at the start of the delay period; whereas the same kind of electrical stimulation did not affect the monkey's correct performance on a delayed matching-to-sample task (Kovner and Stamm, in press), a problem which requires short-term visual memories. Our interpretation is also consonant with the finding (Fuster and Alexander 1971) that prefrontal neurons discharge at increased rates during DR performance, with maximal rates occurring during the early portion of the delay period.

Slow changes in cortical potentials have also been reported in relation to other behavioral tasks with human and animal subjects. The phenomenon of a "contingent negative variation" (CNV), first described by Walter et al. (1964), has been found in experiments with monkeys to be expressed by a surface negative SP shift with maximum amplitude in prefrontal cortex (Low et al. 1965, Borda 1970, Donchin et al. 1971). Other cortical potential changes have been described as related to motor functions, with maximum amplitudes in the human premotor area (Vaughan et al. 1968) and the monkey's post-central cortex (Donchin et al. 1971). Finally, SP shifts have been reported to occur from widespread cortical areas of cats (Rowland 1968) in relation to various forms of reinforcements, with the highest amplitude shifts from the frontotemporal region during food reinforcement.

In view of these reports, which would indicate the implication of prefrontal cortex in several behavioral processes, we have conducted further experiments on the significance of SP shifts from differing cortical areas. One of the present experiments was designed to evaluate several component SP shifts from prefrontal cortex by systematic variations of parameters of the DR task and by correlating the magnitudes of these shifts with response scores.

With the technique of chronic implantation of non-polarizable electrodes, it is also possible to apply direct currents (d-c) to cortical segments during task performance. A number of physiological experiments have shown that application of surface positive (anodal) currents of 10–50 μa will increase the discharge rate of single cortical cells (Bindman et al. 1962, Creutzfeldt et al. 1962), whereas surface negative (cathodal) polarization has the opposite effects. Anodal polarization has also been found to establish a "dominant focus" of excitation for the elicitation of certain motor responses (Rusinov 1953, Morrell 1961). In behavioral experiments, cathodal polarization has been found to retard acquisition of conditioned avoidance responses in rabbits (Morrell and Naitoh 1962, Proctor et al. 1964), but facilitation of performance with anodal polarization has not been clearly demonstrated. In our investigations (Stamm 1964) we were able to markedly increase monkeys' acquisition rates of a delayed alternation task by stimulation of frontal cortex with low voltage pulses, which contained positive current components of relatively long duration. In view of these findings, we thought it possible to demonstrate the facilitatory effects of direct application of anodal currents to prefrontal cortex during task performance. This was attempted in the second of the present experiments.

TESTING APPARATUS AND ELECTRODES

For both experiments the monkey sat in a portable restraining chair during the daily testing session. The chair restricted the monkey's head movements, and his non-preferred hand was restrained by a short chain which was attached to a cuff on its wrist. The chair was placed securely in front of a vertical panel which contained two circular display windows, 3.5 cm in diameter and 6.5 cm between centers, which were mounted at the monkey's eye level. In front of each window was a transparent plastic disk which, when pressed lightly, activated a microswitch. Transparent plastic food cups were mounted beneath each window.

The trial for the DR task began with presentation of the cue, which consisted of several seconds illumination of either the left or right window with bright white light. Both windows were then darkened during the delay period, after which blue fields were projected on both windows. When the monkey then pressed on either window, the illumination was extinguished for the intertrial interval (ITI) and a correct response (to the window on which the cue had been presented) was rewarded with delivery of a 45 mg dextrose pellet to the food cup beneath the correct window and 2-sec illumination of that cup from the rear. On successive trials the cue was presented in the left or right window according to a random schedule, modified so that in every block of ten trials each side was correct five times. Dim overhead illumination was provided throughout each testing session.

During one-stage surgery non-polarizable Ag-AgCl electrodes, similar in construction to those described by Rowland (1968), were chronically implanted bilaterally in dorsolateral prefrontal, precentral, and occipital cortex. Each electrode consisted of a tapered glass capillary tube, filled with a saline agar gel. Immersed in the gel was a 1 cm coil of chlorided silver wire, with a lead that emerged from the wide sealed end of the tube. At the time of surgery the capillary end was cut to the desired length. The open end of the tube presented a circular recording surface of 1–2 mm in diameter. Pairs of electrodes were implanted in each site, with one electrode placed on the pial surface and the other in the adjacent underlying white matter with 5–10 mm separation between tips. For the prefrontal surface placement, the principal sulcus was gently opened and the surface electrode inserted in the posterior half of the sulcus. The electrode leads were soldered to points on Amphenol connectors which were cemented to the skull. Fascia and skin were sutured around the mound of cement.

