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FUNCTION OF CORPUS CALLOSUM IN CONTRALATERAL TRANSFER OF SOMESTHETIC DISCRIMINATION IN CATS[1]

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Monocularly learned visual discriminations transfer readily to the untrained eye in cats with midsaggital division of the optic chiasma (3). However, if the corpus callosum has also been sectioned, the animals are unable to recognize the patterns with the untrained eye (4) and can only relearn the discriminations at rates similar to the original learning with the first eye (6). These findings appear to demonstrate an important role for the corpus callosum in integrating the two hemispheres in visual learning and memory.

In an attempt to obtain further evidence concerning the function of the callosum we have investigated contralateral transfer from one forepaw to the other of trained tactile discriminations. Cats were trained to push the correct one of two pedals which could be reached only with one forepaw and which the cats could not see, but had to discriminate by touch alone. Transfer to the contralateral paw of roughness, softness, and form discriminations in unoperated cats was compared with that obtained in cats with midsaggital section of the corpus callosum.

METHOD

Animals

Eight cats were used. They were 8 to 12 months old at the start of the experiment and had been reared in the laboratory from the age of approximately 2 months. The corpus callosum was sectioned in four of the cats at least 3 weeks before the beginning of training. With the exception of one cat, *Hrr*, the *S*s had received no previous training. *Hrr*, in which the optic chiasma as well as the callosum was sectioned, had been used in a previous experiment on visual discrimination (6).

Apparatus

Training box. The discrimination box, shown in Figure 1, was designed to permit the cat to reach through a hole to press two test pedals with the right but not the left forepaw, and conversely. The cat was closely confined in the choice chamber. A set of interchangeable sliding screens allowed the cat complete, partial, or no view of the test pedals. A vertical partition inside the chamber helped to prevent the cat's using the wrong paw. The pedals, mounted in a separate box, were pulled out of reach between trials. Duplicate pairs of pedals mounted side by side in the pedal box were used for reversing the right-left placement of correct and incorrect discriminanda. Adjustments could be made so the four pedals had equal strokes and counter-tensions, and the proper height for individual cats. When a pedal was completely depressed, it closed a microswitch which activated electric circuits to release a food pellet after a correct response, or to sound a buzzer after a wrong response. An observation window in the top of the box made it possible to observe the cats while they were working.

The discriminanda could be attached interchangeably to the ends of the pedals. After preliminary tests with discriminations of varying difficulty, three problems were selected that could be learned with a moderate amount of training. In order to reduce generalization and interference effects between the problems, each pair of discriminanda was made distinct in shape or surface characteristics. The following problems were used:

Form. A triangular prism with a 90° edge on top, placed crosswise, versus a flat square block. Both pieces were made of wood and were covered with plastic cloth.

Softness. Three degrees of softness were used: a foam rubber block 2 cm. high, a foam rubber block ½ cm. high mounted on wood, and a wooden block 2 cm. high, all covered with cotton cloth. The two discriminanda selected for each cat are listed in Tables 1 and 2.

Roughness. Two half-cylinders of wood, placed crosswise with rounded surfaces up, one covered with No. 2 sandpaper, the other sanded smooth.

Procedure

Preliminary training. The cat was trained first to press a wood block (2 cm. high), mounted on a pedal directly in front of the choice chamber. At the beginning *S* could view the pedal, but vision was restricted increasingly as training progressed. Toward the end of preliminary training, with vision now excluded entirely, the block was shifted at random to the right and left positions until *S* learned to discriminate between the block and the blank pedal. After this habit had been learned, *S* was trained to do the same with the other forepaw. Except at the start of this introductory training, vision of the pedals by the *S*s was completely excluded.

