Physiology and Behavior. Vol 3, pp 703–707 Pergamon Press, 1968 Printed in Great Britain

Instrumental Conditioning of Sensorimotor Cortex EEG Spindles in the Waking Cat[1]

WANDA WYRWICKA AND MAURICE B. STERMAN

Departments of Anatomy and Physiology, School of Medicine, University of California at Los Angeles, and the Veterans Administration Hospital, Sepulveda, California

(*Received* 26 *December* 1967)

WYRWICKA, W. and M. B. STERMAN. *Instrumental conditioning of sensorimotor cortex EEG spindles in the waking cat.* PHYSIOL. BEHAV. 3 (5) 703–707, 1968.—The spontaneous occurrence of a 12–20 cps slow-wave spindle recorded from sensorimotor cortex in waking food-deprived cats was systematically reinforced by presentation of milk. This specific EEG pattern was detected by a filter-relay system, the discharge of which was capable of activating the feeding apparatus within an experimental behavior chamber. After several sessions, with 50 reinforcements per session, this sensorimotor rhythm appeared more frequently and demonstrated a regular temporal pattern of occurrence. The consistent behavioral correlate of this EEG response was the assumption of stereotyped postures, characterized by a complete cessation of spontaneous activity. Withholding milk reinforcement resulted in a considerable enhancement of the sensorimotor rhythm during the initial period of extinction. Such changes were not observed, however, when other patterns of sensorimotor cortex electrical activity were reinforced in a similar manner. We conclude that, in the present experiments, it was possible to establish a conditioned sensorimotor cortex slow-wave response of the instrumental type, and that this sensorimotor rhythm has functional significance as a conditioned "central state" related to the inhibition of phasic motor behavior.

Instrumental conditioning Sensorimotor cortex EEG Somatic inhibition

EXPERIMENTS WITH INSTRUMENTAL conditioning have shown that essentially any behavioral act may be conditioned. Recently, it has become evident that not only somatomotor reactions, but also autonomic responses [9, 10, 15] and electrocortical activity [4, 5] can be successfully regulated through instrumental conditioning. With regard to the latter, the most distinctive changes which can be detected in EEG recordings are those associated with the behavioral transition from wakefulness to sleep. Low-voltage, high-frequency (desynchronized) activity which characterises the alert animal is progressively replaced by a sequence of high-voltage, low-frequency (synchronized) patterns indicative of the several stages of "slow-wave" sleep. Classical conditioning of both spontaneous [12] and electrically-induced [16] EEG slow-wave patterns has been demonstrated in cats. Using a shock-avoidance procedure, Izquierdo *et al.* [4] were able to establish a conditioned EEG desynchronization to tone in sleeping cats, who showed no visible signs of an associated behavioral awakening. Kamiya [5] has obtained evidence for instrumental conditioning of the EEG alpha rhythm in man by using verbal reinforcement.

Our laboratory has been interested in patterns of localized EEG slow-wave activity which can be recorded from the cortex of the awake cat in relation to certain specific behaviors. One of these patterns, which we have termed the "sensorimotor rhythm" or SMR, can be detected over coronal and peri-cruciate cortex during the extinction of an instrumental response and in association with negative conditioned responses [11, 13]. This rhythm consists of a 12–20 cps burst of synchronized EEG activity over motor cortex in an awake animal whose EEG from other cortical areas is clearly desynchronized. The specific details of cortical localization, electrical characteristics and other salient features of this rhythm have been published elsewhere [11]. In the present investigation we attempted to utilize this EEG rhythm as an instrumental response and to determine whether or not this response could be subjected to modification through instrumental conditioning procedures. Moreover, we were interested in establishing more clearly the functional significance of the SMR by reference to its direct behavioral correlate.

