

Modification of Reflex Behavior in Spinal Dogs

JAMES DEESE AND W. N. KELLOGG, Indiana University

The first indication that relatively permanent changes in reflex behavior can take place in spinal preparations, aside from the effects of fatigue, was found by Prosser and Hunter (2). Following complete spinal transection of laboratory rats they found various spinal reflexes could be extinguished with stimuli repeated at intervals of from 10 to 15 seconds. The extinction was considered to be a central process. The process involved the gradual dropping out of "active units" and the diminution in the duration of the response. This was thought to indicate that extinction was a gradual lowering of the excitability.

Shurrager and Culler (4) reported the establishment of a conditioned response in the spinal dog. The spinal cord was completely severed near the third cervical vertebra. Both semitendinosus muscles (S-T MM.) were exposed and freed of fascial attachments, and then fastened to recording tambours. The conditioned stimulus, either mechanical or electric, was administered to the tip of the tail. It consisted of three short shocks or pressures given one second apart, the third one being presented simultaneously with the unconditioned stimulus. The unconditioned stimulus was a shock of sufficient intensity to evoke a full contraction of the left S-T M. when applied to the left paw. A conditioned response to the conditioned stimulus appeared within 25 to 50 trials (4). "The CR is much smaller than the UCR and is generally confined to a small area near the peripheral end of the muscle. The right muscle remains flaccid throughout" (4). Repeating the conditioned stimulus without the unconditioned stimulus resulted in extinction (3).

Pronko and Kellogg (1) found that there are two types of conditioned responses in shock-shock conditioning. One of the types of response having a much shorter latency is similar to the "conditioned response" observed in spinal dogs by Shurrager and Culler. This response, of smaller magnitude and briefer latency, does not conform to the more typical frequency curves of conditioned responses. It rises to a relatively high frequency early, but then does not increase much. This type of response was characterized by the authors as "a kind of flexing jerk or muscle twitch" (1) appearing in the limb to be conditioned shortly after the conditioned stimulus. This muscle twitch is distinctly different from both the unconditioned reflex and the conditioned reflex of the more usual type. Wendt (5) earlier reported a similar condition in conditioning the knee-jerk in human beings with the unconditioned stimulus being a blow to the limb opposite the one to be conditioned. This is, of course, analogous to shock-shock conditioning. The author interprets the bilateral type of response as being mediated by "a lower level integration." (5) This integration is thought to be already present before conditioning as revealed by the strong

facilitating effect of a blow to one knee on the response of the opposite knee. In an occasional individual a crossed-extension reflex is present instead. Repetition of the conditioning trials increases the bilateral secondary response more than the crossed-extension. The presence of the crossed-extension response in this type of conditioning bears important relation to the finding of the present study.

Operation and care of the animals. The use of morphine sulphate or other depressing drugs was strictly avoided, and ether alone was employed as the anesthetic agent. The purpose of this technique was to permit recovery from the anesthetic as quickly as possible. A skin incision about 3 inches in length was then made at the level of the third lumbar vertebra. The muscle tissue was incised by electro-surgery and the spinus and transverse processes of the spinal column were removed by rongeurs. The vertebrae above and below the third lumbar nerves were drilled with a dental burr and the dura exposed for a distance of about an inch. The cord was ligated in two places to prevent the loss of spinal fluid and was then completely transected between the ligatures. Sulphanilimide was placed in the wound and the muscle tissue and fascia were closed with interrupted silk sutures.

Since the animals were kept for about three weeks following the operation it was necessary to build a special device for keeping them active and healthy. A system was finally arranged which permitted a maximum degree of freedom without danger of the animal irritating his wound, or otherwise damaging himself. When not in the conditioning stock the animals were supported in a canvas sling attached to a metal frame from above. This could be raised and lowered, permitting the animal's legs to be on a level with the body or suspended from above, as needed.

Conditioning technique. Four animals were used in the experiment. Shock-shock conditioning was used in the following manner: Two conditioned stimuli were administered to the left rear paw, one second apart. The unconditioned stimulus was administered to the right rear paw one second after the last conditioned stimulus. All measurable upward changes in contour on the kymograph record occurring 9/5 of a second after the conditioned stimuli and before the unconditioned responses were considered conditioned responses in the animals before the operation. Frequency, latency and amplitude were measured in sessions recorded before the operations. Following the operation all changes in an upward direction in the right rear leg simultaneous with the conditioned stimuli in the left rear leg were classified as "bilateral flexion" responses. All changes in a downward direction in the right leg simultaneous with the conditioned stimuli in the left rear leg were classified as "crossed-extension" responses. Only frequency of these responses was measured, since latency and amplitude were for all purposes the same throughout.