Experimental training. The training schedule as a rule consisted of six daily sessions per week, with 70 to 120 trials per day. The right-left placement of the

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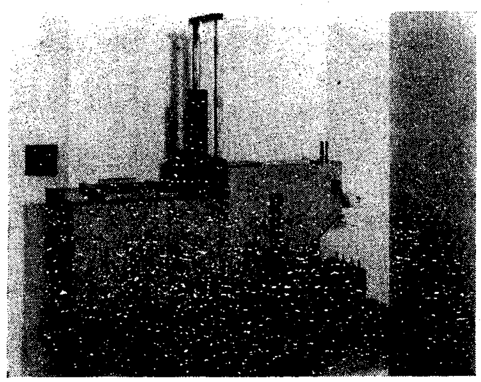

FIG. 1. Tactile discrimination apparatus.

two discriminanda was alternated in accordance with Gellermann's principles (2), except when a position habit developed. When *S* had consistently pressed the right or the left pedal for as many as 10 trials, the correct discriminandum was placed at the nonpreferred side until *S* made two consecutive correct responses. If, then, 4 successive incorrect responses were made, movement of the incorrect pedal was blocked until *S* pressed the correct one. It was found that most cats developed a position habit on beginning a new discrimination. After this had been broken, they tended to form the opposite position habit, after which they would learn to touch both pedals before responding and generally showed no further position preferences.

The *S*s were trained on each discrimination until they responded correctly for at least 50 successive trials or until the response level no longer rose during 200 or more trials. A minimum of six daily training sessions was given for each discrimination with each paw. Retraining with the second paw always started one day after training with the first paw had been terminated. Two days prior to the first transfer trial, *S* received at least 30 trials with the second paw on a previously learned discrimination. The order in which *S*s were trained on successive problems, the paws used for initial training, and the total number of training trials with the first paw are given in Tables 1 and 2.

The apparatus permitted *E* to watch *S*'s paw during the response process, so it was easy to see when the pedals were being selected by touch. That learning was achieved on the basis of touch was evident throughout with a single exception as follows: On the roughness discrimination *Drl* attained an above-chance performance without appearing to feel both pedals, whereupon it was noticed that this cat, being smaller than the other *S*s, was moving sufficiently far back in the chamber to enable it to see the pedals through the hole for the forepaw. Proper precautions were then taken to be certain that *Drl* learned all subsequent discriminations by touch. The other *S*s, when watched through the observation windows, kept their heads above the opaque screen and did not attempt to view the pedals.

The use of auditory and incidental somesthetic cues was prevented by moving the pedal box forward and sideways in a random manner between trials and by attaching the discriminanda to different pedals between successive training sessions. In order to make valid comparisons between the two groups, we attempted to apply similar training procedures and schedules to all cats.

Treatment of Data

The *S*s' responses were recorded in groups of 10 trials. The criterion of learning selected was 17 or more correct responses within two successive groups, provided the performance remained above the .01 probability level during overtraining. The first of these 20 trials was taken as the point at which learning had occurred and where overtraining started.

The degree of contralateral transfer is expressed by the "saving score," which is the ratio of the trials saved in relearning to the trials required in initial learning, stated as a percentage. A negative "saving score" indicates that more trials were required to reach criterion during retraining than during the original training.

The mean percentage of correct responses for the number of trials to criterion with the first paw was computed for training and for retraining. The difference is stated as the "transfer level." Its significance was evaluated by computing the *t* ratio for the difference between proportions of right and wrong responses. A negative "transfer level" signifies that *S*'s performance was lower with the second than with the first paw.

RESULTS

Transfer Tests with Corpus Callosum Intact

Substantial transfer, as expressed by the saving scores listed in Table 1, was evident in all four cats. The saving scores were, with one exception, between 58 per cent and 99 per cent, with a median of 76 per cent. The only exception was *Hnr*'s zero saving score on the form discrimination. This *S* made consistently fewer errors, however, during retraining than during training with the first paw. If one applies the .05 criterion level (15 correct responses in 20 trials) to this performance, 80 trials were required with the first paw, but only 30 with the second, giving a saving score of 62 per cent.

Positive transfer effects were also revealed by the learning curves. The curves for *Jsp*, shown in Figure 2, are representative for this group. When the shift was made to the second paw, the performance level dropped somewhat, but remained considerably above the initial performance with the first paw and reached the final level more rapidly. This was observed for every discrimination which these *S*s learned. The terminal performance levels were approximately equal for both paws at 85 per cent to 100 per cent correct responses.