STEADY POTENTIAL SHIFTS

Method and Procedure. For the recording experiment the subjects were four adolescent stumptail monkeys (*Macaca speciosa*) of 2–3 kg bodyweight. The monkeys were adapted to sitting in the restraining chair and were then gradually trained to respond on the DR task with the preferred hand. Training at 120 trials per session was given with 2-sec cue presentation, 8-sec ITI, and with gradually increasing delays. After recovery from surgery the monkeys were retrained and generally given additional testing with increasingly longer delays. The parameters of the DR trial were then systematically varied as explained in the Results section.

During the recording session, the Amphenol plug was connected by shielded low-noise cables to d-c preamplifiers (Grass, 5P1) of a Grass Model 5D Polygraph. Output from the power amplifiers led to a 7-channel FM magnetic tape recorder (Honeywell, Model 7600) on which 4 channels of ECG data, as well as the monkey's response and electronic triggering information were stored. Off-line data averaging was obtained with two different computer arrangements. Plots of normalized (truly averaged) data and variance estimates were obtained with a TMC CAT-1000, in conjunction with a Variance Computer and Resolver Integrator. Computations of the *magnitude* of the SP shift in terms of the area circumscribed by the shift and a projection of 6 sec of averaged SP baseline recorded prior to the cue was obtained with a PDP-12A (DEC) computer. This apparatus was also programmed for product-moment correlations between SP shift magnitudes and other variables. The ECG data were computed generally for electrode locations in *cortex* contralateral to the responding hand.

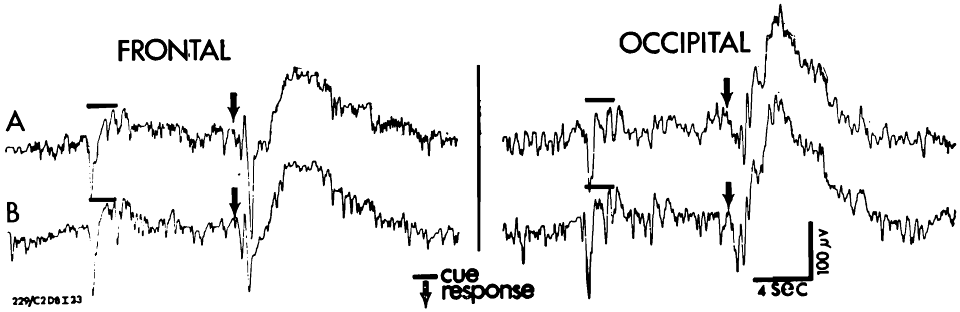

Fig. 1. Averaged SP shifts from prefrontal and occipital cortex during 8-sec DR performance. The monkey had been trained with 8-sec ITI which was then changed to 23 sec. (*A*) Averages for the first 40 trials with 23-sec ITI; (*B*) last 40 trials during same session. Cue presentation, instrumental response, and calibration as indicated. Surface negativity in this and subsequent Figures is upwards.

Results. When monkeys respond at a high level of correct performance under conditions of constant settings for cue duration, delay period, and ITI, the recording from the principalis electrode indicates three definable surface negative SP shifts (Fig. 1*B*). These occur: (i) toward the end of the ITI, prior to the onset of the cue; (ii) at the end of cue presentation and during the early delay period; and (iii) following the monkey's instrumental response. The temporal occurrence of these shifts during the course of the DR trial suggests that they are reflections of: expectancy, mnemonic processes, and reinforcement, respectively.

