The role of the superior colliculus in facilitating visual attention and form perception

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ABSTRACT   When interhemispheric transfer in cats is studied from an intact hemisphere to a hemisphere with a suprasylvian cortical lesion, excellent transfer of grating discriminations, but no transfer of forms, is present. Stimuli with global, repetitive features covering a large visual field (gratings), which can be discriminated by preattentive vision, are transferred; perception of stimuli with local features (forms), which require serial exploration using focal vision, is defective in the hemisphere with cortical lesion and transfer is lacking. Influence of the midbrain in facilitating focal vision is shown by the restoration of form discriminations after section of the superior collicular commissure. It is hypothesized that the perceptual defect after lesion in the suprasylvian cortex is due to poor spatial attention and its restoration after midbrain lesion is due to improved function of those collicular cells that mediate orienting of attention.

Recent experiments from this laboratory have broadened considerably our understanding of the interaction between cortex and midbrain in two types of related visual behavior— (*i*) visuomotor orienting and (*ii*) orienting of attention. These experiments have revealed two new phenomena; the first was initially described in 1966 (1) and has been developed further in 1989–1990. The second is the subject of the present paper.

Sprague (1) removed all known visual cortical areas unilaterally in the cat and found a contralateral, homonymous hemianopia that endured for periods up to a year and a half (cortical blindness). However, visual responsiveness in the form of orientation to salient stimuli could be restored to the "blind" field by removal of the superior colliculus contralateral to the cortical lesion or by section of the intertectal commissure. In view of the known participation of the colliculus in orienting, why, after the cortical lesion, is the ipsilateral superior colliculus (which receives input from the hemianopic field) not functioning? Apparently it is functionally depressed, either because of removal of facilitation normally mediated by corticotectal fibers, or because of an influx of cross-tectal inhibition, or both. Lesion of the opposite colliculus or section of the tectal commissure would appear to abolish the inhibitory influx and to restore function to the colliculus ipsilateral to the cortical lesion, and pari passu visual orienting responses reappear in the previously blind visual field. This work has received support from a number of studies by others (2–5).

The neural system responsible for this crossed inhibition was initially assumed to be the pathway connecting the two colliculi, described by Edwards (6). This part of the hypothesis was proved untenable by recent experiments by Wallace *et al.* (7), who demonstrated that restoration of orienting also follows lesion in the contralateral substantia nigra, pars reticulata (SNr), which is known to give rise to a nigrotectal tract (8).

We asked the question whether this tectal commissural system, which is clearly involved in visuomotor orienting, is also concerned with the orienting of attention related to perception (i.e., pattern and form discrimination). If this proved to be the case, it would provide evidence of an additional role of the midbrain in a function (form discrimination) that has been considered wholly cortical and as such would shed considerable light on the neural mechanisms underlying visual perception. The experiments summarized here give a positive answer to that question.

These experiments have used the paradigm of interhemispheric transfer, which studies the movement of the memory trace, or engram, from one area of the brain to another by using a known commissure pathway (corpus callosum; ref. 9). Interhemispheric transfer of a visual discrimination is tested after splitting the optic chiasm so that each eye is connected directly only with the ipsilateral hemisphere. Then a discrimination problem can be trained monocularly, with the other eye occluded; after performance reaches criterion, the trained eye is closed and responses are tested using the opened naive eye. If the cat knows the discrimination with little or no relearning, then transfer of the engram has occurred. Previous work (10) has shown that transfer of shape discriminations can be blocked by removal of the "association" cortex in the suprasylvian gyrus of the hemisphere into which the transfer is being received. When the lesioned hemisphere is used for initial learning, attainment of criterion performance is prolonged but transfer to the intact hemisphere is present (Fig. 1).

This deficit in transfer to the lesioned hemisphere is not due to a general sensory loss in this hemisphere because no such deficit occurs when visual sensory areas 17, 18, and 19 are removed (11). It is also not due to a defect in the transfer mechanism because when gratings rather than forms are used for the learned discrimination, transfer is present at a high level (Fig. 2 *A*, *B*, and *C Upper*). Consideration of these facts has suggested that a lack of transfer of form discriminations is due to a perceptual deficit in the hemisphere with the suprasylvian lesion. Since one type of stimulus (gratings) transfers and one type (shapes or forms) does not, it is possible that the perceptual problem is due to a defect in spatial attention related to the nature of the stimulus. The general strategy of the experiment was as follows.