METHOD

Each of four adult cats (3 males and 1 female, weighing 3–4.5 kg) were surgically prepared with ⅛-in. jeweler's screws threaded into the skull in pairs over coronal gyrus bilaterally, and in an anterior-posterior sequence, 2 mm apart, over lateral (also termed marginal) gyrus, on one side. After recovery from surgery the animals were observed individually in a sound-attenuated behavior chamber supplied with a one-way viewing window and a relay-operated, dip-type

---

[1] This investigation was supported by the Veterans Administration and by P.H.S. grant No. MH-10083. Additional support for preliminary studies, carried out at the Nencki Institute of Experimental Biology, Warsaw, Poland, was provided for W. W. by the Foundation's, Fund for Research in Psychiatry, New Haven, Connecticut.

liquid feeder apparatus. They were attached by a 20-connector cable, slip-ring assembly and counterweight mechanism to a Grass VI electroencephalograph.

Training sessions were carried out three times a week on alternate days. The animals were food-deprived for approximately 22 hr when brought to the experimental chamber. They received condensed milk during experimental testing, supplemented by dry meat or fish 1–2 hr after its termination. The animal initially learned to obtain liquid food from the feeder apparatus through manual random presentations of 0.5 cc milk in the feeder cup. In order to achieve the objectives outlined above it was necessary to establish an instrumental conditioning situation, utilizing the SMR as the response to be reinforced. This was accomplished in the following manner. Spontaneous SMR activity, which is "easily" detected visually, was initially reinforced by manual operation of the feeder device. The rhythm was usually visualized over both left and right sensorimotor areas simultaneously, but was seldom absolutely symmetrical (Fig. 1). Recordings from the electrode pair yielding the highest voltage of SMR activity were thus utilized for conditioning tests. The experiment was initiated with three test sessions during which milk reinforcement was presented randomly. In the fourth session visual detection of an episode of SMR activity lasting for at least one-half second was utilized as a criterion for reinforcement by contiguous presentation of milk. The discrete nature of this rhythm and the contrasting low-voltage pattern of desynchronization in its absence made this criterion quite reliable. After one such "shaping" session, reinforcement of the SMR was accomplished automatically. Sensorimotor EEG signals were fed into a series of solid-state amplifiers with twin "T" feedback networks. These networks were tuned to select a number of very narrow frequency bands and to reject all others (including harmonics of selected frequencies). In this manner the frequency components of SMR activity from each animal were determined. Peak frequencies were established as 13 cps for two animals and 17 cps for the two others. Calibrated attenuation circuits were used to adjust the voltage output of a given filter. This output was fed to an integrator circuit, which specified that a signal containing at least 4–6 waveforms of the appropriate peak SMR frequency, at a voltage 100 per cent above background level, would activate the feeder mechanism (Fig. 2).

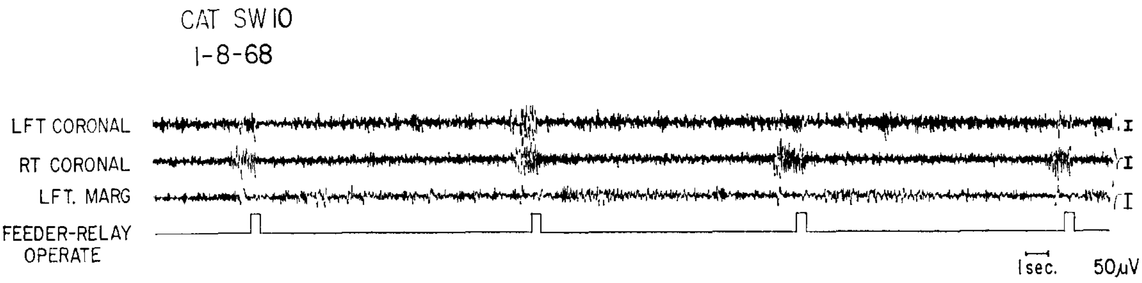

FIG. 1. Example of recurrent conditioned SMR activity recorded bilaterally from sensorimotor cortex in the cat. In this animal milk reinforcement was presented for SMR from right coronal gyrus. Asymmetry of SMR activity from the two hemispheres is usually observed, and may be attributed to differences in electrode placement or individual differences among the animals. Note the absence of spindle activity from marginal gyrus during coronal SMR discharge.