The characteristics of the expectancy shift can be observed by variations in the duration of the ITI. As indicated by Fig. 1, when the ITI is first lengthened from 8 to 23 sec, the 6 sec pre-cue baseline is constant (*A*), but continued training with a constant ITI (*B*) results in a gradually increasing surface negative shift which reaches maximum amplitude of 25–50 μv at the onset of the cue presentation. The magnitude of an expectancy shift was computed as the area between the SP for the last 4-sec of ITI and a baseline determined by the SP level for the preceding 2-sec. The magnitudes, as shown in Fig. 2, increase linearly as functions of successive blocks of trials. Figures 1 and 2 also show that acquisition

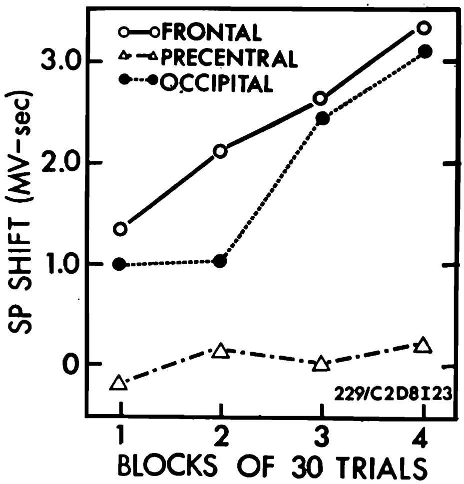

Fig. 2. Magnitudes (MV-sec) of SP shift for 4 sec prior to cue presentation for successive 30-trial blocks during DR training with 23-sec ITI.

of this SP shift is not restricted to prefrontal cortex, but is observed from other electrode locations, including occipital and precentral areas. The sample of data shown is one of innumerable instances in which this phenomenon was observed from the majority of bilateral recording locations in all our monkeys while they were responding above the 90% criterion level.

In order to evaluate the significance of the large 50–100 μv negative SP shift which appears 2–6 sec after the monkey's response, a series of extinction procedures was conducted. As shown in Fig. 3, omission of the

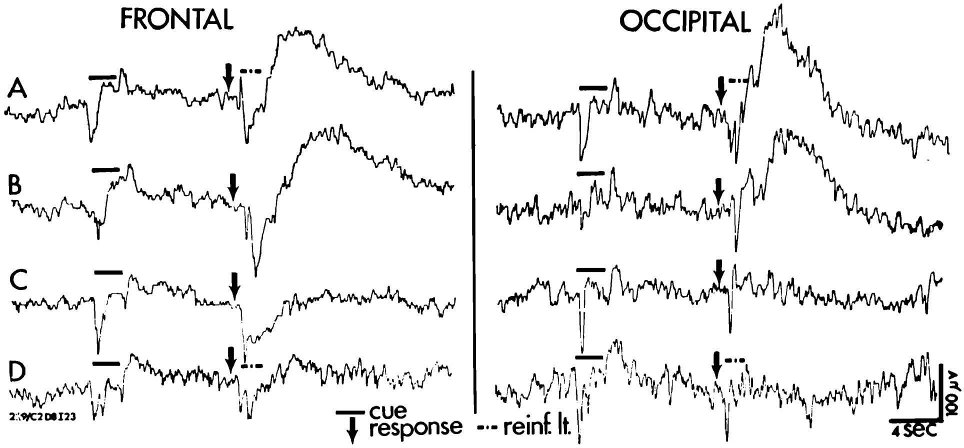

Fig. 3. Averaged SP shifts (40-trial blocks) from prefrontal and occipital cortex during performance on 8-sec DR. (*A*) Standard reinforcing conditions; (*B*) omission of 2-sec illumination of food cup; (*C*) omission of food reward and of cup illumination; (*D*) reinstatement of cup illumination. Cue presentation, response, reinforcement illumination, and calibration as indicated.

2-sec illumination of the food cup (*B*), which serves as a secondary reinforcement, had little effect on this SP shift. However, when the food reward was also omitted (*C*), this shift was greatly reduced at all electrode locations. Re-introduction of the cup illumination (*D*) resulted in a slight increase in the shift magnitude. Throughout these extinction procedures the monkey continued to respond above the 90% criterion, and the response latencies did not change appreciably during the 40 trials of extinction (Fig. 3C). The post-response shifts were also clearly seen in the raw ECG data, unencumbered by possible chewing artifacts. This supports our interpretation that the averaged shifts are not related to motor activity involved in consummatory behavior, but are an electrocortical correlate of the reinforcement process per se.

