Neural Mechanisms in Sexual Behavior. I. Reflexology of Sacral Segments of Cat.*† (21119)

BERRY CAMPBELL, CHARLES A. GOOD, AND RALPH L. KITCHELL.

From the Departments of Anatomy, Schools of Medicine and of Veterinary Medicine, University of Minnesota.

Most analyses which have been made on conduction and integration in the spinal cord have been based on those spinal mechanisms which are related to locomotion. Less information is available concerning the properties of the centers serving non-locomotor behavior. Sexual reflexes are an example of such and they exhibit features which deviate considerably from the better known cord mechanisms. There is an absence of the proprioceptive component of the segmental reflex. There is a conspicuous crossed ventral root outflow, a feature missing in the lumbo-sacral intumescence. It is the purpose of this report to describe some of the phenomena related to the genital innervation of the cat and to analyze the properties of the caudalmost segments of the spinal cord.

Material and methods. A series of 18 cats was prepared with dial or nembutal anesthesia and used for stimulating and recording experiments of the peripheral nerves, nerve roots, or spinal cord. In some of the animals, transection in the lower thoracic levels preceded the experiments. This had no discernible effect on the reflex phenomena. Silver wire electrodes were used for stimulating and recording from the nerves and nerve roots. The potentials of the spinal cord were obtained with glass coated silver solder micro-electrodes. Both males and females were included in the series.

Observations. Stimulation of the S_2 dorsal root evokes a response on the corresponding ventral root (Fig. 1*a*) which resembles, in its components, the segmental reflexes of the first sacral segment and of the caudal few lumbar segments. This similarity is undoubtedly due to the fact that the second lumbar segment has extensive innervation of locomotor structures. There is a proprioceptive spike, the 2-neuron reflex, followed by a dispersed cutaneous response (the flexor reflex of various authors). A complete absence of a crossed response further substantiates the relation of this segment to the segments cranial to it and raises the question of its innervation in any midline muscles.

The third sacral segment shows an abrupt change in properties from the second and more cranial segments. Stimulation of the dorsal root evokes a response on the corresponding ventral roots (Fig. 1*b*) which lacks the proprioceptive component completely. The cutaneous response is present and resembles that of the S_2 segment in form though remarkable in its great latency which is usually around 4.0 msec. The problem of comparison of cutaneous responses preceded by proprioceptive spikes with those in which the early component is lacking is one which is full of pitfalls(2) and this additional central delay of the cutaneous response is not necessarily indicative of a more complex pathway than in the other segments.

A feature lacking in the S_2 segment and conspicuous in S_3 is the crossed reflex. Stimulation of a dorsal root of the S_3 segment evokes a response not only in the corresponding ventral root but also in the opposite ventral root (Fig. 1*c*). The form of the response is similar to that on the homolateral side, but the amplitude is usually decreased. The latency is greater, varying from an additional several tenths of a millisecond to as much as 3 msec.

The first caudal (Ca 1) segment shows a pattern of segmental response different from its predecessor. It shows a proprioceptive spike which gives it the appearance of the segmental response of the lumbar region (Fig. 1*d*). Following the spike is a distinct cutaneous component. The crossed reflex (Fig. 1*e*) lacks the proprioceptive spike and has a

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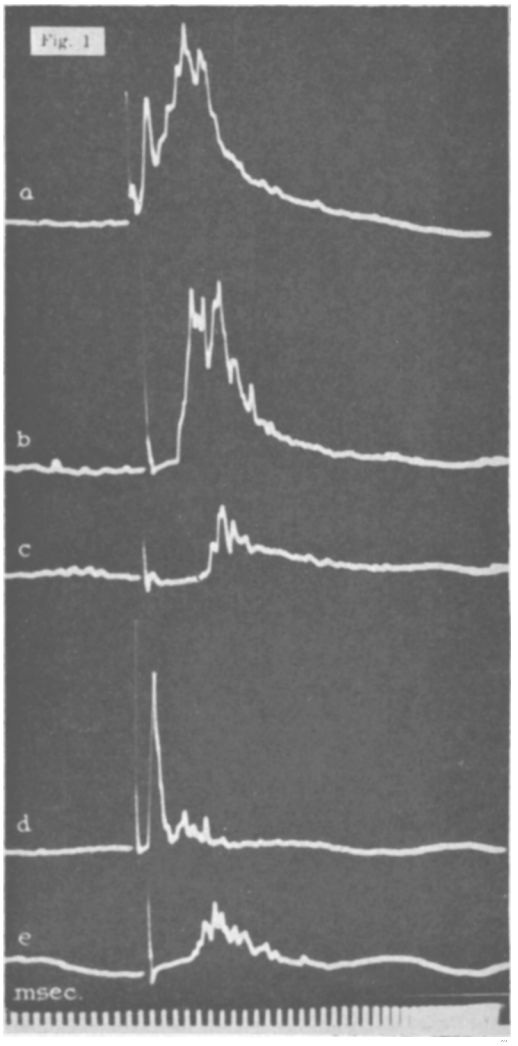

FIG. 1. *a*. Response on S_2 ventral root from stimulation of ipsilateral S_2 dorsal root. *b*. Response on S_3 ventral root from stimulation of ipsilateral dorsal root. *c*. Same from stimulation of contralateral S_3 dorsal root. *d*. Response on Ca_1 ventral root from stimulation of ipsilateral dorsal root. *e*. Same from stimulation of contralateral dorsal root.

later and more continuous cutaneous response. However, the remarks above, relevant to the interpretation of the cutaneous component when complicated by the preceding firing of the neurons in a proprioceptive spike, are also relevant here.

