With such light cycles one can detect recurring phases of responsiveness to light about 24 hours apart (*13*). Two golden-crowned and six white-crowned sparrows died during the experiment.

I found previously (*10*) that 6 weeks of short days (LD 8 : 16) were enough to terminate the refractory period in both species. Therefore, after 6 weeks of exposure to the experimental light cycles, all birds were transferred to an LD 16 : 8 cycle to determine in which groups the refractory period had been broken. At the time of transfer, measurements of testicular size indicated that all birds were still in a state of complete testicular regression.

The effectiveness of the various light cycles in breaking the refractory period is shown in Fig. 1. Maximum testicular increase after 4 or 6 weeks of the LD 16 : 8 cycle is plotted for the various preceding light cycles. Testicular enlargement occurred in all golden-crowned sparrows (Fig. 1a) previously subjected to cycles of 24 hours (LD 8 : 16), 48 hours (LD 8 : 40), and 72 hours (LD 8 : 64). No enlargement occurred in golden-crowned sparrows subjected to cycles of 16 hours (LD 8 : 8), 36 hours (LD 8 : 28), or 60 hours (LD 8 : 52). The 24-, 48-, and 72-hour cycles all had the effect of short days; these cycles terminated the refractory period and resulted in photosensitivity to long days (LD 16 : 8). On the other hand, 16-, 36-, and 60-hour cycles maintained the refractory state. These cycles acted as long days, even though each cycle contained only one 8-hour period of light.

These results are consistent with the hypothesis that an endogenous rhythm with a periodicity of about 24 hours is used in measuring the length of the photoperiod during the refractory state of the golden-crowned sparrow. Apparently, photoperiodic refractoriness is maintained when light is coincident with a certain phase of the circadian rhythm. When light is noncoincident with this phase, the refractory period is broken, and testicular growth can again be initiated by long days.

A circadian rhythm is also involved in the termination of the refractory period in the white-crowned sparrow (Fig. 1b). These results differ only in that the 16-hour cycle (LD 8 : 8) did terminate the refractory period in white-crowned sparrows, but not in golden-crowned sparrows. The response of white-crowned sparrows to the 16-hour cycle is not understood, but this result does not negate the hypothesis that a circadian rhythm is involved in this photoperiodic response. The results from the other light cycles indicate that an endogenous rhythm with a periodicity of about 24 hours is involved in breaking the refractory period of the white-crowned sparrow. The peculiar results for the 16-hour cycle reemphasize the importance of understanding the dual action of light, both as an entraining agent of the endogenous rhythm and as the inducer of the photoperiodic response. The phases of the circadian rhythm which are coincident with the light in the 16-hour cycle will be different from the phases which are coincident with the light in the 36- and 60-hour cycles. Without an understanding of how an LD 8 : 8 cycle entrains the circadian rhythm involved in this photoperiodic response, one cannot determine why such a cycle ended the refractory period in white-crowned sparrows.

Farner (*4*) found that an endogenous rhythm may be involved in the initiation of testicular growth in *Z. leucophrys gambelii*. In an experiment similar to that done by Hamner on the house finch *Carpodacus mexicanus* (*3*), I found that circadian rhythmicity is involved in the initiation of testicular growth in both *Z. leucophrys pugetensis* and *Z. atricapilla* (*14*).

In both the white-crowned and golden-crowned sparrows the initiation of testicular growth is normally dependent on long days, whereas the termination of the refractory period depends upon short days. While there exist other possible models for how the circadian clock may be involved in these two photoperiodic responses (*15*), I believe the "external coincidence model" is at present the most likely possibility. Under this hypothesis, the initiation of testicular growth depends on the coincidence of light and a particular phase of the circadian rhythm. The termination of the refractory period depends on the lack of coincidence of light and a particular phase of a circadian rhythm.

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Summated Cortical Evoked Response Testing in the Deafferented Primate

Abstract. *Dorsal rhizotomy from C_2 or C_3 to T_4 in the primate results in failure to elicit summated cortical responses from systematic stimulation of the appropriate peripheral nerves. Under these conditions there is thus no evidence of sensory input into the cerebral cortex. A nonclassical mechanism must therefore be operational to explain the extensive purposive movements observed in the deafferented animals.*

Deafferentation of a single forelimb in rhesus monkeys by means of dorsal root section has long been known to result in an effectively useless extremity when the animal is unrestricted (*1*). However, a monkey can be induced to use the affected limb purposively by increasing the motivation to do so, as in conditioned response situations where reinforcement is made contingent on use of the deafferented member, or by subjecting the contralateral limb to prolonged restraint (*2*).

The ability to make purposive movements following the abolition of somatic sensation and autogenetic spinal reflexes is even clearer in the case of deafferentation of both forelimbs. Use of the limbs is then not restricted only to certain specialized situations (*3*), but occurs spontaneously in the free situation as well (*4, 5*). Under the latter conditions animals with bilateral dorsal rhizotomies are able to execute complex movements of the forelimbs for climbing, running, and even prehension by the fingers, and they retain this level of motor ability after deafferentation of the entire spinal cord, when all spinal reflex arcs have been interrupted (*6*).

