

THE EFFECT OF DISSECTION OF CORPUS CALLOSUM ON DIFFERENTIATION OF INSTRUMENTAL REFLEXES TO SYMMETRICAL TACTILE STIMULI IN DOGS

Czesława DOBRZECKA and Jerzy KONORSKI

Department of Neurophysiology, Nencki Institute of Experimental Biology
Warszawa, Poland

Abstract. In normal dogs a differentiation task consisting of lifting the left or right foreleg in response to the tactile stimuli administered to the left or right side of the body respectively is very difficult, requiring from 500 to 1,000 trials. On the contrary the same task presented to other dogs after transection of the corpus callosum is mastered immediately after the animals have learned to perform the instrumental movements. These results are explained as being due to the role played by callosal connections in the transfer of the afferent information from one side of the body to the other side.

INTRODUCTION

In the preceding paper of this series (2) it was mentioned that when two rhythmic tactile stimuli (TSs) are administered to either of two symmetrical parts of the trunk and the dog is required to place his right or left foreleg on the feeder in response to the ipsilateral TS, this task is very difficult and is mastered only after 500 to 1,000 trials. On the other hand, when the two TSs are administered to the distal parts of the forelegs, which then perform the instrumental response, the differentiation task is very easy and is accomplished in a few trials.

According to anatomical evidence obtained in experiments on cats (5) and monkeys (6) the cortical areas representing symmetrical parts of the body other than the extremities, are interconnected by the corpus

callosum. Hence, one could conclude that callosal interconnections may hamper the discrimination of TSs administered to symmetrical spots of the body. The present paper is devoted to the testing of this hypothesis.

MATERIAL AND PROCEDURE

The experiments were performed on dogs in a standard sound-proof CR chamber. The procedure was described in detail in the preceding paper (2). Briefly, after the dogs had been habituated to the chamber, rhythmic 1/sec TSs were administered to the anterior parts of the trunk on the left or right side. In the presence of the TS the ipsilateral fore-leg was lifted by the technician and placed on the feeder. Then a bowl with food was moved into the aperture of the feeder by remote control. Nine trials per session separated by ca. 1 min intervals were given, the right and the left TS being administered in randomized order. After a few sessions the dogs learned to perform the trained movements to every presentation of the CS; from that time on they were left alone in the chamber. When the dog performed the correct movement, food was presented. When the movement was incorrect, the TS was immediately discontinued and food was withheld. The no-correction method was then used. The criterion for learning was 5% of errors in the last 10 sessions (90 trials).

The experiments were performed on two groups, each consisting of seven animals. Group I included normal dogs and group II, dogs subjected to transection of the corpus callosum before training. In these dogs the training began 1 week after surgery.

Surgery and anatomy

The operation was performed under Nembutal narcosis (36 mg per kg). A longitudinal incision was made in the midline and the temporal muscles were retracted. The bone covering the fronto-parietal area was removed, the frontal sinuses having been opened and then closed by wax. The transection of the dura matter was semicircular and its free end was fixed with a ligature. The hemispheres were pushed carefully aside with the help of spatules inserted slowly into the sagittal fissure. Then the corpus callosum was severed by suction under visual control. Following this the dura matter, muscles, subcutaneous tissue and skin were sutured in separate layers.

Postmortem examination of the brains showed that in all animals the anterior part of the corpus callosum was completely dissected.

RESULTS

The left leg-right leg differentiation to symmetrical TSs in normal dogs is presented in Table I, and the typical course of training is demonstrated in Fig. 1. Table I shows that the training was exceedingly difficult requiring an average of about 1,000 trials. One of the dogs was unable to reach criterion.

As seen in Fig. 1 the course of training may be divided into three periods.

In the first period the performance of the trained movements to the CSs had to be done with the help of the technician (white parts of the columns). This period lasted for about a dozen sessions (100–150 trials).