TABLE 1

Summary of Training Sequence and Results for Unoperated Cats

Subject†	Problem‡	Paw Trained First	Total Trials with First Paw	No. Trials to Reach Criterion: Learn	No. Trials to Reach Criterion: Relearn	Saving Score (%)
Hnr	s₁*	L	680	260	110	58
	r	R	890	360	50	86
	f	L	630	90	90	0
Jsp	r	R	750	340	80	76
	f	L	480	100	30	70
	s₃	R	750	170	10	94
Frn	f	R	600	110	40	64
	s₂	L	450	90	10	89
	r	R	1,250	820	10	99
Gdf	f	L	600	90	20	78
	s₂	R	660	330	120	64

* Negative stimuli.

† The table is arranged according to the order of training of *Ss* and discrimination problems.

‡ Discriminations: s—softness; r—roughness; f—form. The positive stimulus is the softer pedal, the sandpaper surface, or the edge, except where an asterisk (*) indicates that these were the negative stimuli. For softness discrimination the positive and negative stimuli were, respectively: s_1, 2-cm. rubber pad vs. wood; s_2, ½-cm. rubber pad vs. wood; s_3, 2-cm. vs. ½-cm. rubber pad.

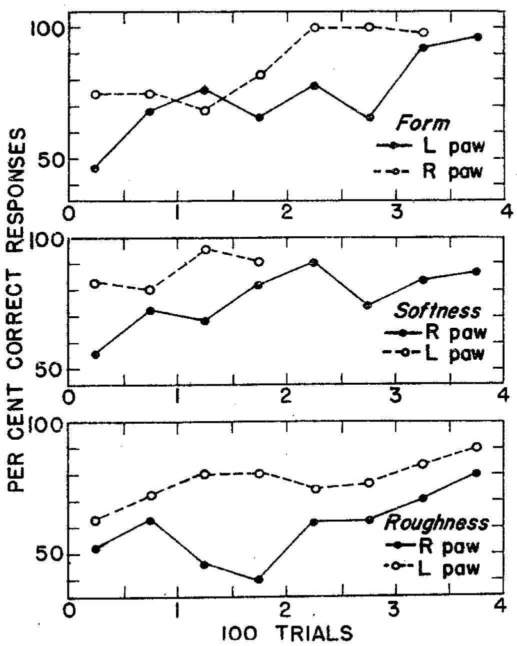

FIG. 2. Learning (solid) and relearning (dotted) curves for three discriminations by *Jsp* with callosum intact. The terminal portions of some of the curves are omitted.

According to the *t* ratios for the transfer levels, the cats gave significantly more correct responses with the second than with the first paw on all tasks, except *Hnr*'s form discrimination. One *t* was slightly above the .01 probability level, while nine ratios fell well beyond this criterion.

Transfer Tests with Corpus Callosum Sectioned

No cat in this group showed consistent transfer, as indicated by the saving scores listed in Table 2. Five saving scores were positive and six were negative, with a group median of −8 per cent. An appreciable positive saving score was obtained only by ***Hrr*** on the roughness problem. This is accounted for by the exceptionally long training with the first paw. ***Hrr*** did not reach criterion with the second paw until trial 260, which is more than twice the highest number of trials needed by any of the unoperated *S*s to attain criterion during retraining.

The lack of transfer in these cats is apparent also from their learning curves. The curves of *Bnj*, shown in Figure 3, are representative for this group. When the shift was made to the second paw, the performance dropped to chance level and the relearning curves then followed the course of the curves for the first paw. The marked agreement between the two curves of each task was evident in the majority of discriminations of the other three cats.

TABLE 2

Summary of Training Sequence and Results for Cats with Sectioned Callosum*

Subject	Problem	Paw Trained First	Total Trials with First Paw	No. Trials to Reach Criterion: Learn	No. Trials to Reach Criterion: Relearn	Saving Score (%)
Bnj	f	R	420	170	210	−23
	s₂	L	510	110	80	+27
	r	R	840	270	380	−41
Crr	f	R	980	300	340	−13
	s₂*	L	500	150	200	−33
	r	R	610	270	200	+26
Drl	s₂	L	600	240	260	− 8
	f	R	500	210	180	+14
Hrr	r	R	1,350	680	260	+62
	f	L	620	350	330	+ 6
	s₂	R	650	180	270	−50

* See footnotes of Table 1.

