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MECHANISMS OF INTERHEMISPHERIC TRANSFER OF VISUAL INFORMATION IN RATS

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Abstract. Pattern discrimination learning in functionally hemidecorticate rats leads to formation of memory traces in the intact hemisphere. The interhemispheric transfer (IHT) of such lateralized engrams is more efficient when the untrained eye rather than the trained eye is used during interdepression training (10 trials) preceding the retention test with the contralateral hemisphere, probably because the untrained hemisphere is indispensable for readout in the first case (imperative IHT) but can be completely bypassed in the second case (facultative IHT). Monocular acquisition of a pattern discrimination habit induces a strong primary engram in the contralateral and a weak secondary engram in the ipsilateral hemicortex. The primary trace is further improved with overtraining while the secondary engram is abolished. During interocular transfer, the primary trace is at first read out through commissural fibers while a secondary trace is rapidly transferred to the untrained hemisphere. Pretraining administration of 2-pyrrolidone acetamide (Piracetam, 100 mg/kg) improves the secondary trace acquired during monocular pattern discrimination learning almost to the level of the primary trace, and facilitates the imperative IHT. Uncrossed optic projections and subcortical storage may contribute to IHT of brightness but not of pattern discrimination. It is concluded that IHT of visual engrams is mainly due to transcommissural encoding activated during learning or by transcommissural readout of lateralized traces.

INTRODUCTION

In spite of the application of sophisticated electrophysiological methods, research into the physiological nature of memory is seriously limited by the lack of information about the locus of engram storage. Difficulties of the search for the ubiquitous memory trace summarized twenty years ago by Lashley (19) are still valid today. From this point of view even a 50% reduction in the uncertainty of engram location must be considered as highly desirable. This aim can be simply achieved by the lateralization of memory traces in the split brain preparation (11, 32), which has recently obtained a new experimental dimension of reversibility in the functional split brain studies (3, 4). With the reversible split brain preparation it is possible not only to compare the properties of the trained and untrained hemisphere in the same animal but also to study the further fate of the initially lateralized engrams, the dynamics of their growth or decay, their accessibility to readout and their integration with the rest of the memory system.

In the surgical split brain preparation lateralization of engrams is achieved by directing the sensory input into one hemisphere, while section of commisural pathways prevents spread of the information to the opposite half of the brain. Absence of the engram in the untrained hemisphere is revealed by the absence of savings when contralateral sensory input is employed during retention testing. The functional split brain technique achieves lateralization of engrams in a different manner: during acquisition engram formation is blocked in one hemisphere by Leão's (20) spreading cortical depression. A few hours later the depressed hemisphere recovers and intact commissural pathways are available for interhemispheric transfer of the initially lateralized memory trace. Retention testing under cortical spreading depression (CSD) in the trained hemisphere reveals, however, complete absence of savings for difficult sensory discriminations, operant habits and classically conditioned skeletal reactions (4). The absence of spontaneous interhemispheric transfer under the above conditions indicates that engram location is determined during learning and that the quiescent trace remains stationary. Activation of the trace may initiate its growth, however. Thus a few trials performed with an intact brain after acquisition of the lateralized trace, facilitate subsequent retrieval with the untrained hemisphere (3, 4, 27). It can be surmised that the interdepression training induces information transfer from the trained (transmitting) hemisphere into the untrained (recipient) hemisphere and formation of a secondary engram in the latter.