In the second period the instrumental responses were performed in every trial, but the animals committed many errors (black parts of the columns). In Fig. 1 (left) the course of training in good learners is presented; in Fig. 1 (right) bad learners are shown. It may be seen that

TABLE I

Differentiation of instrumentae responses to symmetrical TSs in normal dogs

Dog	Total number of trials till criterion	Right TS		Left TS		Total number of errors
		Passive movements	Errors	Passive movements	Errors	
N1	720	60	65	40	73	138
N2	520	63	62	72	51	113
N3	920	36	131	14	123	254
N4	1200	58	127	61	166	293
N5 ^a	1160	53	133	52	166	299
N6	1280	42	82	38	135	217
N7	720	9	115	23	170	285
Average	931.42	45.86	102.14	42.85	123.42	228.43

^aNo criterion reached.

the most frequent strategy demonstrated by the animals in that period was to perform the trained movements with either the left or the right leg only. In this way instead of solving the task correctly, they solved it by the method of irregular feeding, since with such a strategy half of all trials were certainly reinforced. Interestingly enough the dogs were not consistent in this strategy, because after a long phase of performing the trained movement exclusively, or mainly, with one leg, they switched to using the other leg.

In the third period the errors decreased significantly, and then they

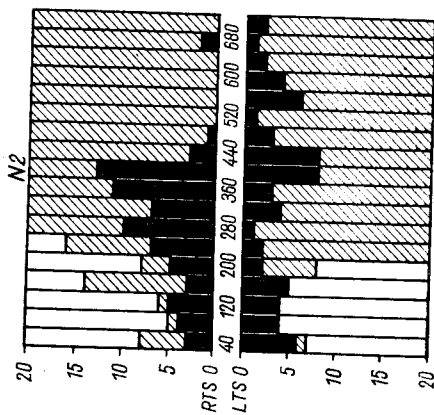
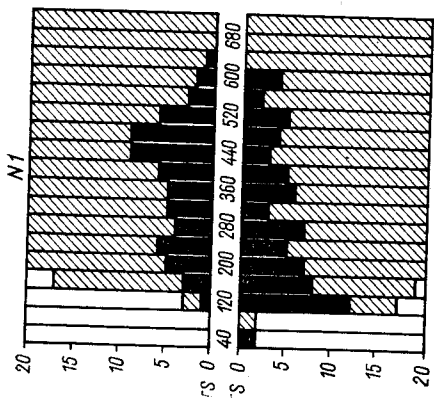
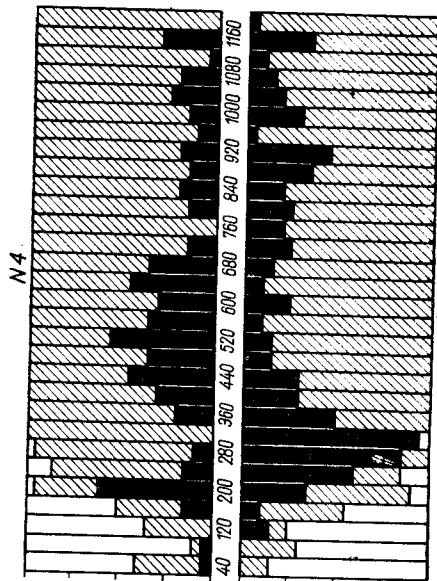
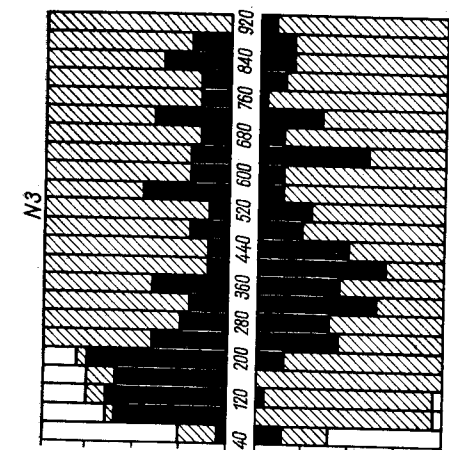


Fig. 1. Normal dogs.

