

Two-cue learning by brain-damaged cats

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Thirty-seven intact cats, 20 with lesions in posterior association cortex, 8 with ablations of auditory and 9 with ablations of visual projection cortex learned to approach a compound stimulus, noise plus lights, for food. Two different procedures investigated whether one or both elements had come to control the cats' behavior. When the noise or light were presented singly, the group with auditory cortex damage was more successful on light trials; the other groups responded more frequently to noise. When noise and light were opposed by simultaneous presentation at different loci, the cats with injuries to auditory cortex preferred the visual stimulus. The other groups responded more frequently to noise. Lesions in the auditory cortex appear to reduce attention to discriminable acoustic signals, and to reverse cats' ordinarily strong preference for auditory over visual cues. This result is consonant with views that postulate nonsensory functions for projection cortices. We speculate that similar results were not obtained from the cats with damage to visual cortex because of a ceiling effect. Removal of posterior association cortex had no discernible effect upon performance in this experiment unless the lesion included inferior temporal cortex. Thus the idea that the extramarginal cortex is critical for intermodality learning in a general sense was not supported.

If an animal is conditioned to a compound stimulus consisting of strong (more salient) and weak (less salient) components, later tests with each of the components presented alone show that conditioning occurred predominantly to the strong element and that little or nothing was learned about the weak stimulus. This phenomenon, which Pavlov (1927) termed overshadowing, occurs under conditions in which the weaker stimulus is clearly discriminable and adequate for conditioning when used on its own. Thus, it is the relative salience rather than the absolute intensity of the stimulus elements that determines the degree to which one element overshadows the other.

The relative salience of different stimuli seems to vary from one species to another even without variations in the physical characteristics of the stimuli. Presumably, these differences in the functional significance of various sensory modalities in different species reflect underlying differences in neural organization (Diamond, 1967; Diamond & Hall, 1969; Warren, 1973). For example, the auditory projection cortex in cats is quite extensive (Neff & Diamond, 1958; Woolsey, 1960), and audition seems to be the predominant sensory mode in

terms of behavioral control. Diamond and his colleagues (cf. Diamond, 1967) demonstrated this in several previous experiments. They found that auditory cues overshadowed visual cues, even when both cues were equally valid predictors of reinforcement and even when the visual cue appeared to be more conspicuous to the experimenter. Ablation of the auditory cortex reversed this overshadowing effect. However, the manner in which the cortical lesion produced its behavioral effect is not entirely clear. Such a result might be obtained for any of several reasons, including disruption of the animals ability to perceive or attend to the auditory cue, to associate the cue with reinforcement, or to integrate the auditory cue with other stimuli in the test situation so that the appropriate response could occur.

Since the overshadowing effect implies a dynamic interaction between equally relevant but redundant stimulus elements, it figures prominently in contemporary learning theory. For the same reason, we felt that it might offer a particularly effective way to check some of our current notions about the relative roles of primary sensory and association cortex. As Mackintosh (1974) points out, the overshadowing data refute older views "that animals attend to only one stimulus at a time . . . or that learning proceeds independently about all available stimuli." Two prominent contemporary theories hold that overshadowing results from selective attention (Mackintosh, 1975) or from limitations in the associability of the stimulus elements with the reinforcer (Rescorla & Wagner, 1972). Therefore, ablation of

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primary sensory or association cortex might be expected to disrupt overshadowing to the extent that these cortical areas are involved in the perception of or attention to one or both elements of the stimulus compound or the associability of these elements with one another or with reinforcement.

Historically, the function of the sensory neocortex has been thought to be the sensation and perception of stimuli within the associated sensory modality. The function of the "silent" association cortex, on the other hand, has been thought to include the integration of the perceived sensations from several modalities, the association of one or more of these perceived stimuli with specific behavioral outcomes, and/or selective attention to the various sensory modalities. This conception of association cortex function received support from demonstrations that the association cortex of cats under chloralose anesthesia is activated in an equivalent and nonspecific way by visual, somatosensory, and auditory stimulation (Thompson, Johnson, & Hoopes, 1963). The amplitude of these "association responses" was strongly influenced by the behavioral state of the animal. Furthermore, cats with lesions in the association cortex failed to show sensory preconditioning between auditory and visual cues (Thompson & Kramer, 1965). These authors argued that their results support the hypothesis that association cortex plays a critical role in attentional aspects of behavior.