Although the above results are readily reproducible, they can be interpreted in different ways. The straightforward assumption that unilateral CSD limits engram formation to the nondepressed hemicortex (the memory confinement view) was challenged by Schneider (28, 29) who claimed that learning under unilateral CSD leads to formation of bilateral subcortical engrams (Fig. 1). The absence of savings during retention testing with the contralateral hemisphere is not due to the elimination of a lateralized engram but to a generalization decrement, i.e. to the inability of the brain to recognize the old sensory cues in a new context. Kinesthetic stimuli and sensory neglect caused by the lateralized CSD form, with the specific cues of the learned behavior, a complex conditioned stimulus which changes so drastically during CSD in the contralateral hemisphere that the previous experience becomes meaningless and the task has to be completely relearned. According to this interpretation which resembles in many respects the so called state dependent learning (26), transfer trials help to bridge the gap between the two unilateral CSD states by facilitating the transfer of the conditioned response from one set of stimuli to another via a stimulus generalization process. Already this assumption raises serious doubts since it is intuitively apparent that unilateral CSD resembles contralateral CSD more than either bilateral CSD or an intact brain (33). A serious argument against the generalization decrement hypothesis is the disruption of transfer caused by CSD evoked in the untrained but not in the trained hemisphere shortly after the transfer trial (1, 5) and the dependence of transfer on the intactness of the commissural pathways (22).

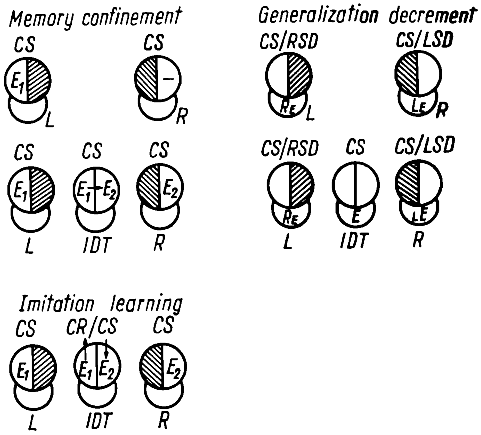

Fig. 1. Schematic illustration of three different interpretations of interhemispheric transfer. CSD indicated by shading. L, learning; IDT, interdepression training; R, relearning. CS, conditional stimulus; CR, conditioned reaction; CS/RSD or CS/LSD combination of specific CS with CSD generated symptoms. E_1, E_2, primary and secondary cortical engrams; R_E, L_E and E, subcortical engrams generated by the CS/RSD, CS/LSD and CS.

Transcommissural information flow is, however, not necessarily postulated by the memory confinement view. The possibility must be taken into the account that during interdepression training the trained hemisphere guides the animal to the correct solution of the task and that the untrained hemisphere simply "observes" this behavior through its own sensory channels (Fig. 1). Such extracerebrally mediated interhemispheric transfer was recently demonstrated in split brain monkeys (16) but is not likely to be important in rats with poorly developed imitation learning.

Some of the ambiguities of the above interpretations can be resolved by detailed analysis of the processes underlying interhemispheric transfer. Combined use of unilateral CSD and unilateral sensory input makes it possible to separate the write-in and readout components of interhemispheric transfer and to specify their respective roles. The present paper summarizes the main results of this research project.

METHOD

Male hooded (Druckray strain) or albino (Wistar) rats aged 2–3 months were trained in a discrimination box to avoid electric shocks by reaching the safe goal compartment through the vertically striped door (CS^+) while the locked horizontally striped door served as CS^-. Footshocks (0.5 ma, 0.5 sec, 1/3 sec) were applied 5 sec after the door of the starting box had been raised, and continued until the animal entered the goal compartment. The intertrial intervals varied from 40 to 80 sec. Position of the vertical and horizontal stripes was changed in a random manner. Training continued until a criterion of 9 correct responses out of 10 (or 12 out of 13) consecutive trials was reached. CSD was elicited by application of a filter paper soaked with 25% KCl on the frontoparietal cortex exposed by a trephine opening 4 mm in diameter made 24 hr before the training. During experiment the trephine holes were protected by a plastic ring (12 mm internal diameter, 10 mm high) which was sutured to the scalp and closed by a threaded cover. Vision was eliminated on one side by covering the eye with an opaque plastic occluder similar to that used by Chorover and Chase (12).

