tion of the motor axon are remarkably similar in the cockroach and the vertebrates. In both the vertebrates (13) and the cockroach, the shift of the nucleus to an eccentric position is associated with a high degree of protein production needed to regenerate an injured axon. The primary difference between cockroach neurons and those of vertebrates seems to reside in the organization of cytoplasmic RNA. In the vertebrate neuron the cytoplasmic RNA is grouped in large granular masses termed Nissl bodies (13). These consist of stacks of granular endoplasmic reticulum (14). It is apparently the RNA of the attached ribosomes in these structures that stains with the classical Nissl procedures. The normal vertebrate neuron is constantly producing protein at a high rate (15). When an extraordinary demand for protein synthesis, such as the need for regeneration, is placed on the vertebrate neuron the Nissl bodies break down (chromatolysis) causing the cytoplasmic RNA to become finely dispersed. In this condition the cell has shifted to a "superactive" level of protein production (15). The cockroach neuron normally has cytoplasmic RNA in a finely dispersed state; there are no prominent Nissl bodies (5, 16). When a high demand for protein synthesis is placed upon a cockroach cell, it forms a perinuclear aggregate of RNA which resembles in part the vertebrate Nissl body. These aggregates in the cockroach neuron then break down to a finely dispersed state once again, and at this time the cell shows obvious evidence of protein production by regenerating a new axon. This breakdown can be considered similar to vertebrate chromatolysis. This implies that the secondary dispersed state of RNA in the cockroach neuron, stemming from the breakdown of the perinuclear ring, differs in some critical manner from the normal, dispersed state of RNA in these cells. Perhaps the ribosomes require structural alignment on the cisternae of the endoplasmic reticulum in order to combine with messenger RNA needed to produce new protein for axon regeneration. In insects such as the locusts which do not show axonal regeneration (11), our studies indicate that injured neurons do not form a perinuclear ring of RNA.

In the cockroach, changes within specified cells can be related to alterations in the connections between these cells. The similarity with respect to neural regeneration between the cockroach and the vertebrates indicates that information from the insect preparation may lead to some general conclusions about the factors which determine connections between cells in excitable systems.

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Evoked Cortical Potentials: Relation to Visual Field and Handedness

Abstract. The amplitude of evoked responses of occipital cortex in man depends on the visual field in which the stimulus appears. Greater responses occurred repeatedly for two of three subjects, both left-handed, when the stimulus appeared in the left field than in the right. Subsequent tests of 13 right- and 13 left-handed males indicated that the magnitude of the response of the right lobe, relative to that of the left, was greater for left-handed individuals. We conclude that the difference in amplitude between the two lobes is related to handedness.

We recently demonstrated that reaction time and evoked potential (EP) latency and amplitude vary concomitantly with variations in site of retinal stimulation. Reaction time parallels changes in EP latency and varies inversely with EP amplitude (1). These results provide evidence for the existence of a relationship between reaction time and EP's, in agreement with other studies (2).

In that study our observations were limited to the temporal retina of the right eye. Since stimulation of the nasal retina yields shorter reaction times (3), we subsequently attempted to demonstrate the generality of the relation between reaction time and EP's by showing that the cortical responses to nasal retina stimulation are of larger amplitude and shorter latency than to temporal retina stimulation. However, EP's obtained from the right occipital lobe due to nasal stimulation of the right eye were consistently smaller than those obtained from temporal stimulation of that eve (4).

Since the nasal retina of the right eye projects to the left lobe and the tem-

poral retina to the right lobe, it is possible that the nasal-temporal effects being sought were masked by hemispheric differences. That such differences may exist also is suggested by photic driving studies indicating that one hemisphere tends to be more susceptible to driving than the other (5). One purpose of the present study, therefore, was to determine whether differences actually do occur in EP's obtained from the two lobes when flashes are presented in the right and left visual fields. A second purpose was to determine whether such differences, if they do occur, are related to handedness.

To investigate the first question, three of the authors served as subjects in two experimental sessions each. In each session, 10 retinal sites located 10° apart along the horizontal meridian were stimulated, red light being used in one of the sessions, blue in the other. Both eyes were stimulated simultaneously. There were five trials in a given session. Each trial was separated by a 15-minute rest interval during which the subject was required to leave the experimental room. In a given trial a total of 100 or 200 flashes were presented at a rate of one per second to two retinal sites symmetrically located in opposite hemispheres. The order in which the two sites were stimulated was balanced over the trial by alternately presenting flashes to each site in blocks of 25, using an ABABBABA design. For control purposes, responses in the absence of light flashes were obtained, as were responses to foveal stimulation.