With automatic reinforcement established, conditioning

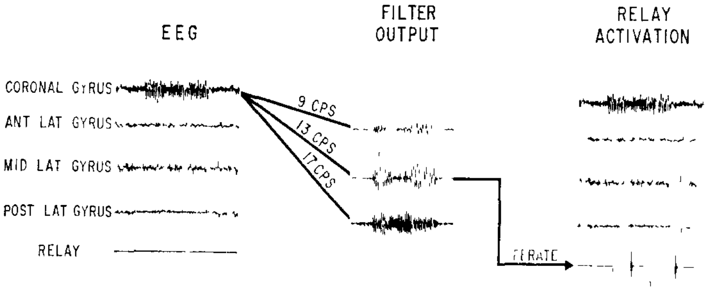

FIG. 2. Samples of spontaneous spindle activity recorded from the coronal gyrus of waking cats were subjected to frequency analysis as shown above. Solid state twin "T" feedback networks then passed the precisely-selected frequency signal through adjustable voltage attenuator and integrator circuits, which were adjusted to establish certain criteria for the operation of a final relay circuit. During training sessions this relay activated the chamber feeder apparatus.

sessions consisted of 50 automatic presentations of milk in relation to the occurrence of the SMR. After 20 consecutive conditioning sessions the experimental series was terminated by an extinction session. This was accomplished by withholding reinforcement for 30 min after 15 normally-reinforced trials. After a two-day interval, a control series was initiated in which milk was presented manually only in relation to a desynchronized pattern visually detected in the coronal gyrus (also utilizing the absence of automatically-registered SMR activity). This series was terminated by an extinction session identical to that described above.

Following another two-day interval, a third series was carried out in which the previously-conditioned SMR was again reinforced during 20 consecutive sessions, followed by an extinction session.

Throughout each of these series visual observations were carried out simultaneously with the recording of EEG activity, and of the relay discharges associated with the occurrence of the SMR (see Fig. 2). Quantification of the SMR for evaluation of experimental effects was achieved by measurement of the frequency and duration of relay closure. During extinction sessions the relay system continued to indicate the presence of the SMR, but was no longer connected to the feeder mechanism of the chamber.