In our previous communication (Stamm and Rosen 1969), we have described the mnemonic SP shift, which was found to occur only in prefrontal cortex. The preliminary findings have indicated that the magnitude of this shift was unaffected by variations in cue presentation of 2–8 sec, but was related to the level of correct performance. The significance of this shift was further examined by relating its magnitude to variations in brief cue durations, the delay period, and performance scores. When monkeys, which had been initially trained with 2-sec cues, were then tested with varying cue durations of 0.06 sec to 8 sec, we found that performance scores were maintained at 90% correct and that the magnitude of the prefrontal shift remained essentially constant. By contrast, the SP shift from occipital cortex had appreciably lower magnitudes for cue presentations below 0.2 sec, which would indicate that the occipital shift is a reflection of the amount of visual input from the cue. However, the frontal shift reflects some other process which occurs as long as information is available to the monkey for making a correct response.

When monkeys were tested on differing delays of 4–20 sec, there also seemed little variation in the magnitude of the prefrontal SP shift. The recordings in Fig. 4, which were obtained for 40-trial blocks while the monkey was responding above 90% correct, show that for delays of 10-sec and longer, the prefrontal shifts return to baseline level approximately 5-sec after the start of the delay and remain at this level for the remainder of the delay period. The data presented in Fig. 4 show an overall decline in shift magnitude as a function of increasing delay. This result, however, is exceptional, and for the group of monkeys the correlations between delay and shift magnitude are insignificant.

The results presented thus far have all been obtained with highly trained monkeys who responded above the 90% criterion level. However, when monkeys are first trained on DR with delays of 8-sec or longer,

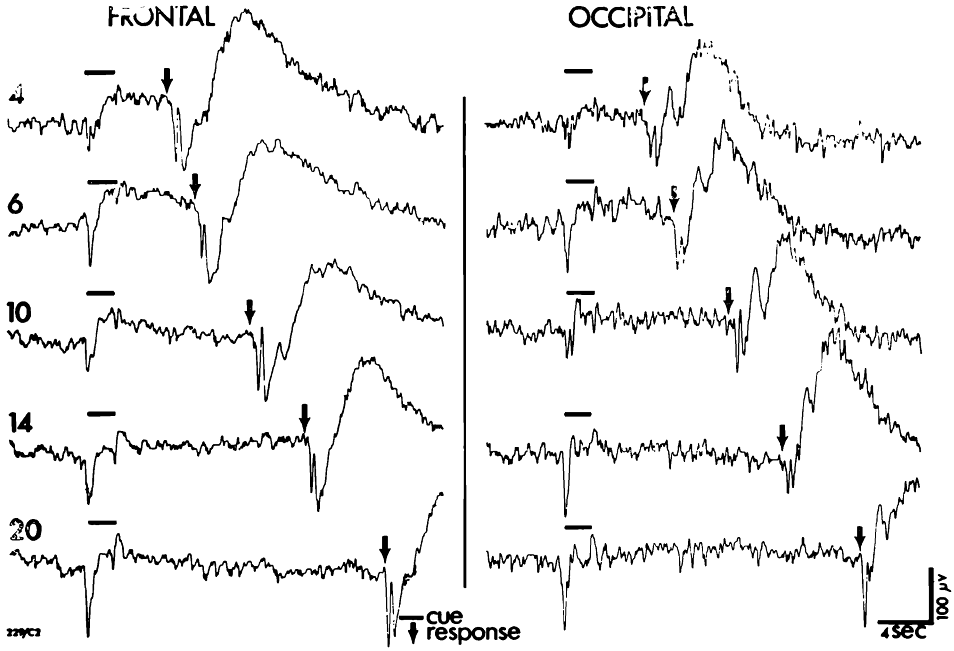

Fig. 4. Averaged SP shifts (40-trial blocks) from prefrontal and occipital cortex during DR performance with delays varying from 4 to 20 sec, as indicated at left of each trace. Cue presentation, response, and calibration as indicated.