The total latency of the proprioceptive spike is less than 1.5 msec. and exhibits a central latency consonant with the 2-neuron reflex. The cross response commences at 4.0 msec.

The signal delivered to the spinal cord from stimulation of the genitalia operates within the segmental system described above. Apparently in this species the principal innervation of the penis and vulvar vestibule is from the S_3 segment. Stimulation of the penis gives a marked dorsal cord potential (Fig. *2a*) which is confined to that segment. In this record, the conduction spike does not show, probably because of the dispersed nature of the volley. The latency of the dorsal cord negativity is 3.2 msec. Placing the electrodes on the intact S_3 dorsal root in the same experiment (Fig. *2b*) shows a volley (resulting from a single condenser discharge across the intact penis) which shows considerable dispersion commencing at 2.0 msec. In another experiment, a record made from the peripheral end of a cut pudenal nerve yielded a potential which begins at 1.2 msec., and continues for at least 6 more msec. The complex form indicates several groups of fibers were participating. The dispersion is more clearly illustrated in Fig. *2c*. This was a female cat. The stimulating electrodes were placed in the vulvar vestibule and, from a small filament of the S_3 dorsal root, the activity following a single shock to the vestibule was recorded. Because of the recording conditions, much of the activity is shown as single unit spikes. The considerable dispersion of the volley is illustrated. In response to stimulation of the genitalia, a reflex on the S_3 ventral root is evoked. In Fig. *3a* and *b*, the dorsal roots on the left side were cut. The response on the right, thus, was an ipsilateral reflex. The total latency is about 8.0 msec. of which 3.2 msec. may be taken as the afferent conduction time. The outflow potential rises to a rapid peak and terminates within 4.0 msec. after its commencement. As it ceases before the afferent volley has ceased, some quenching mechanism is indicated. There is no sign of a proprioceptive component. The crossed reflex in the S_3 ventral root following stimulation of the penis or vestibule resembles the uncrossed outflow described above. The latency is from 0.6 msec. to 2.0 msec. more than that of the uncrossed reflex.

From similar stimulation of the genitalia, no response is to be obtained from the S_2

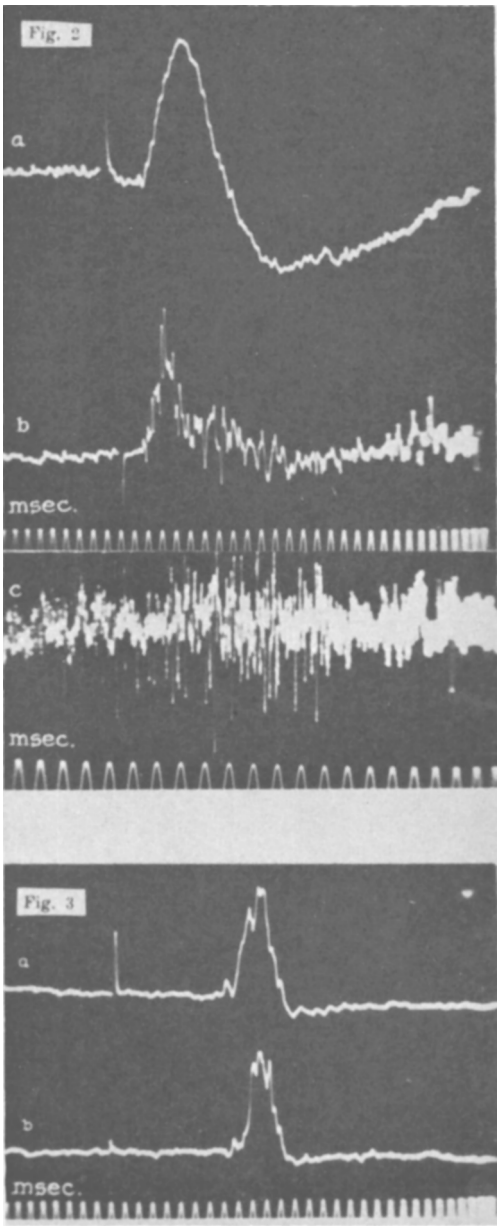

FIG. 2. *a.* Male cat. Response at dorsum, of cord, S_3, following stimulation of penis. *b.* Record from S_3 dorsal root, stimulus as in *a.* *c.* Response on S_3 dorsal root, following stimulation of vulva.