Learning and transfer of visual discriminations were carried out in a two-choice test box, consisting of a start chamber with a transparent door that opens into an approach alley at the end of which are two top hinged doors carrying the discriminanda (see refs. 10 and 11 for details). The stimuli were square-wave gratings covering the entire panels (14 × 11.5 cm) or forms projected on the lower third of the panels. The positive stimulus was shifted from right to left on a quasi-random sequence. The door carrying the negative stimulus was locked; correction was allowed but without reward (beef spleen). Training was continued until perfor-

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Transfer intact   ◄——— Prolonged learning
left eye   right eye
                                                          } ⊢ After lesions
Normal learning ———► No transfer   1 and 2
left eye   right eye

Normal learning ———► Transfer intact   After lesions
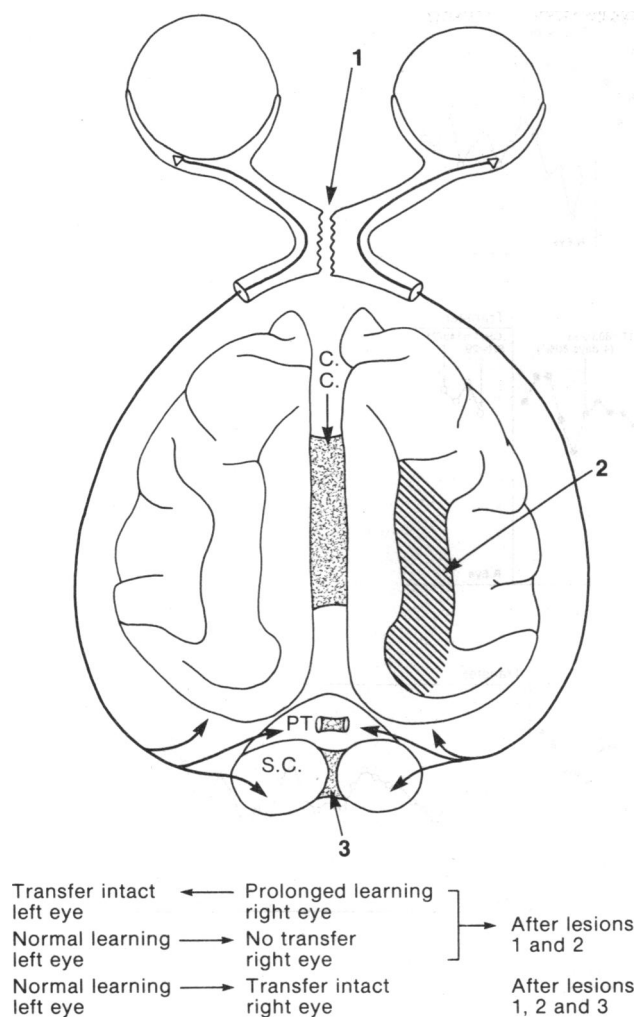left eye   right eye   1, 2 and 3

FIG. 1. Schematic drawing to show retinae, optic nerves and tracts, cerebral cortex, and midbrain of the cat. Lesion 1, split of optic chiasm; lesion 2, removal of suprasylvian cortex; lesion 3, split of commissure of superior colliculi (S.C.). C.C., corpus callosum; PT, pretectum and posterior commissure. Learning and transfer are of two-dimensional forms.

mance reached an arbitrary criterion of 90% or more correct responses for 2 successive days or 80% or more for 4 successive days.

Step I. The cats were shaped in the test apparatus on a simple luminance discrimination, first binocularly and then monocularly.

Step II. The optic chiasm was split (Fig. 1), and the animal was returned to the colony for a 3- to 4-week recovery period. The success of the operation was then checked in the perimetry test for bitemporal hemianopia and good orienting responses using either eye. The animal was retrained in the flux discrimination to adopt the necessary oculomotor strategy when shifting the occluder from eye to eye (i.e., the right eye had a visual field from 0°–45° left, and the left eye had a visual field from 0°–45° right).

Step III. The cortex of the middle suprasylvian gyrus was removed unilaterally (Fig. 1), and after a recovery period, the animal was again tested in perimetry to assure good responses in both visual fields and for retention of the luminance discrimination.