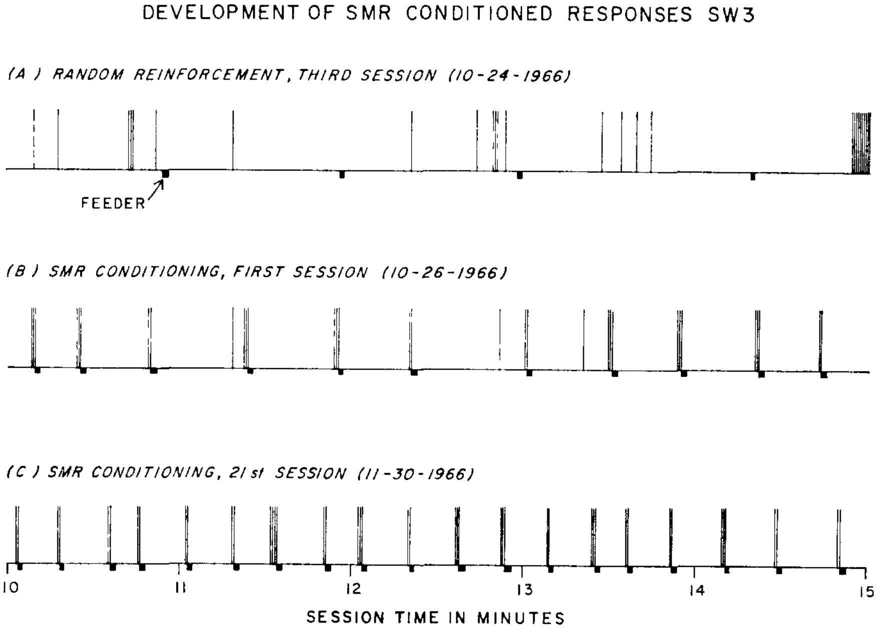

FIG. 3. The charts shown above indicate the time distribution of 0.25 sec epochs of SMR activity during (A) initial random milk reinforcement, (B) first training session, and (C) last training period before extinction test. Each vertical line represents and individual epoch, and adjacent lines indicate continuing SMR activity. These data samples were taken, in each instance, during a continuous five-min period, ten min after the initiation of a given session.

RESULTS

Conditioning of the Sensorimotor Rhythm

In the early stage of this series bursts of synchronized activity occurred transiently over the coronal gyrus when an animal appeared to "freeze" briefly during normal activities, such as walking or searching (Fig. 3-*A*). In the first training session the cats usually began to assume a definite motionless posture between reinforcements and to display the SMR regularly (Fig. 3-*B*). The previously random behavior was replaced by a systematic alternation between feeding and the assumption of motionless stereotyped postures. Each animal developed its own specific posture. One cat (SW-1) characteristically arched its back while its eyes were fixed straight ahead. Two other animals (SW-2, SW-3) went to a fixed location at the front of the chamber and stood "at attention." The fourth cat (SW-4) assumed a half-sitting posture at the wall opposite to the feeder. Other observations suggest that a decrease in muscle tonus and a suppression of respiratory activity accompany the occurrence of SMR activity. With the development of such behavior the SMR, which previously had appeared only randomly or in relation to the onset of sleep [13], showed not only an increase in percentage occurrence, but also a systematic temporal distribution, recurring periodically in relation to these various stereotyped postures (Fig. 3-*C*). When milk was delivered upon the occurrence of the SMR the animals immediately approached the feeder. After consuming the milk they returned quickly to their original positions.

Extinction was carried out after 20 conditioning sessions. Following the first 15 trials of the twenty-first session, milk was withheld for 30 minutes and then the session was terminated. The occurrence of SMR activity increased markedly in the first 5 minutes following this procedure, while the electrical activity from other leads remained desynchronized (Fig. 4-*A*). The cats simultaneously showed extended periods of alert but motionless behavior. In the next stage of extinction periods of motionlessness were alternated with periods of general restlessness, accompanied by desynchronization of the EEG in all leads. Finally, brief episodes of sleep, accompanied by synchronized patterns in all leads could be observed.

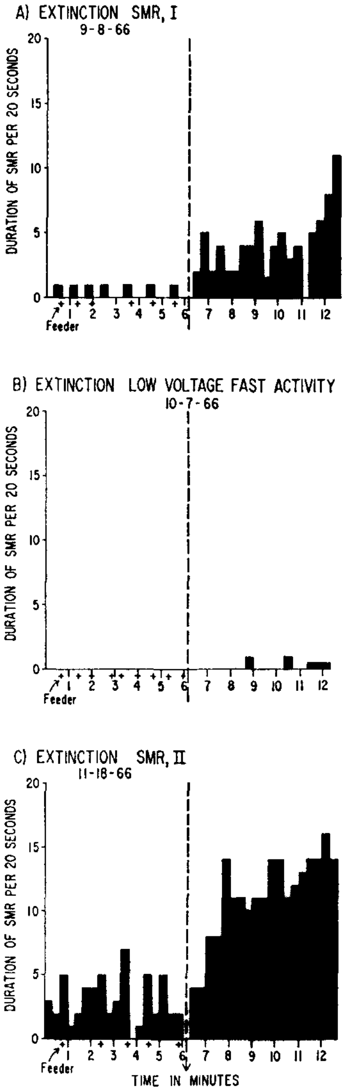

FIG. 4. These graphs indicate the course of events during the initial period of extinction in each training series for one cat. The broken vertical line shows the point at which food was withdrawn in each instance. The absolute amount of SMR activity in sequential 20-sec samples is shown on the ordinate for a period six minutes before and after food withdrawal. Plus marks indicate operation of the feeder prior to the beginning of extinction. In series A and C, SMR activity was the reinforced sensorimotor cortex pattern. In series B, low-voltage fast activity from the same leads was reinforced. Note the specific increase in the occurrence of SMR activity during the initial period of extinction in A and C, and its contrasting absence in B. The enhancement of SMR activity during extinction was usually greater after reconditioning than after the original training series.