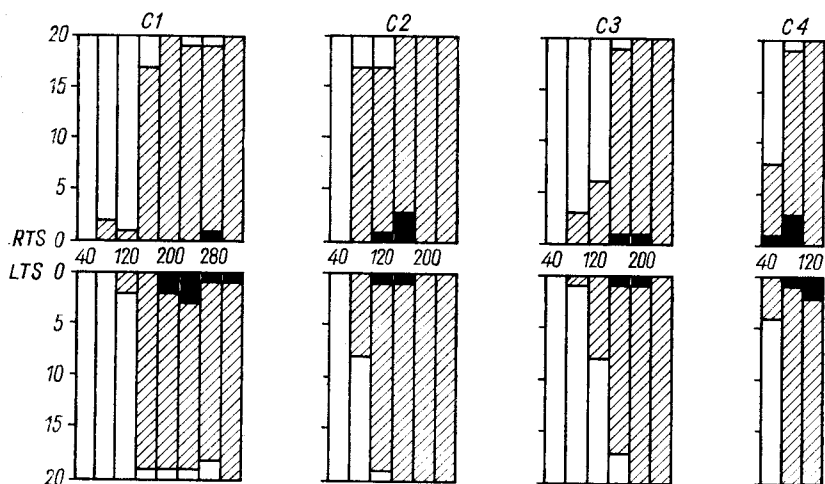


Fig. 2. Callosal dogs.

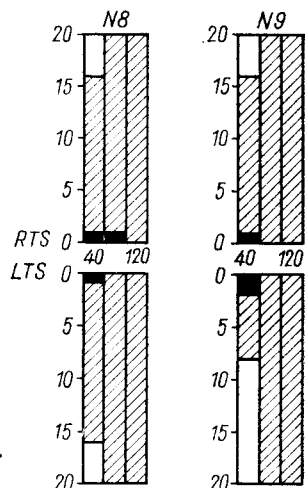


Fig. 3. Normal dogs with TSS administered to corresponding paws.

Fig. 1-3. Each column represents a block of 40 trials. The white parts of the columns denote those trials in which the dog did not perform any movement; the black parts, those trials in which he performed incorrect movements; the hatched parts, those trials in which he performed the correct movements. The columns in the upper row represent trials in which right TSS were given; the columns in the lower row indicate those trials in which left TSS were given. The figures placed between the two rows denote the number of trials from the beginning of training.

were committed almost equally to presentation of either CS. This period ended with the achievement of criterion.

When we compare in Fig. 1 the fields covered with black parts of the columns (errors) with those covered with hatched parts (correct responses), we may notice that above-chance performance was achieved relatively easily, usually not later than by the end of the first half of the training period. This shows that the animals were able in principle to respond correctly before they reached criterion, but that there were some factors which prevented their performing correctly in every trial.

Quite different was the training in callosal dogs (Table II and Fig. 2.) All the dogs solved the problem within about 250 trials and reached criterion almost immediately after mastering the task of placing the forelegs on the feeder. It may be seen that although the first period of training (in which the leg was placed on the feeder by the technician) lasted as long as in normal dogs, as soon as the callosal dogs learned to perform instrumental responses they "knew" which leg to lift. In this respect these animals behaved in exactly the same way as normal animals trained to place the left or right foreleg on the feeder in response to rhythmic TSs administered to the paws (2). The difference was only in the first period of training which was exceedingly short in the latter case (Fig. 3).

TABLE II

Differentiation of instrumental responses to symmetrical TSs in callosal dogs

Dog	Total number of trials till criterion	Right TS		Left TS		Total number of errors
		Passive movements	Errors	Passive movements	Errors	
C1	320	62	1	63	7	8
C2	240	26	4	33	2	6
C3	240	52	2	54	2	4
C4	120	13	4	16	3	7
C5	280	31	6	40	6	12
C6	240	54	1	82	6	7
C7	200	74	3	53	2	5
Average	234.28	44.57	3	48.71	4	7

DISCUSSION

There is a great body of evidence to show that not only are symmetrical parts of particular fields of the cerebral cortex interconnected by callosal fibers, but also that memory traces established in one hemisphere are transferred to some degree by these fibers to the other hemi-

sphere. The most spectacular case of such a transfer has been demonstrated in the visual system (9, 11).