RESULTS

Interhemispheric transfer of lateralized visual engrams

Since in rats most optic nerve fibers cross at the level of the chiasma, monocular acquisition of pattern discrimination is considerably impaired during CSD evoked in the hemisphere ipsilateral to the occluded eye (Fig. 2). The deficit is better expressed in albino rats than in hooded rats and is inversely related to the number of uncrossed optic nerve fibers in the two strains (13, 21, 31). On the contrary, pattern discrimina-

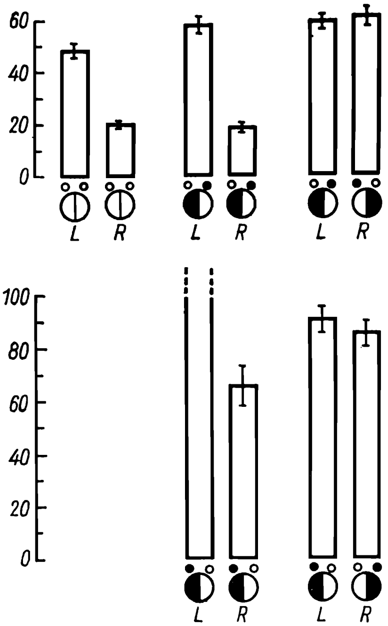

Fig. 2. Pattern discrimination learning (L) and relearning (R) in hooded rats under conditions of binocular or monocular vision with intact brain or under unilateral CSD. Conditions of experiment schematically shown in diagrams (occluded eye and depressed hemisphere black). Ordinate, average number of trials to criterion in groups of 10 animals. Standard error of the mean (SEM) indicated by vertical bars.

tion learning proceeds at almost normal rate when CSD is elicited in the hemisphere contralateral to the closed eye (Fig. 2) (6).

The memory trace formed during monocular pattern discrimination learning with CSD in the hemisphere ipsilateral to the trained eye is highly lateralized. No savings were observed when the same discrimination was relearned with the opposite eye and hemisphere (Fig. 2). Interhemispheric transfer of the lateralized trace can be induced, however, by a limited number ($n = 10$) of interdepression trials during which the animal can employ either the trained or the untrained eye (23, 24). Whereas there is almost no transfer in the first case (direct access to the lateralized engram, Fig. 3) significant savings are observed in the second case (indirect access). It seems that interdepression trials employing the eye contralateral to the lateralized engram are less efficient since they do not require active participation of the untrained hemisphere, which can be completely bypassed during readout of the lateralized memory trace (facultative transfer). On the contrary the eye ipsilateral to the trained hemisphere can get access to the lateralized engram only via commissural pathways passing through the untrained hemisphere, the activation of which becomes an obligatory condition of readout (imperative transfer). At the onset of the imperative transfer, the untrained eye "looks" through the commissural connections into the trained hemicortex (Fig. 4). When the sensory input coincides with the

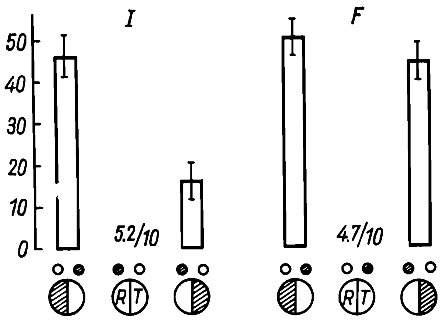

Fig. 3. Imperative (I) or facultative (F) conditions of interhemispheric transfer. Ordinate, average number of trials to criterion. Shading indicates covered eye or depressed hemisphere. R, recipient hemisphere; T, transmitting hemisphere. The numbers indicate ratio of correct responses to all interdepression trials.

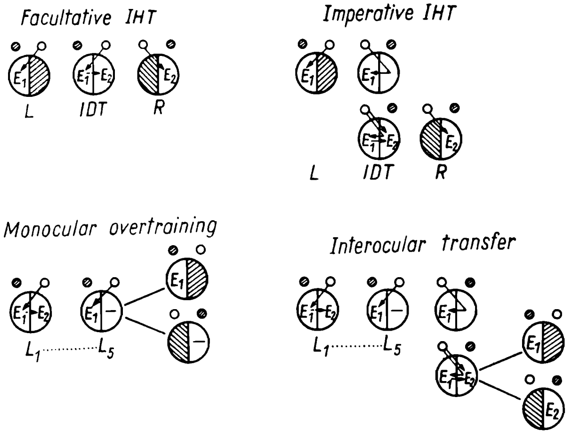

Fig. 4. Schematic illustration of the hypothetical processes underlying interhemispheric transfer (IHT) and interocular transfer. CSD and eye occlusion indicated by shading. L_1–L_5, five successive learning sessions. The arrows indicate the main direction of information flow. Other description as in Fig. 1.