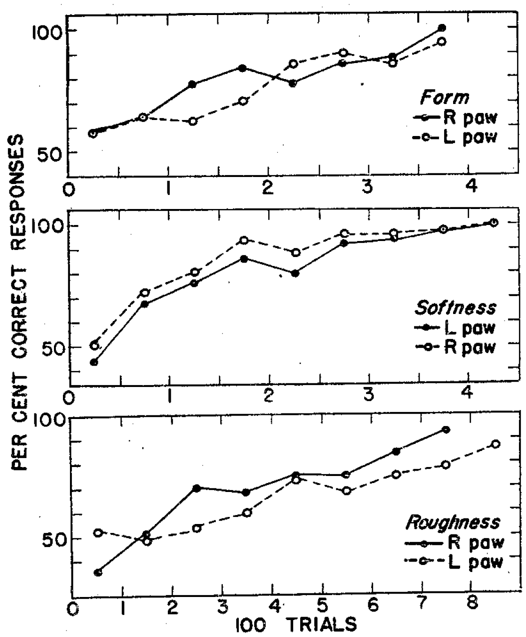

FIG. 3. Learning (solid) and relearning (dotted) curves for three discriminations by *Bnj* with callosum sectioned.

The final performance was also 85 to 100 per cent correct responses. For three cats the right and left curves for each discrimination ended at about the same level, but *Crr* responded better with the left paw during final training on each task, regardless of the paw with which it was first trained.

The transfer levels for this group were consistently low, varying little from the group median of −0.2 per cent and the corresponding *t* ratios did not fall beyond chance, except for *Hrr*'s roughness and *Crr*'s form discrimination. The latter *t* was negative beyond the .01 probability level because *Crr* gave somewhat better than chance responses during training with the first paw and responded below chance for over 250 trials with the second paw.

Comparisons between the Two Groups

The number of training sessions for the three tasks required with the first paw were 6 to 10 for the unoperated and 6 to 11 for the operated group, except for one discrimination in each group which needed longer training. The group medians for the total number of training trials with the first paw were 660 for the unoperated and 610 for the operated *S*s. *Frn* and *Hrr* required exceptionally long training on the roughness discrimination. *Frn* attained the .05 criterion level on this problem after 310 trials, but then responded slightly below the .01 criterion for over 500 trials. This was the first discrimination on which *Hrr* was trained, and *S* did not begin to test the discriminanda until after almost 600 trials, when its learning curve finally rose from chance level.

The unoperated group appeared to learn somewhat faster than the operated group, the respective medians being 170 and 240 trials to criterion. This difference is entirely accounted for in the scores for form discrimination, which required medians of 95 trials for the unoperated and 255 trials for the operated cats. The other two discriminations, however, were learned somewhat more rapidly by the callosum-sectioned cats.

In the performance with the second paw, there was a marked difference between the two groups, with the median number of trials to reach criterion being 260 for the operated, but only 40 for the unoperated group. The difference in the degree of transfer is illustrated in Figure 4.

There was little overlap between the saving scores for the two groups. Only one score of the unoperated *S*s was below 58 per cent, and only one score in the operated group was above 27 per cent, while ten scores in each of the groups were clustered about the respective

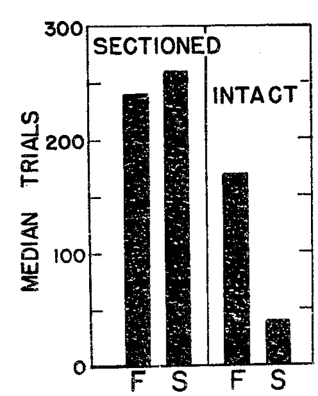

FIG. 4. Median number of trials required to attain criterion for the callosum-sectioned and callosum-intact groups during training with the first paw (F) and retraining with the second paw (S).

medians. For this distribution of scores a chi-square coefficient of 11.6 ($p < .001$) was obtained, further illustrating the significantly higher degree of transfer in the operated cats.