Conditioning of Desynchronized Sensorimotor Area Electrical Activity

In this experimental series milk reinforcement was made contingent upon the occurrence of a desynchronized (low-voltage, high-frequency) electrical pattern from the sensorimotor cortical area. The previous conditioned SMR response faded in the first training session and was replaced by a consistently desynchronized pattern. The behavior of the cats changed also. They became constantly active, searching the chamber, circling and performing frequent discrete spontaneous movements. The previously-observed quiescent postures were absent from their behavior.

Once more an extinction session terminated this experimental series. As can be seen in Fig. 4-*B*, the initial period of extinction was characterized by an absence of the SMR, in contrast to its enhanced status under these circumstances in the first series. The behavior of the cats was also different; they showed an intensification of the restless activity described above. After some 15 min the cats tended to become less active and frequently reclined. During these quiet episodes the SMR was observed to reappear.

Reconditioning of the Sensorimotor Rhythm

For this last series the filter relay system was used again to provide milk reinforcement in association with the occurrence of the SMR. Initially, the animals displayed desynchronized cortical activity and behavioral restlessness. However, they gradually returned to postures resembling those displayed in the first SMR conditioning series, concurrently with the reappearance of related, and systematically-generated, periodic SMR activity over the coronal gyrus. The extinction session produced results similar to those observed in the first series (Fig. 4-*C*). However, the enhancement of SMR activity during the initial minutes of extinction was greater in this series.

DISCUSSION

A comparison of the electrical activity displayed from sensorimotor cortex during the various experimental series described here indicated that the overall pattern was modified by the conditions of reinforcement. That is, in the first and third series when the SMR was reinforced, this activity increased in its rate of occurrence and became systematically distributed in time. Moreover, the SMR was considerably enhanced during the initial period of extinction. Conversely, in the second series when milk was presented in association with the absence of SMR activity, a desynchronized EEG pattern dominated the sensorimotor cortex recordings, and no increase in SMR activity accompanied the initial period of extinction. These findings are in accord with the results usually obtained during the training and extinction of typical instrumental conditioned reactions [6, 7]. From these facts we may conclude that the discrete SMR reinforced by milk in our experiments became an instrumental conditioned response.

Behaviorally, conditioning of the SMR leads to a recurrent alternation between idiosyncratic motionless postures and feeding reactions. This observation may lead some to conclude that the corresponding SMR was simply associated with the development of these stereotyped postures. However, the postures assumed by the animals differed from one another and were sometimes variable in a given animal in the course of training. Moreover, the appearance of a given posture was necessary but not sufficient for the occurrence of SMR activity. The latter typically developed several seconds after the stereotyped posture was assumed. Ultimately, the behavioral feature common to all animals in every session was an absolute suppression of phasic-motor activity in an alert animal. This suggests, instead, the development of a "central state" of inhibition which is reflected both by the suppression of phasic-motor activity and by the change in the electrical activity from sensorimotor cortex. The general nature of this central influence is indicated, also, by the observation of a suppression of respiratory activity in relation to the occurrence of a conditioned SMR.