memory content, the readout mechanism triggers not only the appropriate behavioral reaction but initiates also the transcommissural write-in process which transcribes the primary engram into the recipient hemisphere. Formation of the secondary engram is further enhanced by interaction of the transferred information with the direct sensory input to the recipient hemisphere.

The above explanation is supported by the absence of interhemispheric transfer in callosotomized rats (Fig. 5) (24) and is in good agreement with the effect of reversed interdepression trials. In the latter case

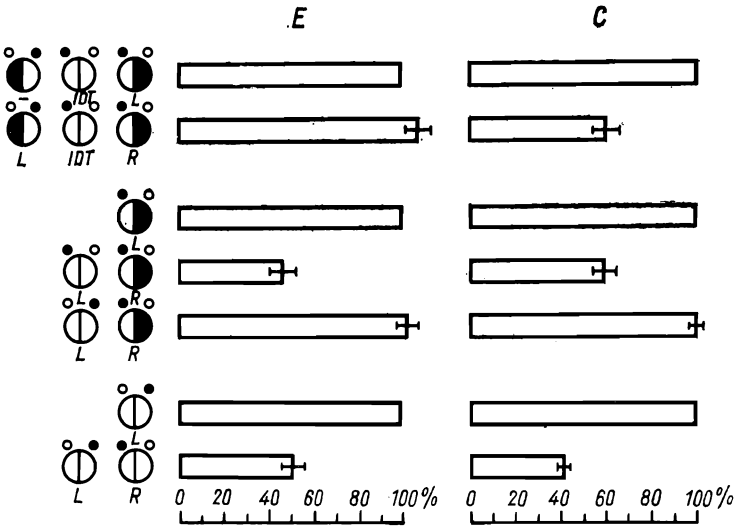

Fig. 5. Interhemispheric and interocular transfer of pattern discrimination learning in normal (C) and callosotomized (E) rats. Above: imperative interhemispheric transfer induced by 10 interdepression trials in hooded rats. Middle: strength of the primary and secondary traces formed during monocular pattern discrimination training in albino rats. Below: interocular transfer of pattern discrimination learning in albino rats. Abscissa: average number of trials to criterion in groups of 10 animals during relearning expressed in percentages of corresponding performance of untrained animals. Denotations as in Fig. 1 and 2.

(8, 25) the animals were trained under unilateral CSD in the usual pattern discrimination (vertical stripes CS^+, horizontal stripes CS^-) and then given with intact brain 10 interdepression trials with reversed meaning of the stimuli (vertical CS^-, horizontal CS^+). Retention of the original discrimination was tested on the next day under CSD in the trained hemisphere. Reversed trials induced interhemispheric transfer when the trained eye but not the untrained eye was used during interdepression training. It seems that the apparent mismatch between the sensory input and memory content activates the interhemispheric write-in mechanism much more than the simple readout obtained with identical interdepression trials. On the other hand transcommissural readout initiated by reversed interdepression training with the untrained eye is not strong enough to activate the primary engram and does not, therefore, induce appreciable interhemispheric transfer.

Interocular transfer

Flow of transcommissural information plays an important role also in the mechanism of interocular transfer. Monocular acquisition of pattern discrimination with intact brain leads to formation of the so called primary trace in the hemisphere contralateral to the trained eye whereas a considerably weaker and less accurate secondary trace is formed in the ipsilateral hemicortex (23). The primary and secondary traces can be separately examined after elimination of one hemisphere by CSD (Fig. 6). Availability of the primary trace during retention testing yields 60% savings, whereas the secondary trace improves relearning only slightly (20% savings). Since the uncrossed optic nerve fibers cannot account for the formation of the secondary trace, the latter is evidently formed by transcommissural write-in during monocular acquisition. With continuing monocular discrimination learning (5 days of to-criterion learning) the primary trace gradually improves while the secondary trace weakens and finally disappears altogether (9). It seems that the continuous use of the primary trace inhibits the interhemispheric transfer and that the unused secondary engram gradually decays.