FIG. 3. *a.* Response on S_3 ventral root on intact side from stimulation of penis. *b.* Response on opposite side.

segment but the Ca_1 segment shows a small return, both crossed and uncrossed. Because of the nature of the records the onset is not easily fixed, but it seems to be slightly earlier than in the preceding segment.

The exact modalities involved in these responses are not apparent from the dorsal root stimulation. To make some test of this, records from the S_3 dorsal root were made on a cat with stimulation of the penis in its retracted position (with the stimulating electrodes in the preputial cavity), on the glans of the everted penis, and on the anus. This shows a latency of 2.5 msec. from the glans penis as contrasted with a latency of 1.8 msec. in the response to stimulation of the prepuce as well as the glans. With the stimulating electrodes within the anus, the corresponding delay drops to 0.9 msec. Between the first 2 figures, some of the discrepancy may be due to the increase conduction distance, certainly less than 2 cm. Probably the greatest factor in these different latencies, is the different spectrum of fiber size concerned in each instance. A question is raised by these figures concerning the muscle sense of the rectal and preputial sphincters. While there is no characteristic 2-neuron spike in this segment, as mentioned above, the possibility that the faster component of the pudenal nerve may be related to some kind of muscle sense must be entertained. The relatively smaller amplitude of the response from the glans probably indicates a rather restricted population of fibers as one might expect from the specialized nature of the organ.

Discussion. The activity described in these experiments is a part of the behavior pattern of the genitalia. It is not specifically concerned with sexual behavior, *per se,* as the genitalia have other behavioral aspects. The properties of the reflex phenomena described resemble the so-called "flexor" reflex—the cutaneous component of the segmental return. This is usually thought to be protective in its function, and may in fact be considered in this instance. It resembles the "flexor" reflex also in form and in its lengthy central time. It is not consistent with our knowledge of the behavioral meaning of the reflex phenomena to identify a given simple response with a particular behavioral entity. As locomotion is not a simple sequence of proprioceptive or cutaneous or crossed extension reflexes, but an integrated behavior utilizing the mechanisms serving these physiological fragments, in the

same sense, the behavior of the genitalia is not to be elucidated by the study of a simple reflex. The phenomena serve to define the properties of the pathways which mediate the activity of the genitalia.

The lack of the proprioceptive reflex from the segmental reflex of S_3 indicates that the striated musculature of the genitalia does not have a myotatic regulation with the same properties as that of the limb or tail muscles. Whether there are different types of muscle end organs, or any muscle end organs at all, must remain questionable until a histological examination has been made.

Summary. Activation of the third sacral and first caudal segment of the spinal cord evokes a segmental response on the ventral root resembling the cutaneous component of the segmental reflex of the more cranial parts of the spinal cord. A proprioceptive spike is absent in S_3, present in Ca_1. In each of these segments, there is a crossed reflex return resembling the cutaneous component and frequently somewhat later and smaller than the ipsilateral response. Stimulation of the penis or of the vulvar vestibule elicits the same response, though without the proprioceptive spike in the Ca_1 ventral root. Spinal transection in the lower thoracic region does not alter these reflexes under the experimental conditions.

1. Riddoch, G., *Brain,* 1917, v40, 264.
2. Campbell, V., Mark, V. H., and Gasteiger, E. L., *Am. J. Physiol.,* 1949, v158, 457.

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Thyroid Feeding and Vitamin B_6 Deprivation in the Rat.* (21120)

J. R. BEATON AND M. E. GOODWIN.
From the Department of Public Health Nutrition, University of Toronto, Canada.

In an earlier investigation(1) it was found that the basal metabolic rate of vit. B_6-deprived rats was not different from that of pair-fed control animals although lower than that of *ad libitum*-fed controls when expressed as oxygen consumption per unit of body weight. There is considerable evidence that the efficiency of energy production is altered by vit. B_6 deprivation. However, attempts to lower the basal metabolic rate by administration of thiouracil or by thyroidectomy did not cause definite alterations in the syndrome of vit. B_6 deprivation(1). It was felt advisable to study the effects of a hyperthyroid state on the deprivation syndrome in rats. The results of this study are presented.

Methods. Forty albino rats of the Wistar strain and of both sexes were divided into 4 groups equal with respect to number, sex distribution and an initial average body weight of 103 g. All animals were housed in individual, screen-bottomed cages with drinking water freely available. The basal diet employed was the 20% casein, 20% corn oil, vit. B_6-free diet previously described(2). Two groups were further provided with 50 μg pyridoxine hydrochloride per rat per day in their food and served as control animals. One vit. B_6-deprived and one control group were given one mg desiccated thyroid (U.S.P., Nutritional Biochemicals) per g of diet. To eliminate differences in analytical results between groups consequent to differences in the amount of food consumed, all groups were pair-fed with the vit. B_6-deprived group given desiccated thyroid such that the average daily food consumption of all groups was 13.4 g per rat. Following an experimental feeding period of 21 days, the animals were fasted for 18 hours and anesthetized with an intraperitoneal injection of 2% butylone in 0.9% saline. Blood was removed from the exposed hearts with the aid of a hypodermic syringe and was heparinized and pooled for each group. The following analyses were done in duplicate on

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