Several authors have recently challenged the belief that the primary sensory projection cortex is concerned solely with the analysis of the physical characteristics of the specific sensory stimuli within that modality. For example, Diamond and Hall (1969) proposed that sensory cortex mediates integrative functions in addition to those traditionally ascribed to projection cortex. Their views appear to have merit, certainly in respect to attentional processes. Cats with extensive destruction of the primary visual cortex can discriminate a circle and a triangle, although this discrimination is far less efficient than that of controls. The severity of the deficit in such cats is exacerbated by training with irrelevant variations in visual dimensions other than shape; it is as if the visually decorticated cats had trouble in maintaining attention to the relevant dimension in the face of distracting cues (Cornwell, Warren, & Nonneman, 1976). In addition, Ravizza and Belmore (in press) have suggested that the auditory cortex is more involved with processes of spatial and sequential memory and with the temporal aspects of hearing than with the conscious perception of sound per se.

Before the present study could be conducted, it was necessary to empirically determine the salience of the auditory and visual elements of the compound stimulus for normal cats. Thus, in several prior experiments in this laboratory, cats were trained in the Nencki test situation (NTS; Divac, 1972) to approach a compound stimulus consisting of a low-intensity white noise and bright flashing lights. Under these conditions, the audi-

tory and visual cues were approximately equal in salience, and normal cats responded appropriately to both cues when they were presented on single-cue tests (Barrett, Nonneman, Stratton, & Warren, Note 1). This pilot work was necessary because the degree of overshadowing of one cue by another in a compound stimulus depends on the relative salience of the individual elements. There is little or no overshadowing if the two cues are equally discriminable (Pavlov, 1927; Mackintosh, 1974, 1975). Salience or discriminability of cues is typically measured by the rate at which animals learn with each cue separately. Thus, the salience of the two cues of the compound were equated by adjusting the cues until equivalent learning rates were obtained with each.

The observation that normal cats can associate appropriate responses with both elements of the compound stimulus afforded an opportunity to test two hypotheses concerning the functions of sensory and association cortex. We expected that cats with near-total ablations of auditory or visual projection cortex would ignore perceptible cues in the affected modality, and fail to respond at better than chance levels to this stimulus on single-cue tests. In contrast, we expected ablations of association cortex to interfere with intermodality associations. Specifically, we thought that cats deprived of much of the association cortex would be inferior to controls in learning about both cues in the compound situation.

METHOD

Subjects

Seventy-four cats with identical histories of testing on visual performance tasks (Cornwell, Overman, Levitsky, Shipley, & Lezynski, 1976; Cornwell, Warren, & Nonneman, 1976) served as subjects in this experiment. The prior testing consisted of preoperative acquisition and postoperative retention of a shape discrimination with variable numbers of irrelevant cues plus postoperative tests on size, brightness, and depth discrimination tasks. There were 37 intact controls (Group C); the experimental groups consisted of cats with lesions in the marginal and splenial gyri (Group MS, $N = 9$), in the auditory cortex (Group AC, $N = 8$), and in the posterior association cortex (Group EM2, $N = 9$, Group EM3, $N = 11$).

Apparatus

The NTS has been described and illustrated by Divac (1972). Briefly, the NTS is a rectangular chamber, containing a central cage that can be raised and lowered, and two feeders, opposite each other on the short sides of the rectangle. The front wall is a vertically sliding door equipped with a half-silvered mirror covered on the inner surface with window screening. This allows access to the interior of the apparatus when raised and unobtrusive observation of the subject when lowered. Small (approximately 65-mm) cubes of pork kidney are dispensed at the feeders when the experimenter activates a Davis Universal Feeder. A speaker is mounted just above each feeder. In this experiment, the auditory cue presented through these speakers was a 68-dB re 20 $\mu\text{N}/\text{m}^2$ white noise (measured from the center of the apparatus with the door lowered). This cue was produced against a 53-dB re 20 $\mu\text{N}/\text{m}^2$ background noise produced by the air handling system. A row of three 12-V bulbs, 3.2 cm apart, lies just above the speaker. The side lamps flashed on and off

4 times/sec; the center light was on constantly. The intensity of the signal lights was 3.0 log fL. The white panel on which the lights were mounted reflected 2.0 log fL when the signal lights were on and 0.5 log fL when illuminated only by the 7-W house-light.

