INTERACTION OF EXTEROCEPTIVE AND INTEROCEPTIVE REFLEXES

COMMUNICATION I. EFFECT OF UNCONDITIONED EXTEROCEPTIVE AND INTEROCEPTIVE STIMULI ON A SPINAL MOTOR REFLEX

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It is known that under normal conditions exteroceptive stimulation is of prime importance in motor system activity. Numerous researches [2, 10, 22, and others] have elucidated the effect of exteroceptive stimuli, such as light, color, sounds of various tones and harmonies, smells, and tastes, on voluntary movements of human subjects (ergograms), or on their capacity for performing work requiring precision of movement. It was found that some of these stimuli exerted a stimulatory, and others an inhibitory effect. It is also known that the activity of the motor system of animals and humans is much less affected by changes taking place within the organism, i.e., by interoceptive stimuli.

Many workers have, however, shown that manipulation of internal organs in the course of operations, or their stimulation under experimental conditions, cause changes in the activity of skeletal muscles [13, 15, 16, 21, 23].

It is also known that stimulation of interoceptors leads to changes in the activity of skeletal muscles, such as in coughing, vomiting, swallowing, micturition, and parturition. According to some clinicians, the effect of interoceptive stimulation on voluntary muscular activity may be particularly pronounced in certain morbid conditions, and may, in a number of cases, be the cause of the development of disturbances of the motor system.

M.R. Mogendovich showed in 1941 [12] that stimulation of certain viscera caused changes in the chronaxie of voluntary muscles.

A systematic study of exteroceptive and interoceptive conditioned reflexes of the skeletal musculature has been undertaken by K.M. Bykov and his associates [7].

V.N. Chernigovskii and his associates have made a detailed study of reflexes released by stimulation of interoceptors, and established the existence of two basic types of effects – a "releasing" and a "correcting" effect [8, 9, 17, 18, 19, 20]. I.A. Bulygin [3, 4] has also shown that various types of internal organ stimulation evoke reflex reactions of skeletal muscles.

It may thus be said that the effects of interoceptors on voluntary muscles, under conditions of acute experimentation, have been investigated very thoroughly. Much less work has, however, been done under conditions of chronic experimentation [5, 11, 16, 23].

Still less attention has been paid to the comparative analysis of the correcting effects of exteroceptive and interoceptive stimulation on voluntary muscles. The only reference to this subject that we have been able to

trace is an abstract of a Doctor's thesis by I.D. Boenko [1]. In his animal experiments, this author determined the chronaxie of limb muscles and of the corresponding areas of the cerebral cortex, before and after various interferences with the organism, and found that the chronaxie changes in the same direction in both these systems, and in the same way, irrespective of whether the animal was subjected to stimulation of exteroceptors or interoceptors.

The present paper is devoted to the comparison of the effects of interoceptive and exteroceptive stimulation on a spinal motor reflex which is already in progress.

EXPERIMENTAL METHOD

The experiments were performed on eight dogs. All the animals were provided with a gastric fistula, and were subjected to a Thiry-Vella operation for exteriorization of the intestine. The unconditioned spinal motor reflex (withdrawal or raising of an extremity) was elicited by electrical stimulation of the sole of a fore or hind limb. We used ac current from the mains, supplied to a rheostat, connected potentiometrically.

The current was switched on for periods of 0.5 seconds, at a frequency of 12 impulses per second. At the beginning of each experiment we determined the threshold by moving the slide of the rheostat, and then slightly increased the current to give a pronounced reaction. The threshold varied from 0.5 to 1.5 v for different animals. We repeated the stimulus 15-20 times, over 5-10 minutes. Respiratory movements, and those of the stimulated limb, were recorded on a kymograph. In addition, electrocardiograms were recorded in some of the experiments.

We were not interested in the electrocardiograms as such, except as a means of registering heart rate.