The cat was next trained using the eye on the side of the intact hemisphere, in a grating discrimination, using either vertical vs. horizontal bars or the same bars placed obliquely at 35° and 125° from vertical. After criterion was reached, 5

days of overtraining were given to stabilize performance, following which transfer was tested by occluding the trained eye and exposing the naive eye; training was continued until criterion was reached.

When viewed through the transparent door of the start box, 100 cm away, the gratings had a frequency of 0.87 cycle/degree. It is not known at what point in the approach alley the animals made the discrimination, but it appeared to be much closer than 100 cm. Hence it is likely that the effective spatial frequency was much lower.

The cat was then trained in one of two shape discriminations (△ ▽; + ○) in exactly the same sequence as described above. After learning the shape discriminations using the eye on the side of the intact hemisphere and testing for transfer to the lesioned hemisphere, the cat was returned to the colony for 2 weeks and then tested using each eye for retention of flux, gratings, and form in the original sequence.

Step IV. The commissure of the superior colliculus was split or the colliculus opposite the cortical lesion was ablated (Fig. 1), and after a 3- to 4-week recovery period, the animal was tested monocularly for retention of the previously learned tasks. Then a new grating with the same spatial frequency composition as that used in step III and a new form were learned sequentially using the intact hemisphere and tested for transfer to the hemisphere with the cortical lesion.

Learning and transfer were assessed using three measures comparing performance using the first eye with that using the second eye: (*i*) number of trials/errors in the last two sessions of overtraining with the first eye and the first two sessions with the second eye; (*ii*) total number of trials/errors required to reach the final criterion using each eye; and (*iii*) total number of trials required for performing the first run of correct responses with only one error, with a chance probability of occurrence equal to or lower than 0.01 for each eye (a "significant run"; see refs. 10–12). The second measure is an index of the ability to reach a high level of performance, whereas the third measure estimates the beginning of learning as the first significant deviation above chance performance.

Interhemispheric transfer is usually considered to be perfect when the initial performance on the first one or two blocks of trials using the second eye is equal to the performance on the last two blocks of trials with the first eye during overtraining. More often the result is a successful, but imperfect, transfer in which there is significant savings in trials/errors to reach a significant run and criterion.

All surgical procedures were performed using strict aseptic conditions. Anesthesia was induced with an initial intramuscular injection of ketamine hydrochloride (Ketalar, 15–20 mg/kg), which included 0.02 mg of atropine sulfate. The femoral vein was cannulated and an initial loading dose of 20–50 mg of pentobarbital was given followed by tracheal intubation. Electrocardiogram leads were placed under the skin of the chest to monitor heart rate, and procaine penicillin G (200,000 units) was injected i.m. All subsequent anesthesia was given i.v. as a 1:1 mixture of pentobarbital and thiopental diluted in sterile saline, whenever the anesthetic plane lightened as evidence by increased heart and respiratory rate.

At the completion of the testing, the cats were sacrificed under deep Nembutal anesthesia by intracardiac perfusion of saline followed by 10% formaldehyde in saline. The brains were sectioned and stained with cresyl violet and Mahon–Heidenhain. The lesions were reconstructed using anatomical (13) and physiological (14) criteria. The cortical lesions included areas 5, 7, and 21a and the part of 19 containing the representation of area centralis and upper visual fields. Invasion of cortex in the suprasylvian sulcus was minimal. Areas 17 and 18 were intact, as were laminae A and A_1 of the lateral geniculate complex.