performance scores may vary in successive blocks of trials from 50 to 100%. Under these conditions it appears that the magnitude of the mnemonic shift is positively correlated with the level of performance. This observation is illustrated by Fig. 5 which shows areas under negative SP waves (stippled) from several electrode locations for 40-trial blocks with correct performance at 60 and 92%. The product-moment correlation coefficients between the integrated measures of SP shift magnitude, following the onset of the cue, and performance scores on 8-sec DR by the 4 subjects are presented in Table I. High positive and statistically significant coefficients, ranging from 0.86 to 0.90, were found only for prefrontal SP shifts in 3 monkeys. The prefrontal coefficient for Monkey 226 was just below significance level, because of the relatively small amount of data that was available ($n = 5$; for other monkeys, $n = 8$). The magnitudes of SP shifts from the other electrode locations ranged from −0.56 to +0.41 with occipital and 0.14 and 0.74 with precentral placements, and are not statistically significant. The positive coefficients for the "precentral" locations might in part be attributed to the spread of the prefrontal shifts to adjacent cortical areas, since these electrodes were placed on premotor cortex and their distances from the border of

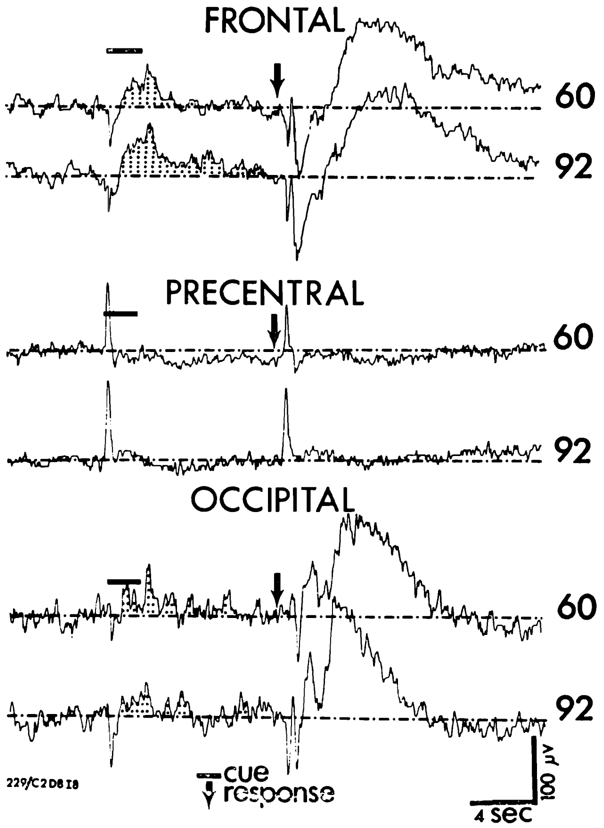

Fig. 5. Averaged SP shifts (40-trial blocks) from prefrontal, precentral, and occipital cortex during 8-sec DR performance. Response levels are 60 and 92% correct, as indicated. Stippled areas indicate magnitudes of SP shifts. Cue presentation, response, and calibrations as indicated.

the prefrontal area (arcuate sulcus) varied considerably in individual monkeys.

Discussion. The present results of three distinct SP shifts would indicate that dorsolateral prefrontal cortex is implicated in several functions during DR performance. We consider the first as an expression of "expectancy", because it becomes most prominent during prolonged training conditions with constant ITI's, when the monkey would anticipate the presentation of the cue. An expectancy wave has also been described with the CNV paradigm (Walter et al. 1964, Donchin et al. 1971), where the temporal contingencies between a preparatory and imperative stimulus elicit a surface-negative SP shift during the interstimulus interval. These potentials have been reported to be widespread over the cortical surface, with the highest voltages from the frontal

TABLE I

Correlation coefficients between SP shift magnitudes (mv-sec) and correct performance on 8-sec delayed response[a]

Monkey	Cortical area		
	Frontal	Precentral	Occipital
221	0.90*	0.16	0.41
223	0.89*	0.20	—0.42
226	0.74	0.74	—0.56
229	0.86*	0.14	0.54

[a] Average SP shift magnitudes (40 trials) were computed for 6 sec periods, following onset of 2-sec cue.

* Significant at 0.01 level.

areas. The SP shift following the reinforcement on DR seems to correspond to similar potentials which have been recorded over widespread cortical areas in cats in relation to reinforcement contingencies (Rowland and Goldstone 1963). Thus, these two prefrontal shifts seem to reflect general processes of cortical excitation which involve a wide range of neuronal structures.