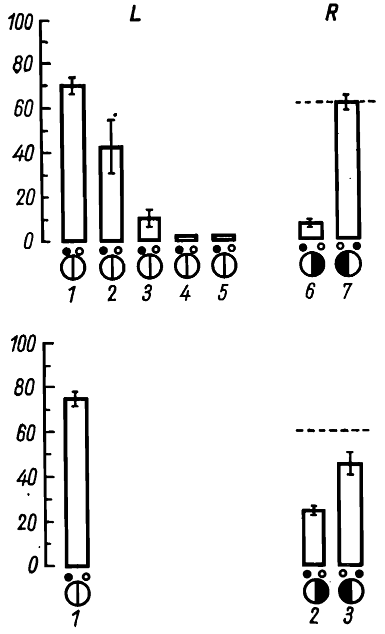

Fig. 6. Primary and secondary engrams formed during monocular acquisition of a pattern discrimination during a single to-criterion learning session (below) or during five to-criterion training sessions (above). The dotted horizontal line indicates the average performance of untrained animals with functional elimination of the hemicortex contralateral to the occluded eye. Ordinate, average number of trials to criterion. Abscissa, days of experiment.

The relative weakness of the secondary trace contrasts with the marked interocular transfer. Pattern discrimination acquired with the right eye can be relearned with the left eye with 90% savings. Control experiments show that this result cannot be explained by readout of the primary engram through the uncrossed optic nerve fibers. It must be assumed, therefore, that the left eye obtains access to the trained left hemisphere through commissural pathways. This transcommissural readout activates transcommisural write-in processes, which together with the sensory information directed into the right hemisphere, facilitate formation of the secondary trace. Even a few trials with the untrained eye induce considerable increment of the secondary engram (Fig. 7).

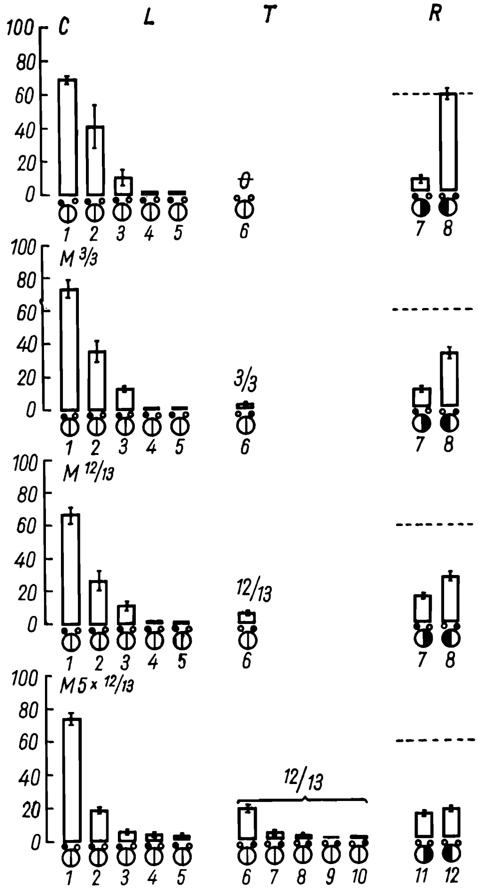

Fig. 7. Effect of limited monocular training with naive eye on lateralization of memory traces formed during monocular overtraining of a horizontal-vertical discrimination habit. L, learning; T, transfer trials; R, retention testing. C, M 3/3, M 12/13 and M 5 × 12/13, control and monocular transfer groups trained to different criteria. Procedures on days 7 and 8 were counterbalanced over those 2 days. Other description as in Fig. 6.