Dorsal rhizotomy has generally been believed to abolish all sensory input from relevant portions of the body. It is important for the interpretation of these experiments that this contention be clearly verified. Moreover, in an animal the size of a rhesus monkey the dorsal root filaments are very fine and offer relatively poor optical contrast to the underlying spinal cord. They are therefore frequently difficult to visualize, leading to some uncertainty as to the inclusiveness of the procedure. In earlier work the completeness and precision of dorsal rhizotomy were determined by (i) use of magnification (×10 to ×40) during operation for direct visualization of dorsal rootlets, (ii) observation of clinical behavior in the immediate postoperative period, any but the most rudimentary use of the affected extremities indicating incomplete deafferentation, (iii) gross postmortem examination, and (iv) anatomical studies with longitudinal and horizontal sections of the spinal cord (*4*). The study reported here utilizes the technique of summated cortical evoked responses to peripheral nerve stimulation to determine whether input data are transmitted to the cerebral cortex of rhizotomied animals. This technique is complementary to the above validating procedures and constitutes a new critical determinant of the functional effectiveness of the experimental surgery (*7*).

Six animals were used in this investigation, five monkeys (*Macaca mulatta*) and one baboon (*Papio* sp.). Two monkeys and the baboon had been subjected to bilateral cervical and thoracic dorsal rhizotomy (C_2 or C_3 to T_4) on the first day of life, within hours after birth (*8*). Another monkey had received a unilateral rhizotomy (C_2 to T_4) during adolescence. Surgery was carried out as in earlier work (*4*). At testing the three operated infants were 7 to 8 months old; the adolescent animal had been subjected to surgery 3 months earlier. Two intact animals were used as controls, one adolescent and one aged 8 months.

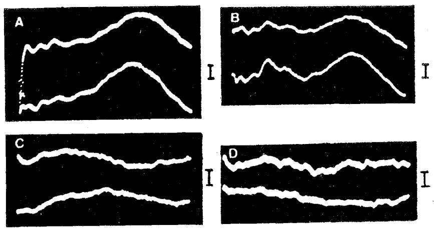

Fig. 1. Summated cortical response (SCR) to percutaneous peripheral nerve stimulation in intact and rhizotomied animals. (A and B) Normal control, 8-month-old rhesus. (A) SCR to left median nerve stimulation, 69 stimuli. (B) SCR to right median nerve stimulation, 97 stimuli. (C and D) Bilateral rhizotomy, 8-month-old baboon operated on first day of life. (C) SCR to left median nerve stimulation, 157 stimuli. (D) SCR to right median nerve stimulation, 158 stimuli. In each pair in all figures the top line is from the right cerebral hemisphere, and the lower line is from the left. All sweeps are 250 msec. Calibration is 200 μv, root mean square.

The recording electrodes were 16-mm nickel-chrome Michel clips to which thin-stranded wires were soldered. They were applied bilaterally in a coronal array corresponding to the postcentral gyrus, with an electrode placed approximately 5 mm anterior and 5 mm superior to the external acoustic meatus, and another electrode placed approximately 4 mm from the midsagittal plane. Prior to electrode placement the scalp hair was removed with an electric shaver. The animals were restrained in a primate chair without drug immobilization; the head was held manually during the actual recordings.

Amplification was achieved by using Brush electroencephalograph high-gain a-c amplifiers, operating with a bandpass of 1 to 600 hertz. The amplifier output was directly applied to a CAT 1000, and was also monitored intermittently by a two-gun oscilloscope. The summated outputs were photographed directly from the CAT oscilloscope.

A Nuclear-Chicago constant-current stimulator was employed to deliver monopolar, square-wave pulses of 0.1 msec in duration, ranging in current between 2.5 and 9.5 ma. Stimuli were applied percutaneously at different times over the median, ulnar, and radial nerves at a rate of one per second through electrodes fixed by tape. The index of stimulation was appropriate rhythmic movements of the thumb, fingers, and wrist, respectively; evoked responses were recorded at both threshold and suprathreshold values.

In the intact animals, peripheral nerve stimulation generated well-defined, summated cortical evoked response patterns from right and left median, radial, and ulnar nerves. Samples of the response to right and left median nerve stimulation are shown in Fig. 1, A and B. It may be observed that there is an initial series of oscillatory potentials during the first 50 msec, which is followed by a higher-amplitude, longer-duration wave, peaking at around 175 msec from the triggering stimulus. The absence of any recognizable summated cortical responses to similar stimulation of a bilaterally rhizotomied animal is apparent in Fig. 1, C and D. The unilaterally rhizotomied animal was its own control; this animal showed a prominent multispike response to stimulation of the intact limb and complete lack of response for the affected limb. In this animal the radial nerve stimulus generated an angular movement at the wrist joint of approximately 20°; nevertheless, it gave rise to no summated cortical evoked activity in repeated tracings. For some animals with deafferented limbs the peripheral nerves were stimulated several hundred times; even under these extreme conditions no recognizable cortical evoked responses were observed.