The learning curves of three cats are shown in Fig. 2. In each case the initial learning uses the eye on the side of the
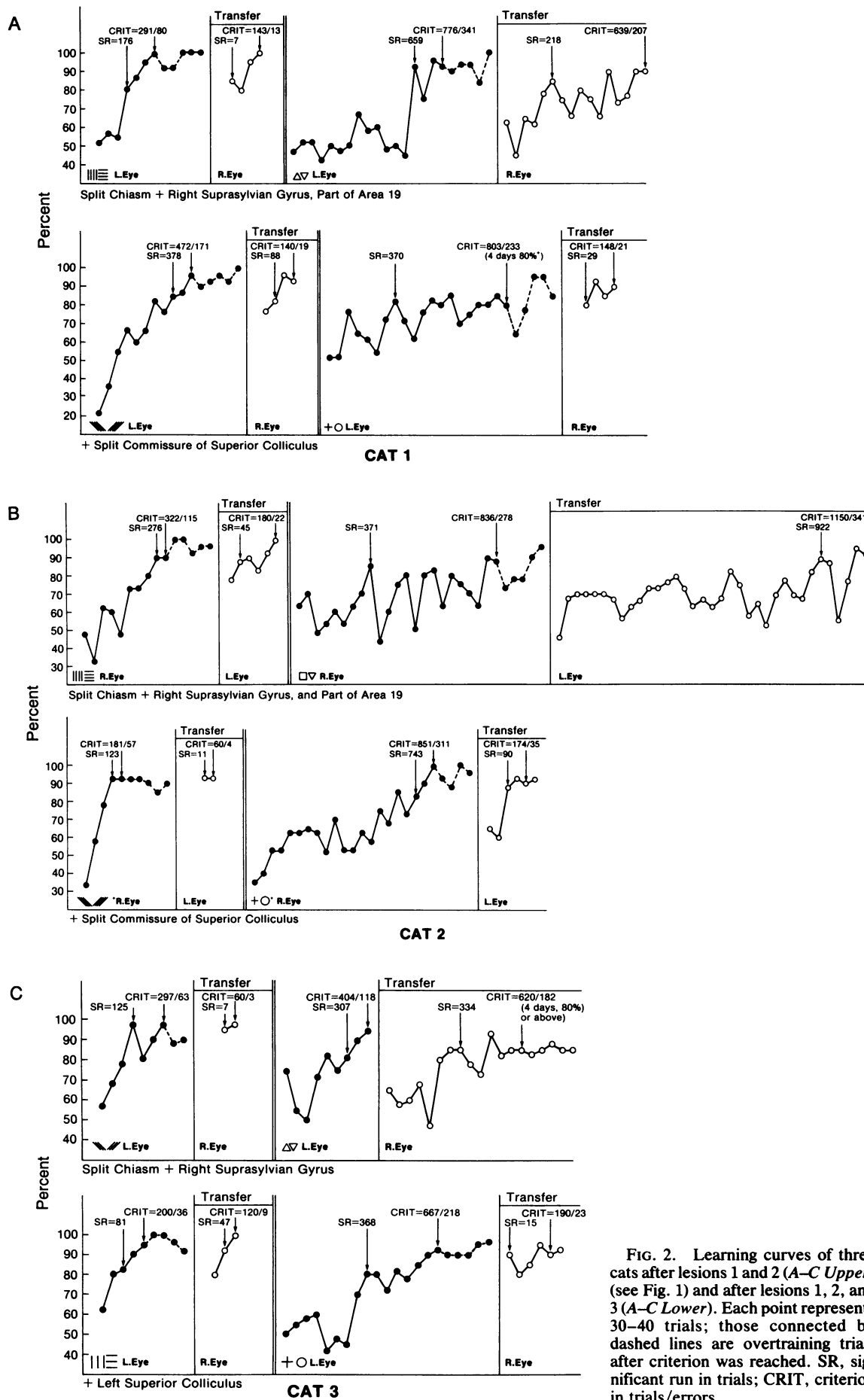
FIG. 2. Learning curves of three cats after lesions 1 and 2 (*A–C Upper*) (see Fig. 1) and after lesions 1, 2, and 3 (*A–C Lower*). Each point represents 30–40 trials; those connected by dashed lines are overtraining trials after criterion was reached. SR, significant run in trials; CRIT, criterion in trials/errors.

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intact hemisphere, and transfer is measured using the eye on the lesioned side of the brain. Fig. 2 *A–C Upper* shows performance after chiasm split and unilateral suprasylvian lesion. In each case, transfer at a high level is present using a grating, but no transfer occurs when shapes are used, and in the case of cats 2 and 3, there was no savings either. Cat 1 showed no transfer in the first five blocks of trials (206 trials) but some savings in the number of trials necessary to reach the first significant run and in the number of errors to reach criterion.