The "mnemonic" SP shift appears more specific to prefrontal cortical areas, since recordings in the present and previous studies did not reveal this shift from occipital, parietal, or premotor electrode locations. The physiological evidence that surface negative SP shifts are concomitant with increased discharge rates from the underlying neuronal elements, has received more direct support by unit recordings during the performance of behavioral tasks. The findings that prefrontal neurons discharge during the delay periods of both the DR (Fuster and Alexander 1971) and delayed alternation (Kubota and Niki 1971) tasks adds strong support to the concept of specific prefrontal functions in the short-term mnemonic process. The present results, together with those from stimulation experiments (Stamm and Rosen 1969), further specify the locus and time of implications of the cortical structures, namely: posterior two-thirds of principal sulcus and the early portion of the delay. Our findings that the prefrontal SP shift returns to baseline level at approximately 5 sec after delay onset and remains there during the subsequent delay period, would indicate that prefrontal cortex is of particular importance in the formation of the short-term memory, rather than in mnemonic storage per se. However, the neuronal systems which are implicated in short-term memory formation have not been well defined. In view of Konorski's (1967) interpretation of prefrontal functions in terms of "kinesthetic analyzers", this afferent system may be of special importance. Alternatively, prefrontal cortex has been considered as an integral part in a neuronal monitoring system for motor functions (Cohen 1970). Further investigations should be concerned with the implications of the relevant subcortical structures in short-term mnemonic functions. The present technique of recording of SP shifts during task performance may provide an appropriate approach toward finding answers to this important question.

ANODAL POLARIZATION

Method and Procedure. Three experimentally naive stumptail monkeys of 2–3 kg bodyweight were adapted to the DR testing procedure. Nonpolarizable Ag-AgCl electrodes were implanted on the surface and in underlying white matter of prefrontal, precentral, and occipital cortex. The prefrontal surface electrode was placed in the mid-portion of the depth of principal sulcus. Following electrode implantations the monkeys were trained (120 trials per session) on DR, with 4-sec delay, 2-sec cue presentation, and 10-sec ITI. Direct currents, controlled by a modified Grass S4 stimulator and isolation unit, were applied unilaterally across principalis cortex, contralateral to the responding hand. Surface anodal polarization was applied during alternate 30-trial blocks, which were counterbalanced over successive testing sessions. In order to reduce possible damaging effects of prolonged d-c stimulation, the currents were applied for 8-sec of each trial, starting 1-sec before cue onset and terminating after the first second of the ITI. The current levels at the start of testing were 10 to 15 μa and were subsequently increased, at the discretion of the experimenter, in steps of 0.5 or 1.0 μa, to maximum of 24 μa.

One of these monkeys (Monkey 260), which met the 90% criterion on this task, was subsequently trained on DR with 8-sec delay (2-sec cue, 14-sec ITI). Anodal polarization was applied continuously to the prefrontal cortical surface throughout some of the testing sessions of 100 trials each.

Results. The 90% criterion performance on the DR-4 task was attained relatively rapidly by two subjects, whereas the third subject (Monkey 248) showed only gradual performance improvements. His average response scores increased slowly during the first 30 sessions and continued to fluctuate around this level for the subsequent 30 sessions, when training was terminated. Correct performance during the first 30 sessions was slightly, but significantly higher under the anodal than the non-polarization condition, with means of 59.3 and 53.6%, respectively (for the difference between means $t = 4.80$; $p < 0.005$). The facilitatory effects of anodal polarization appear most clearly in a within-session analysis of performance scores, as shown in Fig. 6. This Figure presents separate curves for sessions which started with 30 trials of polarization and for those which began without polarization (each point on the graphs represents a mean for 150 trials). Comparisons of the results under these two conditions indicate significantly better performance for sessions which start with polarization ($t = 2.97$; $p < 0.05$), although under both conditions 60 non-stimulation trials were given. The effects of polarization are demonstrated, moreover, by consideration of performance changes during successive 10-trial blocks. During polarization the response scores increased consistently at a mean rate of 3.27% per 10-trials, whereas for nonstimulation testing there was a mean decrease of 2.27% per 10 trials. The difference between these means is statistically significant ($t = 2.94$; $p < 0.01$). Taken together, these results indicate significant facilitatory effects of anodal polarization which generally outlast the duration of stimulus applications.