These findings indicate that dorsal rhizotomy abolishes somatosensory input to the cerebral cortex, thereby in fact achieving a somatosensory deafferentation. Thus, the remarkable prehensile ability and other relatively fine movements observed in monkeys following complete upper limb dorsal root section are not mediated by primary cortical action induced by peripheral signals from the affected extremity. Moreover, in other experiments (*4*) it has been shown that virtually the full range of deafferented activity can be observed in the forelimbs both after blindfolding and after sensory isolation of the entire spinal cord by division of all dorsal roots. Monkeys can even learn to perform new conditioned responses with deafferented extremities with vision occluded. It would thus appear that most patterns of purposive movement can be set into operation and guided by the central nervous system without any contribution from somatic sensation or other forms of topographic sensory input.

How, then, does the deafferented monkey with vision occluded obtain information about its own motor activities, as would be necessary, for example, when learning new movements? In this regard it is worth considering the possibility of the operation of central feedback mechanisms. Intracentral loops located appropriately could provide a means of monitoring central efferent activity before it has emerged into the periphery. Several pathways that could fulfill this function have been demonstrated to exist both anatomically and electrophysiologically, with points of inflection involving: afferent collaterals from the medullary pyramids to the dorsal column nuclei (*9*), laminae 4 to 6 of the dorsal horn (*10*), and the deep nuclei of the cerebellum (*11*). Other pathways of a similar nature probably exist elsewhere in the central nervous system. Descending activity could also be converted into a return pattern of signals by electrotonic or ephaptic conduction between descending and ascending fibers in adjacent tracts (*12*). A number of indications have made the dorsal spinocerebellar tract a subject of interest for current study in this regard. Another possibility is that no topographic feedback whatever, whether of central or peripheral origin, is necessary for the central nervous system to obtain information about movement-producing patterns of discharge. A set of neurons need only fire, and this event by itself would be sufficient to produce the encoding of that information. Feedback return would not be necessary to reiterate the data or to report on the consequences of the discharge. These different alternatives need not be viewed as mutually exclusive.

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Electrodynamic Sailing: Beating into the Solar Wind

In a recent report Alfvén (*1*) suggests and comments upon a novel means of spacecraft propulsion based upon the extraction of energy from the electromagnetic field of the solar wind. He claims that it is conceptually possible to sail upwind by coupling the energy extracted to an appropriate engine, likely an ion engine. His emphasis upon energy is important, but both energy and momentum requirements must be met.

An electrically conducting spacecraft such as Alfvén proposes suffers from two energy loss mechanisms. One is associated with magnetohydrodynamic wave drag, and the other with internal ohmic losses in the unipolar circuit which the system comprises. To make propulsion feasible in the sailing sense of "beating into the wind," or even a "close reach," there are two requirements: (i) the spacecraft must be able to do work upon the solar wind in excess of the work done upon it by wave damping and ohmic losses; and (ii) the momentum exchange must favor the thruster (ion engine). It seems possible to achieve the second requirement since an engine ought to be able to partition momentum in the necessary way. However, it appears to be impossible to meet the first requirement, that is, to satisfy the principle of conservation of energy for sailing upwind.

Alfvén's suggestion that electric propulsion devices be used for attaining high exhaust velocity is basically the means whereby high momentum flux can be obtained while decreasing the fuel mass so that it is not necessary to accelerate as much dead weight of unburned fuel. This mass of unburned fuel which must be accelerated is really the cause of the inefficiency, and it explains why, in the theory of rocket propulsion, the specific impulse is a key parameter. This reasoning also explains why the high exhaust velocities attained in ion engines are so attractive. On the other hand, it has not been possible to design an ion engine capable of yielding the momentum flux required for escape from strong local gravitational fields such as that possessed by the earth, nor does such an accomplishment seem likely in the foreseeable future.

I would now like to turn in detail to Alfvén's scheme for "sailing in the solar wind." The electric field is given by

$$\mathbf{E} = (\mathbf{V} \times \mathbf{B})/c$$

where **V** is the velocity of the spacecraft seen from a frame co-moving with the solar wind bulk speed, **B** is the interplanetary magnetic field, and c is the speed of light. The production of 10^3 amperes in the example of Alfvén will produce a magnetohydrodynamic bow wave in front (on the upstream side) of his wire and result in wave drag from the production of waves which radiate away from the tips of the wire. Other geometries will produce similar results. The consequence is drag. In effect what takes place is a retardation of the spacecraft by distortion of the interplanetary field lines. This retardation can be viewed as a propulsion mechanism, but only in the sense that the spacecraft tends to come up to solar wind speed as the wind drags it along. Thus, in sailing terminology the spacecraft can only sail downwind (run before the wind) by this means.

In order that the spacecraft sail upwind magnetohydrodynamically the sense of current flow must be opposite to that derived from the electric field. In this case radiating Alfvén waves will be produced which tend to propel the spacecraft against the solar wind. Clearly these waves must still heel backward because of the supermagnetosonic speed of the solar wind with respect to the spacecraft, but the body forces