Interoceptive or exteroceptive stimulation was applied during the period of electrical stimulation of the leg, i.e., while the unconditioned motor reflex was in progress. We called these "extra stimulations." Leg movements were recorded in some experiments by means of a V.P. Petropavlovskii splint, and in others by the method of N.N. Poliakova [14], using a rubber tube partly filled with mercury and connected with a rubber bellows fitted with a writing stylus. We applied the following exteroceptive stimuli: light (L), ringing of a bell (b), intermittent ringing of a bell (int. b), a metronome (M_{100} and M_{300}), a skin stimulator applied to the right shoulder (St.rt.), or to the left hip (St.l.), electric shocks applied to the skin of an ear, or a flank, or of a leg (El.e., El.f., and El.l.), irrigation of the mouth with 0.3% hydrochloric acid (HCl_m). Interoceptor stimulation was effected by dilating the ampulla of the rectum by means of a rubber balloon (R), applying a pressure of 70-80 mm Hg, distension of the stomach (Sto.), by inflating a rubber bag at a pressure of 40 mm Hg, and irrigation of the small intestine with 0.2-0.3% hydrochloric acid (HCl_i). In most of the experiments the duration of action of the stimuli was 25 seconds. In one series of experiments, we applied rhythmic stimulation to the left hind leg, and in another to the left fore leg.

EXPERIMENTAL RESULTS

It is evident from the kymograms that extra stimulation, whether of exteroceptors or of interoceptors, may either not affect the spinal motor reflex (Figure 1: 1, 2, 3, 4), as is found in 15% of the experiments, or it may affect it, as in 85% of the experiments. In those cases in which a correcting effect appeared, the motor reaction which was in progress varied differently for different tests. In some cases, the extra stimulation strengthened the spinal reflex (Figure 1: 5, 6, 7, 8), while in others it weakened it (Figure 1: 9, 10, 11, 12), sometimes completely abolishing it. In other cases, extra stimulation gave rise to a diphasic type of reaction (Figure 1: 13, 14, 15, 16). Restoration of the initial motor reaction followed immediately after discontinuation of the extra stimulation (Fig. 1: 5, 8, 9, 12), or some time after (Figure 1: 10, 11), i.e., after-effects could be observed.

When additional movements appeared (Figure 1: 6, 8), we evaluated the effect as one of stimulation, taking the effect as being one of strengthening of stimulation in the corresponding motor centers. We also considered a halt at the summit of the myogram tracings to be evidence of stimulation (Figure 1: 7). Conversely, we took abolition of spontaneous movements (Figure 1: 10) to be evidence of inhibition.

The respiratory changes were characteristic. The first change was seen on beginning rhythmic stimulation of the limb. If the pulsed current was applied when the animal was breathing regularly, we usually observed an acceleration of the respiratory rhythm, frequently associated with uncoordinated respiratory movements (Figure 1:

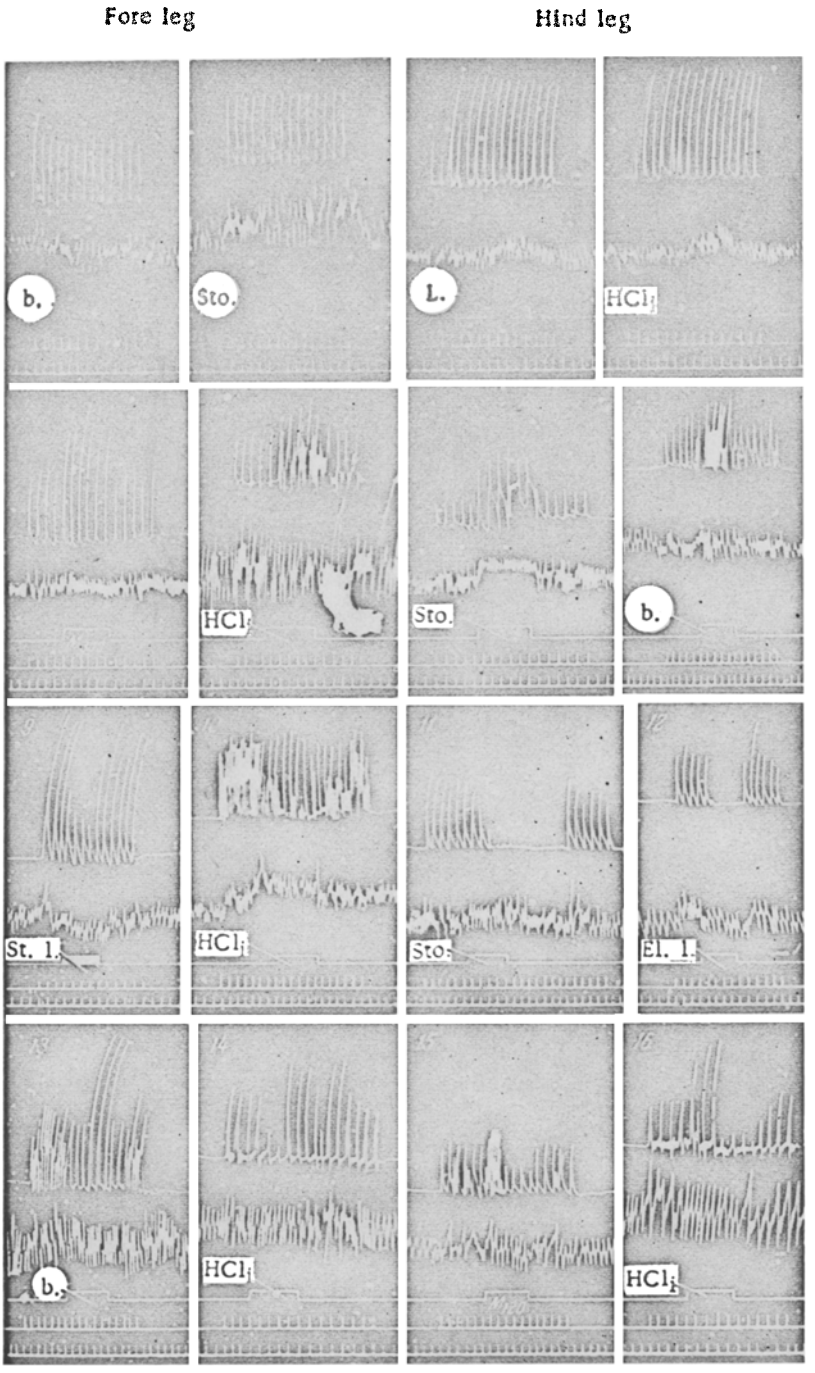

Fig. 1. Effect of exteroceptive and interoceptive stimulation on a spinal motor reflex reaction. Explanation of tracings (from above down): reflex movements of the leg, respiration, extra stimulation signal, rhythmic stimulation signals, time marker (five seconds). Fragments of kymograms 1-16, recording results of tests of different stimuli. Explanation in text.

6, 7, 10, 11). We often observed steep respiratory waves, which appeared at the moment when stimulation was started, and were in synchrony with the electric pulses (Figure 1: 7, 11, 14, 16). When the rhythmic stimulation was applied during a phase of hyperpnea the effect, in the majority of cases, was to abolish the hyperpnea, which was immediately replaced by a much slower respiratory rhythm, which was not in all cases regular (Figure 2: a).

Extra stimulation also affected respiration. The uncoordinating effect of rhythmic stimulation usually disappeared, and in about 60% of the cases a type of "normalization" of respiration ensued for the duration of action of the extra stimulation.