The above experiments closely resemble the results of the preceding section. Absence of the secondary engram in the monocularly overtained animals corresponds to the low efficiency of facultative transfer. Rapid growth of the secondary trace after a few interocular transfer trials is analogous to the more efficient imperative transfer (Fig. 4). That obligatory use of the recipient hemisphere is an essential condition of interhemispheric transfer as demonstrated in an experiment with binocular transfer trials (9), (Fig. 8). Although the animals performed better with both eyes than with the untrained eye alone, no secondary

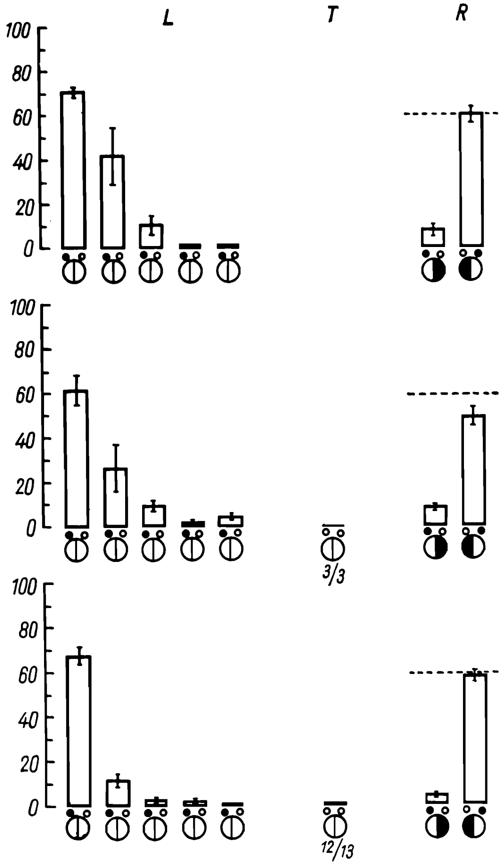

Fig. 8. The effect of limited binocular training on lateralization of memory traces formed during monocular overtraining of a horizontal-vertical discrimination habit. Above, control group; middle and below, 3/3 and 12/13 binocular transfer groups, respectively. Other description as in Fig. 6 and 7.

trace was formed, probably because the easy readout of the primary trace did not trigger interhemispheric write-in and the sensory input to the untrained hemisphere was inadequate for engram formation.

Although no secondary trace is formed during monocular training in albino rats, section of corpus callosum does not interfere with interocular transfer (7,30) which is probably sustained by readout of the primary engram through the remaining commissures (Fig. 5). It appears that callosotomy impairs transcommissural write-in more than transcommissural readout. Recognition of a strong memory trace obviously represents an easier task which can be mastered even by a faulty communication channel inadequate for generation of new engrams.

Pharmacological facilitation of transcommissural write-in

The above experiments led to the assumption (10, 23, 24) that the quality of the secondary trace formed during monocular pattern discrimination learning in the hemisphere ipsilateral to the trained eye is limited by the low transfer capacity of the commissural pathways and by the absence of the correcting effect of direct afferent input. This conclusion had to be modified in the light of experiments with Piracetam (UCB 6215), 2-pyrrolidone acetamid, which specifically facilitates callosal responses and accelerates the consolidation of some engrams (14). The effect of Piracetam on secondary trace formation was studied in rats which received 100 mg/kg of the drug 30 min before the monocular pattern discrimination training was started. Piracetam reduced the number of trials to criterion during acquisition (Fig. 9). Subsequent relearning of the discrimination under unilateral CSD demonstrated that the primary trace remained unchanged, whereas the secondary trace was considerably improved and almost equalled the primary one. Control experiments indicated that Piracetam affects mainly the transcommissural encoding mechanism, since learning with uncrossed optic fibers was not improved.