If a given discrimination task is established by presentation of two objects to one eye, it is transferred to the other eye even if the optic chiasma has been transected (8). Moreover, because of this transfer it is impossible to establish two opposing discriminations in opposite eyes (e.g. circle positive vs. cross negative for one eye, and cross negative vs. circle positive for the other). On the other hand, if the corpus callosum has been transected, memory traces established in one hemisphere cannot be transferred to the other hemisphere; and opposite discrimination tasks for each eye are easily mastered.

Interhemispheric transfer of learning in the somatosensory system has also been demonstrated in various types of experiments by Krasnogorskii (7), Bykow (1), Stamm and Sperry (12) and Myers and Hensen (10).

With these ideas in mind let us now try to explain the difficulty of left leg-right leg differentiation to symmetrical TSs in normal dogs and the easiness of this task after callosal transection.

To begin with, it was shown in our earlier study (2) that tactile sensation in dogs (and similarly in cats (4)) is represented mainly in the contralateral SII area. Thus the left TS is directly projected to the right SII area and indirectly replicated through the callosal fibres in the left SII area. As a consequence, when the dog is trained to place the left

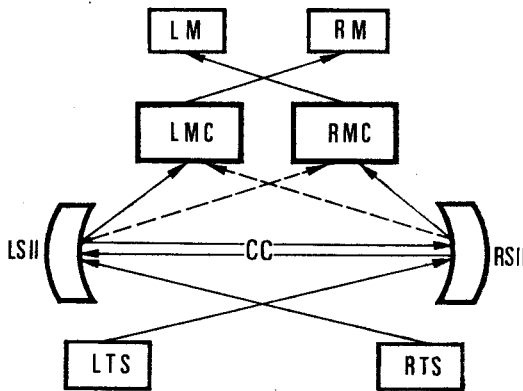


Fig. 4. A block model to explain the difficulty of learning left leg-right leg differentiation to TSs administered to symmetric parts of the body, and its ease after transection of the corpus callosum. LTS, RTS, left and right tactile stimuli; L SII, R SII, left and right SII cortical area. L MC, R MC, motor centers for left and right trained movements (the localization of these centers is not defined). LM, RM, corresponding movements. CC, corpus callosum. Solid-line arrows, "direct" connections; interrupted-line arrows, "indirect" connections mediated by the corpus callosum.

leg on the feeder in response to the left TS, and the right leg to the right TS, he ipso facto learns to perform opposite movements to each of the TSs, because both SII areas are involved in each CR (Fig. 4). Now, if the corpus callosum has been cut such interhemispheric transfer is not possible; and therefore the separate training of each of the two CRs is very easy.

The next question to be asked is why normal dogs are eventually able to learn the left leg-right leg differentiation to symmetrical TSs. The answer is that in the somatosensory system, in contradistinction to the visual system, the symmetrical receptors are not completely equivalent. As a matter of fact, the animal does discriminate stimuli administered to the left side and the right side of the body as may be judged, for instance, by the relative laterality of scratch reflexes. This explains the fact that although dogs reach criterion with great difficulty in the task of left leg-right leg differentiation to two symmetrical TSs, the first signs of differentiation appear much sooner. One can conclude that the animal "knows" which of the two movements he has to perform, but the errors are committed due to some parasitic factors, which handicap correct decision (i.e. the callosal fibers).

To end these considerations we should explain the ease of formation of a left leg-right leg differentiation to TSs administered to the paws of the corresponding limbs. Here at least two factors are in operation. The first is that according to the data of Jones and Powell (6) there are no callosal fibers between the cortical areas representing the paws. Secondly as shown in our earlier paper (3) the instrumental CR elicited by the TS administered to the corresponding paw is facilitated by association U-fibers linking the sensory and motor areas of the same hemisphere. Probably the U-fibers are responsible for the immediate learning of the task of raising the leg touched by the TS; whereas the lack of callosal fibers between the corresponding cortical areas prevents the mutual transfer of TSs administered to the paws.

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Czesława DOBRZECKA and Jerzy KONORSKI, Department of Neurophysiology, Nencki Institute of Experimental Biology, Pasteura 3, 00-973 Warszawa, Poland.