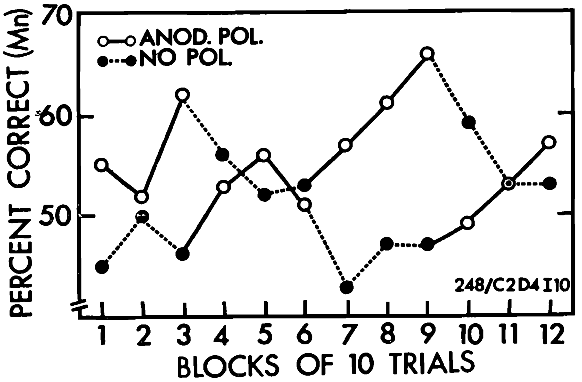

Fig. 6. Effects of anodal polarization of prefrontal cortex on performance of 4-sec DR (Monkey 248). Each curve presents mean scores for successive 10-trial blocks, obtained during 15 sessions. The curves are for sessions (120 trials) which: (a) start with 30 trials of anodal polarization; and (b) start without polarization.

The other two monkeys responded near chance level during the first 5 and 15 sessions, respectively, after which their performance improved rapidly. The 90% criterion was obtained during one session by Monkey 226 and in two sessions by Monkey 260. The effects of anodal polarization (15 to 20 μa) were most impressive for Monkey 226 whose performance scores rose rapidly while polarization was applied and remained at that level during subsequent testing. During the post-criterion sessions, surface cathodal polarization at 20 or 24 μa was applied for 30 trials, which resulted in marked decrements of correct response scores by at least 30%.

The learning curve for Monkey 260 on 8-sec DR is shown in Fig. 7. This Figure indicates that his performance remained near 60% correct for the first 700 trials without stimulation, whereas anodal polarization during the following six sessions resulted in a marked increase in correct performance. The current magnitude was 25 μa during the first session and was subsequently increased in steps to 40 μa during the fifth session, at which level it was maintained during all subsequent polarization sessions. Stimulation also commenced 2 min before the start of testing. The results presented in Fig. 7 show markedly higher performance scores for each session block of polarization than for the preceding scores for the successive non-stimulation sessions. The mean changes in correct performance per 100 trials were +3.0% with the polarization and −1.4% with the non-polarization condition. The Mann-Whitney *U* test indicates that the differences in overall performance changes between the two conditions were statistically significant ($U = 0$; N's = 3, 4; $p = 0.028$). These findings demonstrate the effectiveness of anodal polarization when it is applied continuously throughout a series of testing sessions.

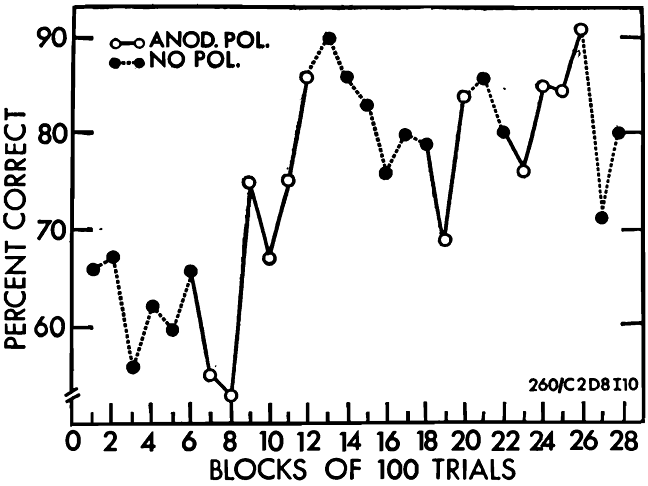

Fig. 7. Learning curve for Monkey 260 on 8-sec DR. Anodal polarization was applied to prefrontal cortex throughout some of the sessions. Currents were initially 25 μa and were increased in steps to 40 μa for the fifth and subsequent polarization sessions.