Anatomical Checks

In view of the nature of the results, anatomical checks seemed uncalled for, and the operated cats have been retained for other investigations. On the basis of the results one would infer that the callosum has been successfully sectioned in all cases. Examination of other brains similarly operated has regularly shown the callosum to have been completely sectioned along with the hippocampal commissure and occasional remnants of the fornix on one or, rarely, both sides.

DISCUSSION

Substantial contralateral transfer was evident in all four cats with intact callosum, the saving score averaging 76 per cent. This is a somewhat lower degree of transfer than was obtained for visual discrimination in a previous investigation (3). The lower degree of transfer in the somesthetic discriminations may be related to the use of different motor patterns in shifting from one limb to the other, whereas the motor response remained the same during the visual testing with right and left eye.

In contrast with the unoperated group, no cat with sectioned callosum showed consistent transfer. The distribution of saving scores, which in this group varied between +62 per cent and −50 per cent (with a median of −8 per cent) on different discrimination tasks, is similar to that obtained for interocular transfer in cats with sectioned chiasma and callosum (6). Since the positive and negative scores were of approximately equal magnitude and since the complete learning curves indicated a lack of transfer, it may be concluded that transfer was absent in the callosum-sectioned cats.

As was found for visual discriminations (6), the independent learning curves from the separated hemispheres of the same animal were much more alike in character than were those from different cats. Also for each individual, variations between right and left curves for the same discrimination problem were small compared with the differences between curves for different tasks. These observations suggest that the individual variability in learning tends to be determined to a surprising degree by intrinsic features of brain organization as opposed to adventitious events in the learning process and general situation.

There was some evidence, not well quantified, that the motor learning involved in pushing the pedals in the present study transferred to a higher degree in the normal than in the callosum-sectioned cats. The learning to press a pedal, which took place prior to the discrimination training, required at least seven days with the first paw. Three callosum-sectioned cats needed as much training with the second as with the first paw. By contrast, all unoperated *S*s were able to press the pedal during the first retraining session.

The present findings are in keeping with an earlier report (1) that cutaneous conditioned responses fail to show the usual spread to contralateral homologous areas in dogs in which the corpus callosum has been sectioned. The apparent disagreement with the observation on human patients that stylus maze learning transfers readily from one hand to the other after section of the callosum (5) remains unaccounted for and may reflect a species difference.

SUMMARY

An apparatus was devised in which cats were trained to press with one forepaw the correct one of two pedals which they could not see and had to distinguish on the basis of touch. Four normal cats and four cats with sectioned corpus callosum were trained to make three discriminations involving differences in form, softness, and roughness. After the discriminations had been learned and overtrained with one forepaw, the cat was retrained to make the same discrimination using the other forepaw.

The group of unoperated cats attained the criterion of 17 or more correct responses in 20 consecutive trials after a median of 170 trials with the first paw, and only 40 with the second paw. The medians for the operated group, on the other hand, were 240 trials for the first paw and 260 for the second. The degree of transfer was expressed by saving scores for which the medians were +76 per cent for the

unoperated group and −8 per cent for the group with the callosum sectioned.

It is concluded that in cats, the corpus callosum is essential for the contralateral transfer of somesthetic discriminations from one to the other forepaw.

REFERENCES

1. Bykoff, K. Versuche an Hunden mit Durchschneiden des Corpus Callosum. *Zbl. ges. Neurol. Psychiat.*, 1924, **39**, 199.
2. Gellermann, L. W. Chance orders of alternating stimuli in visual discrimination experiments. *J. genet. Psychol.*, 1933, **42**, 206–208.
3. Myers, R. E. Interocular transfer of pattern discrimination in cats following section of crossed optic fibers. *J. comp. physiol. Psychol.*, 1955, **48**, 470–473.
4. Myers, R. E. The corpus callosum and hemispheric interaction. Ph.D. thesis, Univer. of Chicago, 1955.
5. Smith, K. U. Experimental analysis of the associative mechanisms of the human brain in learning functions. *J. comp. physiol. Psychol.*, 1952, **45**, 66–72.
6. Sperry, R. W., Stamm, J. S., & Miner, Nancy. Relearning tests for interocular transfer following division of optic chiasma and corpus callosum in cats. *J. comp. physiol. Psychol.*, 1956, **49**, 529–533.

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