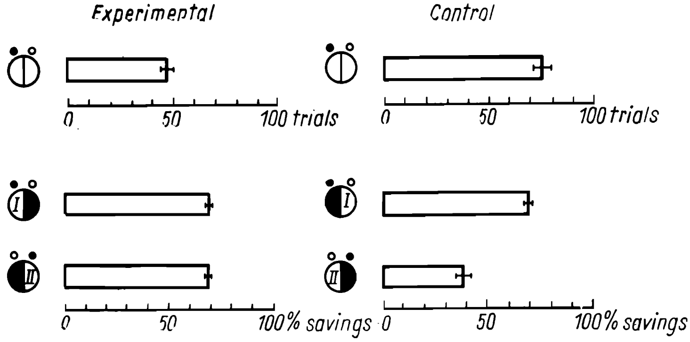

Fig. 9. The effect of Piracetam (100 mg/kg) on pattern discrimination learning (above) and on the strength of the resulting primary (*I*) and secondary (*II*) engrams (below). Abscissa, average number of trials to criterion (above); percentage of savings during relearning compared with uniterally depressed untrained animals (below).

Piracetam did not facilitate interhemispheric transfer of overtrained conditioned reactions. If after 5 days of monocular overtraining of pattern discrimination 10 to 15 trials were applied under the influence of Piracetam with the same eye, the secondary engram was not improved. Similarly Piracetam induced no facilitation of interhemispheric transfer under conditions of facultative use of the recipient hemisphere, probably because at the time of interdepression training the primary trace was already well fixed. Piracetam increased the efficiency of interdepression trials applied without previous unilateral training and significantly improved imperative interhemispheric transfer, obviously again by facilitation of transcommissural encoding (Fig. 10). No changes of retrieval were

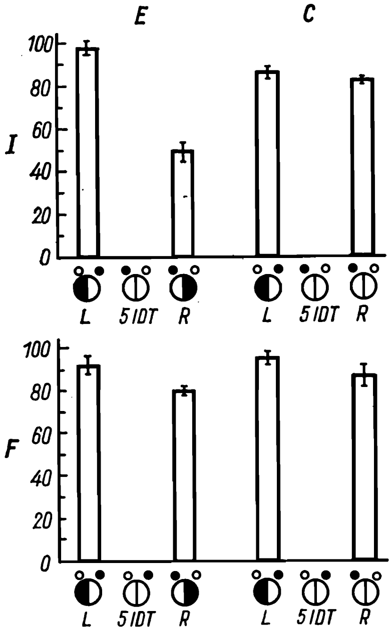

Fig. 10. Facilitation of imperative (I) but not of facultative (F) interhemispheric transfer of pattern discrimination learning by Piracetam (100 mg/kg). E, experimental group; C, control animals. Ordinate, average number of trials to criterion.

found when Piracetam was applied 30 min before retention testing. Facilitation of transcommissural encoding processes was not observed with other drugs (e.g. amphetamin). More experiments are needed to establish the specificity of the Piracetam effects against a wider selection of drugs.

Although the mechanism of the Piracetam effect remains unclear, the possibility of obtaining under conditions of monocular learning, a secondary trace almost equal to the primary engram indicates that the transfer capacity of the commissural pathways can be considerably increased.

Cortical vs. subcortical storage of visual information

The experimental evidence reviewed so far is consistent with ablation studies indicating that visual cortex is indispensable for pattern discrimination learning (18). This is not nocessarily true for the simpler brightness discrimination learning which proceeds according to Thompson (34) at the cortical level while a second set of engrams is simultaneously formed in the posterior thalamus and ventromedial midbrain. Under normal conditions cortical storage is so much more efficient that even prolonged overtraining does not produce an appreciable subcortical trace. It seems that availability of cortical mechanisms inhibits the subcortical storage in a similar manner as overtraining of a monocularly acquired pattern discrimination decreases rather than increases the secondary engram in the indirectly accessible hemisphere (Fig. 4). The relative importance of subcortical engram formation is stressed under conditions of impaired cortical storage.