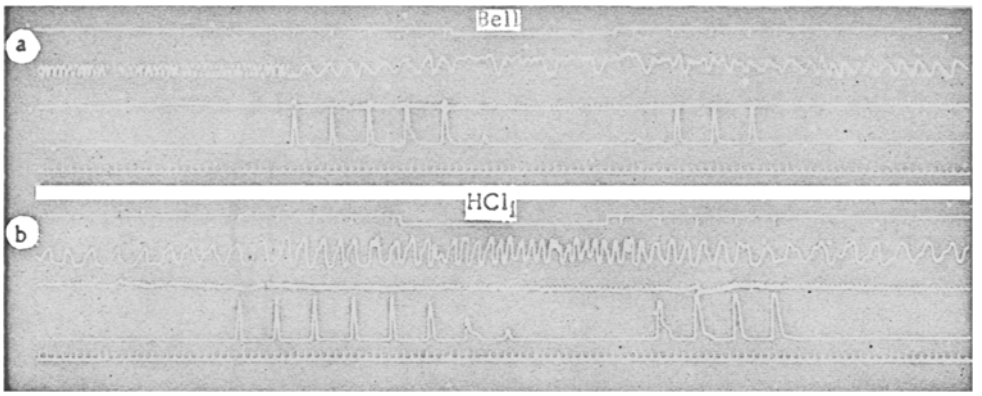

Fig. 2. Effect of rhythmic and extra stimulation on respiration and heart rate. Explanation of tracings (from above down): signals of rhythmic and extra stimulation, respiration, heart beat, reflex movements of the leg, time marker (five seconds).

It is of interest that the respiratory rate again changed during the period of action of the extra stimulus, against a background of rhythmic stimulation. This change consisted, in about half the cases, in a fairly marked retardation of the rate, sometimes with increase in the amplitude of the respiratory movements (see Figure 1: 9, 16). Retardation was particularly pronounced, and most often encountered, with exteroceptive stimulation (Table 1).

TABLE 1

Respiratory Changes During the Action of Extra Stimulation (percentage incidence)

Effect	Interoceptive stimulation	Exteroceptive stimulation	Mean
Retardation	37	63	50
No change	17	13	15
Acceleration	46	24	35

A slight increase in pulse rate appeared when rhythmic stimulation was begun. The superposition of extero- or interoceptive stimulation on a background of rhythmic stimulation usually caused a retardation of heart rate, which in some cases followed a period of acceleration. Acceleration of heart rate again supervened after cessation of the extra stimulus (Figure 2: a, b).

It is evident from the data of Table 2, which shows the percentage incidence in five dogs of inhibitory, stimulatory, and diphasic effects of extra stimulation, that, both for the fore and the hind legs, the most frequently encountered corrective effect of this stimulation on an existing spinal motor reaction is to inhibit the motor reflex, irrespective of whether exteroceptors or interoceptors are stimulated, showing that there is no basic difference between the action of these receptors. This is also shown by Figure 3.

It should, however, be noted that the incidence of inhibition of the motor reflex of the hind leg is higher for interoceptive than for exteroceptive extra stimulation (80%, as compared with 76.4%), whereas the position is reversed for the forelegs (76.5%, as compared with 81%) (see Figure 3: a). We could observe no basic differences between the effects of interoceptive stimulation during rhythmic stimulation of the fore and hind legs. However, here too we found one difference: interoceptive stimulation had less effect on the reflex reaction of the fore than

TABLE 2

Effect of Extra Stimulation On An Existing Spinal Motor Reflex

Exteroceptive stimulation					
hind leg			fore leg		
effect			effect		
inhibitory	reinforcing	diphasic	inhibitory	reinforcing	diphasic
percentage incidence					
82.0	13.8	4.2	82.9	9.5	7.6
80.7	13.2	4.2	82.3	8.0	9.7
71.3	17.7	11.0	78.0	12.4	9.7
69.8	26.6	6.6	–	–	–
78.6	13.8	7.6	–	–	–
76.4	16.4	7.2	81.0	10.0	9.0
Interoceptive stimulation					
hind leg			fore leg		
effect			effect		
inhibitory	reinforcing	diphasic	inhibitory	reinforcing	diphasic
percentage incidence					
72.0	13.0	15.0	78.0	16.5	5.5
83.6	6.4	10.0	77.5	17.5	5.0
87.7	44.9	7.4	73.5	16.5	10.0
77.7	17.7	4.6	–	–	–
79.0	13.0	8.0	–	–	–
80.0	11.0	9.0	76.4	16.8	6.8