Stimulus flashes were generated with a Grass PS-2 photostimulator. The flashes were 10 μ sec in duration and subtended a visual angle of 1°. They were presented onto a white screen with a background luminance of 2 mlam. Their intensity was approximately 1 log unit above the subject's foveal sensory threshold. Color was controlled with Kodak Wratten filters; No. 26 was used for red, No. 48A for blue. While recording, the subject's head was positioned on a chin rest and his eyes were trained on the point of fixation.

The "active" electrodes were attached to the scalp 2.5 cm above the inion and 2.5 cm to the right and left of the midline. Reference electrodes were attached to the right and left ear lobes respectively. Evoked responses recorded simultaneously from both lobes were amplified with an Offner Type R dynagraph and summed with a Mnemotron computer of average transients. The amplified responses of the two lobes were counterbalanced across the two amplifier channels to control for any differences in gain level. Permanent records were obtained with a Moseley X-Y plotter. The responses shown in Figs. 1 and 2 were traced directly from the X-Y plots (1, 6).

Typical EP's evoked by small, 1° light flashes are relatively simple in appearance (1). They consist of trains of sinusoidal, multiphasic waves having a frequency of 8 to 12 cycle/sec which last from 300 to 500 msec. The earliest deflection, observable under certain conditions, has an onset time of 70 to 100 msec, depending on the subject and on the stimulus parameters. This positive (downward) deflection, D1, is followed by a negative (upward) deflection, D2, which has an onset time of 120 to 150 msec. Subsequent deflections (D3, D4, and so on) occur approximately every 50 msec. The largest components in the train are usually D3, 4, and 5. They are readily discernible in most of the tracings of Fig. 1. Their onset times are approximately 160, 210, and

260 msec, respectively. In Fig. 1 the EP tracings have been categorized for each subject by visual field, lobe, distance of stimulation site from the fovea, and color.

In considering the right-left visual field effects, we will refer to the lobe which receives impulses by way of the classical visual pathways as primary and the other lobe as secondary. Thus the right lobe is primary when flashes appear in the left visual field; the left is primary when they appear in the right field. For the two left-handed subjects greater EP's were obtained from the right lobe, when primary, than from the left lobe when primary for every retinal site stimulated with either red or blue light. These differences are immediately evident when



Fig. 1 (above and right). Evoked potentials of right and left occipital lobes to red and blue flashes presented in right and left visual fields from three different subjects.

one compares the tracings in column three to those in column two for subjects RGE and DO in Fig 1. For the right-handed subject, CTW, greater responses were obtained from the right lobe than from the left when the retina was stimulated at the 10° position, but no clear-cut differences were obtained between the two lobes for the other retinal areas stimulated.

For a given visual field condition, the response of the secondary lobe tended to parallel that of the primary lobe. The relatively large primary right lobe responses of the two left-handed subjects (column three) were accompanied by large secondary left lobe responses (column four), whereas the relatively small primary left lobe responses (column two) were accompanied by small secondary right lobe responses (column one). These results suggest that a high degree of interhemispheric interaction exists, although it is not clear whether the highly similar responses were triggered in the secondary lobe by diffuse ascending impulses of subcortical origin or by impulses arriving by way of the cerebral commissures from the primary lobe. Probably both mechanisms are involved.

To answer the question as to whether the differential response magnitudes observed for the two left-handed subjects and one right-handed subject might be related to handedness, we obtained data from a larger sample of right- and lefthanded individuals in a subsequent experiment. A total of 26 subjects, equally divided with respect to handedness, participated in four recording trials each within a single experimental session. No elaborate tests were made for handedness. Each subject was designated as right- or left-handed prior to data collection on the basis of his own impression. Two retinal sites located 20° to the right and left of the fovea were stimulated alternately with blocks of 50 red flashes during each trial, a total of 200 being presented to each site. The flashes were presented at a rate of one per second, using an ABABBABA counterbalancing procedure. All other stimulating and recording apparatus and procedures were identical to those described above, except for the fact that a Grass Model 5 polygraph equipped with 5P5 preamplifiers was used to amplify the EP's.