Results and discussion. Prior to the operation all four dogs were given extensive conditioning training, all animals but one reaching the criterion of 100 per cent frequency of conditioned responses in a 20

trial series. One animal, M74, reached only 85 per cent frequency on the last series. All the animals except M74 had previously been trained in this same conditioning technique, so the frequency on the first series represents retention over varying periods of time. M74 had been previously trained in a slightly different technique. Table I shows the percent frequency on each series for all four dogs. Following the operation

Table I

The Percent Frequency of Conditioned Responses in Right Rear Leg for Pre-Operative Training in all Four Dogs

Series	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
F54	70	60	95	50	50	55	100	100							
M74	45	20	45	55	30	65	80	85	70	60	75	95	75	70	85
M77	95	65	35	55	90	100									
M79	90	100	80	90	100										

1,000 trials were given to each dog, 100 trials on every other day. This necessitated keeping each dog for a period of about three weeks. After the operation the conditioned responses developed during the course of the pre-operative training disappeared. However two distinct kinds of responses appeared in the course of time during the presentation of the conditioned stimuli after the operation. One was a minute muscle twitch or bilateral flexion to the conditioned stimuli, bearing close resemblance to what Shurrager and Culler (4) called a conditioned response in their preparations. The other was a crossed-extension reflex to the conditioned stimuli. These two responses were mutually inhibitory to any given stimulus, but both appeared frequently in the same series. When the frequency of each was plotted graphically it did not resemble a conditioning curve, since both responses appeared and disappeared during the course of the experiment. This may be gathered from Table II and III. However they never appeared immediately on the first trials following the operation in any of the dogs.

In interpreting tables II and III one should consider the mutually inhibitory nature of the two responses to any given stimulus. Under the present conditioning procedure the crossed-extension reflex to the conditioned stimulus was not eliminated as it was in the Shurrager and Culler studies (3,4). It is possible that the bilateral flexion response might have developed more characteristically if the crossed-extension reflex to the conditioned stimulus had been eliminated.

When the percentage frequency of the two responses are combined it suggests the development of a conditioned response of very low frequency. Table IV gives evidence of this. To the 17th series the frequency rises in a fairly regular fashion, after which it declines slightly to a more or less level position. It is extremely difficult to account for this unless one assumes a gradual restoration of physiological function following the operation. It will not do to attribute it to a gradual "spread of excitation" since there are distinctly two responses present,

Table II

The Frequency of Bilateral Flexion Responses in all Four Dogs Combined
Following the Spinal Transection

Series	Per cent	Series	Per cent
1	0.	26	10.
2	3.76	27	21.2
3	7.5	28	13.5
4	0.	29	15.
5	1.25	30	10.
6	2.5	31	7.5
7	6.25	32	12.5
8	3.76	33	3.76
9	2.5	34	1.25
10	1.25	35	2.5
11	12.6	36	0.
12	21.2	37	2.5
13	13.5	38	5.
14	17.5	39	0.
15	12.5	40	1.25
16	0.	41	3.76
17	1.25	42	1.25
18	3.76	43	1.25
19	2.5	44	0.
20	5.	45	0.
21	1.25	46	2.5
22	1.25	47	2.5
23	0.	48	2.5
24	2.5	49	2.5
25	0.	50	2.5

now one appearing now the other. It is quite possible that one response is "inherent" to particular structural limitations here (the crossed-extension) and that the other (bilateral flexion) develops during the process of repeated stimulation. However the functional nature of most spinal reflexes makes an explanation of the *raison d'être* extremely difficult. An explanation would be much easier if the bilateral flexion responses were isolated instances appearing in one preparation, or if they had not appeared under the same stimulus conditions in an intact animal (1). But there is no doubt of their genuine character and the fact that they are unstable (appearing and disappearing) reflexes, though the stimulating conditions remain essentially the same. The most likely hypothesis seems to be that they represent a kind of spinal analogue of startle responses in intact animals. Such an explanation would leave the role of the unconditioned stimulus doubtful. Shurrager and Culler (3,4) emphatically point to the role of the unconditioned stimulus in the appearance of these spinal "conditioned responses" since they are subject to extinction with the elimination of the unconditioned stimulus.