The SMR resembles the activity induced in sensorimotor cortex by stimulation of the basal ganglia or non-specific thalamus, manipulations which are known also to induce and facilitate motor inhibition [2, 3]. Extrapyramidal feedback, moreover, has been attributed an important role in motor inhibition by Massion [8], who demonstrated a filtering process in ventrolateral thalamus which modulates cerebellar input to sensorimotor cortex. Sensory feedback also may influence thalamo-cortical motor mechanisms, as suggested by the findings of Andersson and Wolpow [1]. Transection of the primary somatosensory projection pathways in the spinal cord of cats resulted in the appearance of slow-wave activity, specifically in somatosensory cortex. They suggest that the elimination of afferent input from specific receptor systems can alter the physiological organization of corresponding cortical projection areas. Presumably, therefore, extrapyramidal, proprioceptive and interoceptive stimuli can provide sufficient feedback information for the CNS to define this inhibitory state and to activate the pathways required for its production in order to obtain food. We are presently attempting to determine the subcortical structures involved in the generation of the SMR, with the hope that this will shed light, also, upon the central mechanisms of behavioral inhibition. Findings and implications in this regard have been discussed elsewhere [11, 13, 14].

REFERENCES

1. Andersson, S. A. and E. R. Wolpow. Localized slow wave activity in the somatosensory cortex of the cat. *Acta Physiol. Scand.* **61**: 130–140, 1964.
2. Buchwald, N. A., F. E. Horvath, A. Soltysik and C. Romero-Sierra. Inhibitory responses to basal ganglia stimulation. *Bol. Inst. Estud. Méd. Biol.* **22**: 363–377, 1964.
3. Buser, P., A. Rougeul and C. Perret. Caudate and thalamic influences on conditioned motor responses in the cat. *Boln. Inst. Estud. méd. biol. Univ. nal. Méx.* **22**: 293–307, 1964.
4. Izquierdo, I., W. Wyrwicka, G. Sierra and J. P. Segundo. Etablissement d'un reflexe de trace pendant le sommeil naturel chez le chat. *Actualités Neurophysiol.* **6**: 277–296, 1965.
5. Kamiya, J. Conditioned discrimination of the EEG alpha rhythm in humans. Presented at Western Psychological Association, San Francisco, 1962.
6. Kimble, G. A. *Hilgard and Marquis: Conditioning and Learning.* New York: Appleton-Century-Crafts, 1961.
7. Konorski, J. *Conditioned Reflexes and Neuron Organization.* Cambridge: University Press, 1948, p. 217.
8. Massion, J. M. Etude d'une structure motrice thalamique, le noyau ventrolateral et de sa regulation par les afferences sensorielles. Doctoral Thesis, Univ. of Paris, Paris, France, 1968.
9. Miller, N. E. and A. Carmona. Modification of a visceral response, salivation in thirsty dogs, by instrumental training with water reward. *J. comp. physiol. Psychol.* **63**: 1–6, 1967.
10. Miller, N. E. and L. DiCara. Instrumental learning of heart rate changes in curarized rats. *J. comp. physiol. Psychol.* **63**: 12–19, 1967.
11. Roth, S. R., M. B. Sterman and C. D. Clemente. Comparison of EEG correlates of reinforcement, internal inhibition, and sleep. *Electroenceph. clin. Neurophysiol.* **23**: 509–520, 1967.
12. Rowland, V. Electrographic responses in sleeping conditioned animals. In: *Ciba Foundation Symposium, Nature of Sleep,* edited by G. E. W. Wolstenholme and M. O'Connor. Boston: Little, Brown, 1961, pp. 284–306.
13. Sterman, M. B. and W. Wyrwicka. EEG correlates of sleep: Evidence for separate forebrain substrates. *Brain Res.* **6**: 143–163, 1967.
14. Sterman, M. B. Central mechanisms of forebrain-induced inhibitory states in the cat. *Electroenceph. clin. Neurophysiol.*, in press.
15. Trowill, J. A. Instrumental conditioning of the heart rate in the curarized rat. *J. comp. physiol. Psychol.* **63**: 7–11, 1967.
16. Wyrwicka, W., M. B. Sterman and C. D. Clemente. Conditioning of induced electroencephalographic sleep patterns in the cat. *Science N.Y.* **137**: 616–618, 1962.