of the hind legs. Whereas interoceptive stimulation during rhythmic stimulation of a hind leg had no effect on the spinal motor reflex reaction in 11.6% of the experiments, the corresponding figure for the forelegs was 31.4% (Figure 3: b). The reason for this effect may be that the interoceptive reflex arcs stimulated by us are more closely associated with the hind than with the forelimbs. The greatest incidence of inhibitory effects of exteroceptive stimulation on the motor reflexes of both the fore and the hind legs was found when the stimuli applied were an electric shock to the skin, a skin stimulator, or irrigation of the mouth with hydrochloric acid, i.e., stimuli which had a contact action, while an inhibitory effect was less frequently elicited by stimuli acting at a distance, such as the sound of a bell or metronome, or light. Of the interoceptive stimuli, the most inhibitory was distension of the rectum; the effect of irrigation of the small intestine with hydrochloric acid was smaller, and that of distension of the stomach smaller still.

It appears from the results of our chronic experiments on dogs that extra stimulation emerging from different receptor fields, against a background of an acting spinal motor reflex, exerts a "correcting" action in 85% of the experiments. There is no basic difference between the effects of exteroceptive or interoceptive extra stimulation. In the great majority of experiments an inhibitory effect on the activity of skeletal muscles was seen in both cases.

We cannot say from our experiments whether the vegetative reaction (respiratory and cardiac effects) or the somatic reaction (effect on skeletal muscle activity) appeared first, in response to extra stimulation. Special experiments would be required to provide an answer to this question.

In conclusion we would like to note that, under our experimental conditions, the effects were somewhat more complex than were those reported by authors working under conditions of acute experimentation. Evidently, the higher levels of the central nervous system were involved in the reaction, under our experimental conditions.

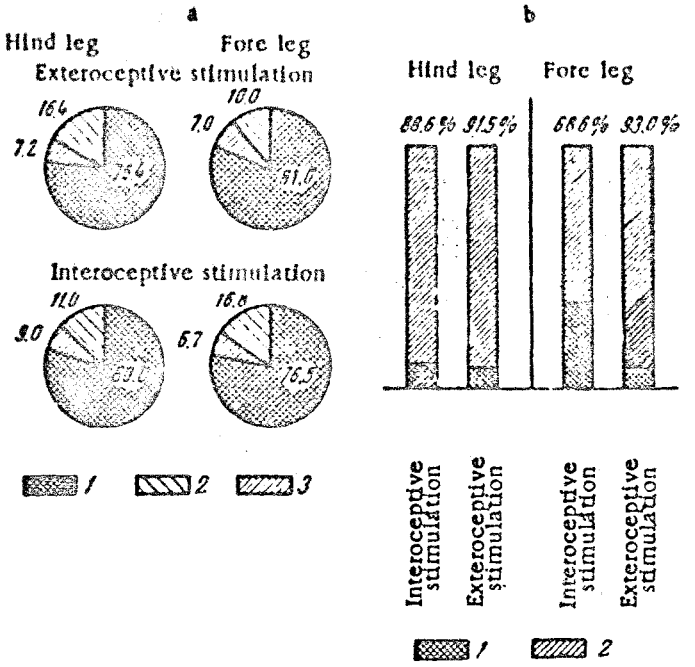

Fig. 3. Effect of extra stimulation on an acting spinal motor reflex: a) effect of exteroceptive and interoceptive stimulation: 1) inhibitory effect; 2) stimulatory effect; 3) diphasic effect; b) presence or absence of effect of extra stimulation: 1) extra stimulation had no effect; 2) extra stimulation had an effect.

SUMMARY

Chronic experiments were performed on dogs. It was demonstrated that stimuli from various fields on the background of a spinal reflex have a "correcting" effect in 85% of the cases. In 80% of cases, this influence is inhibitory, independent of the field from which it was sent. Thus, it may be considered that there is no principal difference in the action of the exteroceptive and interoceptive stimuli on the reflex activity of the skeletal muscles.

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