Table III

The Frequency of Crossed-Extension Responses in all Four Dogs
Combined Following the Spinal Transection

Series	Per cent	Series	Per cent
1	0.	26	2.5
2	0.	27	2.5
3	0.	28	1.25
4	0.	29	1.25
5	0.	30	1.25
6	0.	31	7.5
7	2.5	32	11.2
8	8.75	33	7.5
9	20.	34	16.5
10	25.3	35	10.0
11	22.5	36	15.0
12	10.	37	15.0
13	8.75	38	22.5
14	8.75	39	21.2
15	28.8	40	3.76
16	32.5	41	17.5
17	25.	42	12.5
18	27.5	43	22.5
19	20.	44	16.2
20	13.7	45	7.5
21	8.75	46	13.7
22	13.7	47	16.2
23	8.75	48	20.0
24	13.7	49	16.2
25	12.5	50	15.0

To define "operationally" the appearance of such responses as a conditioning process is easy enough, but it leaves much to be desired. In the present study the responses developed, taken together, seem to bear no particular relation to the appearance of the unconditioned stimulus, but seem to depend entirely for their appearance on the conditioned stimulus. The bilateral flexion reflexes isolated may bear a more direct functional relation to the unconditioned stimulus, but in working with the particular arrangement of shock-shock conditioning used in this experiment it is impossible to eliminate the crossed-extension reflex and still keep the limbs of the animal intact. However, the appearance of both of these "muscle-twitch" phenomena seem to indicate a decided modification of reflex activity as stimulation is continued. However, if they are conditioned responses, as defined not only by the experimental procedure, but also by the measuring techniques used, then they are of a doubtful nature.

This bilateral flexion response seems to stand more or less in between the less variable type of response, such as a direct unconditioned response, and the modified or conditioned response. Modification

Table IV

The Combined Frequency of Bilateral Flexion and Crossed-Extension Responses in all Four Dogs Combined

Series	Per cent	Series	Per cent
1	0.	26	12.5
2	3.76	27	23.7
3	7.5	28	14.75
4	0.	29	16.25
5	1.25	30	11.25
6	2.5	31	15.0
7	8.75	32	23.7
8	12.51	33	11.26
9	22.5	34	17.45
10	26.55	35	12.5
11	35.1	36	15.0
12	31.2	37	17.5
13	22.25	38	27.5
14	26.25	39	21.2
15	41.3	40	5.01
16	32.5	41	21.26
17	26.25	42	13.75
18	31.26	43	24.75
19	22.5	44	16.2
20	18.7	45	7.5
21	10.0	46	14.95
22	14.95	47	18.75
23	8.75	48	22.5
24	16.2	49	18.75
25	12.5	50	17.5

of behavior here has taken place, but the frequency and temporal location were not predictable from any previously given conditions. The exact physiological conditions involved in this modification of response are unknown, and speculations are of little avail in the face of the complexity of the structures involved. However, the common conception of the stereotyped reflex behavior, unmodifiable except for diminution or disappearance upon repeated stimulation, seems seriously in need of revision. Whether the modifiability of the responses may be considered conditioning is another question. Certainly the status of the conditioned response, defined by its investigation, has yielded nothing directly comparable.

Summary. Reflex phenomena similar to the spinal conditioning reported by Shurrager and Culler (4) was found in four dogs after the spinal cord had been completely severed at the level of the 3rd lumbar vertebra. These responses were minute twitches in the limb contralateral to the limb in which the conditioned stimuli were delivered, being the same limb in which the unconditioned response appeared. These responses were intermingled and apparently inhibited by crossed-

extension reflexes to the conditioned stimuli. Both responses appeared, disappeared and reappeared in no regular sequence. There was no indication of incipient avoidance movements to the unconditioned stimulus, though all dogs had been trained to a high degree of proficiency in shock-shock conditioning before the operation. Whether this modifiability of response can be classified under the more customary canons of the conditioned response is doubtful. Rather these reflexes may represent a transition between the clear cut cases of learned responses and those reflexes which are relatively invariable and tied up with the existence of certain crucial structures.

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