Responses obtained from the right and left lobes of the two groups of subjects, when each was primary, are presented in Fig. 2. The EP's obtained during each of the four recording periods from a given lobe have been superimposed to show the degree of consistency with which the responses could be replicated for each subject. To test for significant differences in the degree of responsiveness of the two lobes for the two groups, we determined the average amplitude of D4 for the right and left lobe responses of each subject, based on the four replications. When D4 could not be identified with certainty for a given subject, we measured the deflection corresponding most closely to



23 JUNE 1967

it in time. The deflections actually measured are identified in the tracings by the short horizontal lines drawn below and above each, and which identify the approximate time of onset and termination of each deflection. The average amplitude of the right-lobe response of each subject was then expressed relative to the amplitude of the left-lobe response, that is, as a ratio. For the lefthanded subjects, the magnitudes of the right-lobe responses-relative to those of the left-were: 4.24, 2.06, 1.94, 1.92, 1.91, 1.88, 1.50, 1.38, 1.31, 1.10, 1.09, 0.85, and 0.74. For the right-handed subjects the relative sizes of the rightlobe responses were: 1.88, 1.43, 1.31, 1.29, 1.20, 1.17, 1.00, 0.92, 0.91, 0.80, 0.74, 0.55, and 0.34. A Mann-Whitney U test revealed that the ratio scores of the left-handed subjects were significantly greater at the 0.01 level than those of the right-handed subjects. Based on this result, we conclude that greater responses are evoked from the right lobe, relative to the left, in lefthanded than in right-handed individuals.

Two additional tests, chi square and t, performed on the data for the lefthanded subjects indicated that the right lobe of these subjects is more responsive to incoming impulses than is the left lobe. The chi-square analysis (with 1 df) revealed that the number of cases (11 of 13) in which the right-lobe response was greater than that of the left lobe was significant at the 0.02 level of confidence; the t-test, based on 12 df, revealed that the average magnitude of the right-lobe responses was significantly greater than that of the left-lobe at the 0.01 level. Similar tests conducted on the scores of the right-handed subjects revealed no significant differences. Thus, while the responses of left-handed individuals were found to be greater for the right lobe than for the left, no consistent differences were demonstrable for right-handed individuals.

The results obtained in the statistical analyses are evident in the tracings of Fig. 2. To facilitate comparison, the responses for the left-handed subjects (left two columns) have been arranged in decreasing order with the greatest right-lobe D4 deflection—relative to that of the left—in the top row; the responses for the right-handed subjects are arranged with the greatest left-lobe D4 deflection—relative to that of the right—at the top (right two columns). Except in two instances (last two rows), the right-lobe responses of the lefthanded subjects are visibly greater than those of the left lobe. Only for one lefthanded subject, who claimed to be strongly ambidextrous, are the responses of the left lobe visibly greater than those of the right lobe. It is apparent in the tracings of the right-handed subjects that no consistent tendency exists for the responses of one lobe to be markedly greater than those of the other lobe.

For four subjects (top four rows) the left-lobe responses are clearly greater than those of the right lobe. In all other cases, except one (bottom row), responses of approximately equal magnitude were obtained from both lobes. For the one subject the right-lobe response was markedly greater than that of the left lobe.

These experiments indicate that greater responses to flash stimuli tend to be elicited from the right occipital lobe of left-handed subjects than from the left lobe, whereas no consistent differences were demonstrated for right-handed subjects. The experiments further indicate that the right-lobe responses, relative to those of the left, are greater for left-handed than for right-handed individuals. We conclude, therefore, that the differential amplitude of the responses of the two lobes is related to handedness. Since, however, there is considerable overlap between the two groups in the relative magnitude of the



Fig. 2. Evoked cortical responses of right- and left-handed subjects to flashes presented in right and left visual fields.

1646

RIGHT-HANDED SUBJECTS 5. IFFT LARS

TIME (MSEC. X 100)

2 3 4

responses obtained from the two lobes, handedness cannot be predicted with certainty for a single individual on the basis of observed lobe differences. More data are needed to establish the probability of being correct when predicting handedness from such lobular differences.

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Sleep: The Effect of **Electroconvulsive Shock in Cats Deprived of REM Sleep**

Abstract. Three cats were deprived of rapid-eye-movement (REM) sleep for 10 days, and three were deprived for 12 days. All cats received an electrically induced convulsion on each of the last 3 days of deprivation, as well as on the 1st recovery day just prior to sleep onset. As controls, four cats were deprived of REM sleep for 12 days and one was deprived for 10 days; the controls received no convulsions. Compensatory increases in REM sleep during recovery days were present in the convulsed animals, but were substantially lower than the recovery increases of control animals. During recovery REM sleep, convulsed cats did not display the exaggerated bursts of eye movements and body twitches seen in the nonconvulsed controls.

A major consequence of the selective deprivation of rapid-eye-movement (REM) sleep, whether accomplished by arousals at the onset of each REM period (1) or by drugs (2), is an abrupt rise in the amount of this phase during recovery.

SCIENCE, VOL. 156