Fig. 2 *A–C Lower* shows comparable testing after the addition of complete split of the tectal commissure in cats 1 and 2 and after an extensive lesion of the superior colliculus (which totally interrupts the commissure) on the side of the brain opposite to the cortical lesion in cat 3. Again there was transfer at a high level of a new grating, but in contrast to performance before midbrain lesion, there was equally good transfer of a new shape discrimination in cats 1 and 3. Cat 2 did not show initial transfer in the first two blocks of trials (64 trials) but showed great savings in reaching criterion. The discrimination task + ○ was used *after* midbrain lesion in each case because previous testing in a group of cats has shown it to be more difficult than △ ▽ based on trials/errors to criterion (15). Prolonged learning of the shape discriminations was found using the eye on the side of cortical lesion in all cases except the triangle test in cat 1 (see ref. 10). That improvement in transfer of form discriminations occurs as a result of practice and therefore would be present without the midbrain lesion has been disproved previously by the results of Berlucchi *et al.* (10).

Thus the same lesion in or between the superior colliculi, which restores visuomotor orienting to a previously hemianopic visual field, a midbrain function, also enhances interhemispheric transfer of form perception, usually considered a wholly cortical function. It is the mechanism of attention that may be chiefly involved in the experiments.

According to this hypothesis, when the engram of the form discrimination is initially established using the intact hemisphere, the match between this engram and a corresponding input using the eye on the cortically lesioned side would be made difficult by an attentional deficit on the latter side, hence the lack of transfer. However when the engram is formed initially on the lesioned side, even though the learning is prolonged due to poor attention, the high level of attention to the discrimination on the intact side would greatly facilitate access to an engram laid down in the lesioned hemisphere, resulting in a high degree of transfer (see Fig. 1). It is important to remember that unilateral inattention, as envisioned here, involves not only a bias against the elaboration of signals received by the lesioned hemisphere but also an opposing bias in favor of reception of signals coming into the intact hemisphere (16–18).

The deficit in attention in the hemisphere with the suprasylvian lesion is not solely the result of a malfunctioning cortical mechanism but is due also to the effect of this lesion on neurons lying on the intermediate and deep laminae of the ipsilateral superior colliculus (5, 19, 20). These collicular cells give rise to the tecto-oculomotor and tecto-reticular-spinal pathways, which control and direct orienting of the head and eyes (21–23), and their firing is gaited by inhibitory input from the substantia nigra, pars reticulata in both cat and monkey. It has been demonstrated in the cat that many of these tectoreticular cells give an enhanced discharge to unusual or significant stimuli (24–26), a relationship probably related to the attentional state. It is highly likely that the same holds true for all mammals. The excitability of this subset of collicular cells is depressed by the cortical lesion and inhibited by the nigrotectal path, with the result that in this case directed spatial attention is comprised in the hemisphere with the cortical lesion. Severing the inhibitory nigrotectal fibers

by splitting the tectal commissure or lesioning the opposite superior colliculus would redress the imbalance of orienting mechanisms of the two colliculi and restore the function of the depressed tectal cells that normally control selective attention.

The results reported here on the differential transfer of grating and form discriminations into a lesioned hemisphere suggest that visual perception in cats, like that in humans, operates in two distinct modes. Julesz (27) has used the term "preattentive" vision to describe the detection and discrimination of certain stimuli (simple textures) rapidly and without scrutiny, in contrast to those stimuli that require serial exploration and focal attention to discriminate ("attentive" vision). Posner and Presti (28) have made a similar distinction between the "automatic" processing, which rapidly leads to detection of certain stimuli, and the "effortful" computations requiring time to discriminate more complex stimuli. Those concepts are in keeping with the hypothesis put forward here that stimuli with global, repetitive features, such as gratings, can be distinguished and recognized rapidly without scrutiny or scanning using the preattentive or automatic mode. In contrast, stimuli differing in local features, such as forms, require foveation, serial exploration, boundary tracing, and focal or effortful attention. Thus, failure of transfer of form discriminations to the hemisphere with the suprasylvian lesion may well be due to a defect in attentive vision.

This defect is likely that of "orienting of attention," or in other words the movement of peripheral or central attentional mechanisms toward the target. Orienting of attention is usually followed by eye movements to foveate and serially explore or scan the target in order to recognize and identify the local features of the stimuli. Thus a defect in some aspect of orienting would render it difficult for the animal to link the form stimuli with the appropriate discriminative response. The involvement of the superior colliculus and its interaction with the cortex in the orienting of attention have been previously pointed out by Posner and colleagues (29–32).

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