This assertion was examined in a series of experiments with black--white discrimination learning (6). When the crossed optic pathway was used during lateralized acquisition, retention testing with the opposite eye and hemisphere revealed no savings. Training with the eye contralateral to the depressed hemicortex was so slow that the rats did not reach criterion on day 1, although their performance was significantly above chance level. During the retention test performed with the same eye and hemisphere, criterion was attained on the average within 21 trials. Relearning with the untrained eye and hemisphere was slightly slower (45 trials to criterion) but it was significantly improved in comparison with the first day (Fig. 11). When only the hemicortex, accessible through the uncrossed visual projection, is available during monocular acquisition, formation of the cortical trace is considerably impaired and the relative significance of the subcortical engram is increased. Graded lateralization of brigthness discrimination of increasing difficulty was reported by Hall and Thompson (15) in rats learning and relearning the visual task with alternate hemispheres under conditions of binocular vision.

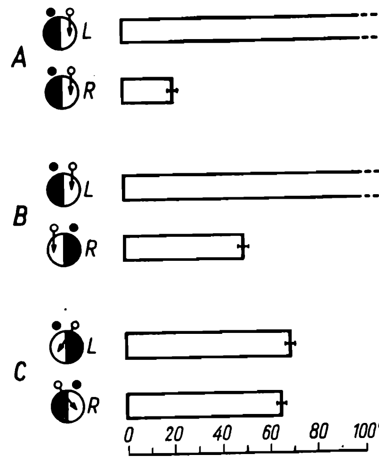

Fig. 11. Brightness discrimination learning in hooded rats using uncrossed (*A*, *B*) or crossed (*C*) visual projections. Retention tested either with same (*A*) or with opposite (*B*, *C*) eye and hemisphere. Abscissa: average number of trials to criterion. Other description as in Fig. 2.

DISCUSSION AND CONCLUSIONS

Combined use of lateralized sensory input and of functional hemidecortication during different stages of the interhemispheric transfer experiments provides strong support for the memory confinement view and rules out some of the alternative explanations. The generalization decrement hypothesis can hardly account for the excellent interocular transfer contrasting with the striking asymmetry of the primary and secondary traces, for the difference between imperative and facultative transfer, for the incomplete lateralization of brightness discrimination learning, or for the absence of interhemispheric transfer of pattern discrimination in callosotomized rats. Extracerebral mediation of transfer is impossible when monocular input is used during interdepression training. Limited importance of observational learning was also demonstrated by the poor results of binocular transfer.

Asymmetry of information storage at the cortical level offers a unique opportunity for investigation of the electrophysiological, chemical and morphological correlates of the formation or activation of engrams. Křivánek et al. (17) found that incorporation of ^{14}C-leucine into proteins of visual cortex contralateral to the trained eye is increased during 1 hr after monocular pattern discrimination training. During monocular pattern discrimination training, difference between cortical evoked potentials elicited by alternating CS^{+} and CS^{-} slowly develops in the hemisphere contralateral to the trained eye (Burešová and Bureš, unpublished results). It is more difficult to find correlates of the interhemispheric transfer process. According to Berlucchi (2) interruption of callosal connections between the visual areas 17, 18 and 19 in cats with split chiasm does not prevent interocular transfer of pattern discrimination, which may employ callosal fibers connecting the suprasylvian and ectosylvian gyri. The contribution of the anterior commisure is highly probable and possible participation of subcortical structures has to be carefully checked.

In spite of the uncertain location of the engram within the trained hemisphere, reversibility of CSD makes it possible to formulate some general properties of the transfer process. The localization of the engram is determined by the input conditions and central states prevailing during learning and during subsequent consolidation. Once formed, the engram remains stationary as long as the neural channels used during acquisition are also employed during retrieval. When the stored information is extracted through other channels, the fixity of the trace is disturbed and the engram is replicated in or expanded to a more advantageously situated locus. In case of lateralized memory traces transcommissural readout represents such a novel route of engram activation. Formation of the transferred trace moves the site of storage closer to the new input against the impulse traffic. More research is needed to prove the general validity of the above principles for other forms of transfer (interocular transfer between crossed and uncrossed projections and different types of cross modal transfer).

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