Discussion. The present findings provide limited support for the beneficial effects of cortical anodal polorization on task acquisition. A number of methodological and procedural problems may account for the inconclusiveness of our results. First, it is difficult to establish the most effective stimulus parameters for each monkey, because of variations in electrode impedance, interelectrode distances, and adeqaucy of contact between electrode tips and the cortical surface. Secondly, in the selection of d-c levels, we may have used insufficient currents in order to minimize the possible lesioning effects, since the highest current density was approximately 20 μa per mm^2. Finally, the facilitatory effects of polarization can only be clearly demonstrated during gradual task acquisition and may be masked by rapid learning rates. We selected a task and training procedure which would result in slow learning rates, namely training the monkeys on 4-sec DR, without prior training on shorter delays. In our other experiments, monkeys who were trained under conditions of gradually increasing delays generally attained criterion on 4-sec DR substantially more rapidly than did the present subjects. The marked individual differences in learning rates, moreover, make it difficult to apply rigorous statistical evaluations to all data.

In spite of the present technical and methodological problems, we were able to demonstrate improved task performance with anodal polarization for every subject. The most effective anodal polarization conditions consisted in the continuous application of relatively high currents throughout successive testing sessions. Under these conditions the monkeys' performance levels were not only higher than for comparable non-stimulation sessions, but the subsequent performance remained better than it had been before application of polarization. Thus, anodal polarization appears indeed to result in long-lasting effects on performance. Furthermore, we have indications that the effectiveness of polarization may be apparent on the day following testing, when performance scores tended to increase further. A similar result has been reported by Morrell and Naitoh (1962) who obtained higher scores of conditioned avoidance responses on days following anodal polarization than during polarization testing. It should also be noted that the effectiveness of polarization was most marked for the slowest learner on DR-4 and again when another monkey was trained on the more difficult DR-8 task. This result appears consonant with our previous findings of low-level stimulation during delayed alternation training (Stamm 1964) where the most dramatic stimulation effects were obtained with the slowest learners.

The present experiment was preliminary, in the sense that we attempted to explore the optimal experimental conditions for obtaining facilitatory effects on task acquisition with anodal polarization. This goal has been partially met and it should now be possible to conduct more definitive experiments on the neuronal processes with are activited with this technique.

CONCLUDING COMMENTS

We believe that the present experiments have demonstrated the feasibility of investigating cortical functions in behaving animals with intact brains. With the technique of recording cortical SP shifts, it has been possible to specify the involvement of prefrontal cortex in several behavioral functions, namely; expectancy, reinforcement, and memory. The first two of these functions appear to be mediated by diffuse neuronal processes which involve a wide range of cortical areas. The third function appears to be more specific to prefrontal cortex, especially the middle and posterior segments of the principal sulcus. The mnemonic function is expressed by the SP shift which appears during the late cue and early delay periods. The magnitude of this SP shift is the only electrocortical measure which we have obtained that correlates significantly with the level of correct performance. Furthermore, the findings that the shift magnitude is unaffected by either the duration of cue presentation, provided this is sufficient to supply the monkey with the necessary sensory information, or by the length of the delay period, permits further specification of the functions of prefrontal cortex. Consideration of the component aspects of short-term memory suggests that prefrontal cortex is specifically implicated in the formation of the mnemonic process, rather than in memory storage or retrieval. Since the results from many ablation studies, as well as from stimulation experiments (Stamm and Rosen 1969, Cohen 1970, Kovner and Stamm, in press), substantiate the view that prefrontal cortex is a neuronal substrate for spatial memory, we conclude that principalis cortex is crucially implicated in the formation of spatial short-term memories.

The findings of higher acquisition rates on the DR task with anodal prefrontal polarization would indicate that performance can be affected with the experimental application of d-c fields to cortical segments. Although our results did not indicate dramatic behavioral changes in ali monkeys, they are to our knowlegde the first reports of successful application of this technique to improved task performance by the intact animal. Further experimentation with anodal polarization may lead to the definition of relatively simple methods and procedures of current applications which will result in marked and consistent performance changes on a variety of behavioral tasks. We are hopeful that investigations with the two techniques that we have described will lead to a clearer understanding not only of the functions of prefrontal cortex, but also of the specific functions of other cortical and subcortical structures.

This research was supported by National Science Foundation Grant GB 13859X. We express our appreciation to Richard Reeder and Harvey Licht for their technical assistance.

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Received 8 October 1971

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