Testing Procedure

The subjects were first shaped to tolerate restraint in the cage and to approach either feeder when released. All approaches to a feeder were reinforced, and no signals were presented in this stage of training, which continued until the cat made consistently prompt responses. Formal training consisted of three phases:

Discrimination training. The cats were trained with differential reinforcement to go to the feeder signaled by the noise and light compound. The two stimuli were presented at one locus while the cat was in the cage. After 5 sec, the subject was released and responded by approaching within 12 cm of either feeder. At this time, the experimenter turned off the noise and light. Responses to the correct feeder were reinforced immediately. Twenty-five noncorrection trials were given at intervals of about 30 sec in each daily session; the learning criterion was 21 correct responses in 25 trials within a single session.

Probe tests. A probe test was a trial on which only noise or only light was presented without reinforcement. Six 25-trial sessions were given in which the noise-plus-light compound was presented and differentially reinforced on 17 trials, as in discrimination learning. Light alone and noise alone were each given on four of the remaining eight trials in the session. Over six sessions, each cat received 24 single-cue trials in extinction with light and 24 with noise.

Opposition tests. An opposition test was a nonreinforced trial with the auditory stimulus at one feeder and the visual stimulus at the other. On 17 of 25 trials in a session, the compound stimulus was given and differentially reinforced, as in the two preceding stages; on 8 trials, the light and noise were presented at different feeders and responses to neither were reinforced. Four sessions yielded a total of 32 opposition tests.

Surgery and Histology

Reconstructions of the lesions in the cats of Groups MS, EM2, and EM3 have been published, together with a description of surgical and evoked potential methods (Cornwell et al., 1976; Cornwell, Warren, & Nonneman, 1976; Hara, Cornwell, Warren, & Webster, 1974). In brief, the lesions were made by gentle subpial suction under aseptic conditions. The lesions of Group MS destroyed most of the cortex of the marginal, posterior marginal, and splenial gyri in an effort to remove areas 17, 18, and 19 as completely as possible. The anterior marginal

association area was deliberately spared. The lesions of Group EM2 removed the cortex of the middle and posterior suprasylvian gyri and the anterior marginal association area. The lesions of Group EM3 were intended to include all of the cortex removed in EM2 cases plus the inferior temporal cortex and the caudal bank of the posterior ectosylvian gyrus. In all extramarginal decortications, great care was taken to preserve the blood supply to the marginal gyrus and to avoid damage to the optic radiations. The procedures followed with Group AC were essentially the same as those used to remove the extramarginal association cortex. The auditory cortex lesions were intended to destroy the anterior, middle, and posterior ectosylvian, and the anterior and posterior sylvian gyri. AI, AII, Ep, and the temporal and insular auditory cortex were ablated, while AIII and most of the suprasylvian fringe were deliberately spared (Woolsey, 1960). Auditory and visual evoked potentials were taken from the animals of Group AC at surgery and at sacrifice to verify that the auditory cortex lesion was complete and that the integrity of the geniculostriate system had not been compromised.

RESULTS

Anatomy and Electrophysiology

Since the anatomical and electrophysiological findings for Groups EM2, EM3, and MS have been published (Cornwell et al., 1976; Cornwell, Warren, & Nonneman, 1976), only surface reconstructions of the largest and smallest lesions in these groups are presented in Figure 1.

The evoked potentials recorded just after surgery and at sacrifice revealed the same picture. Several cats in Group AC had tiny patches of cortex preserved within the auditory projection which could be seen in the brain sections. These islands responded to acoustic stimuli with low-amplitude potentials ($<75 \mu\text{V}$), much smaller than those evoked from the same area in subjects from Groups EM2, EM3, and MS ($>100 \mu\text{V}$), suggesting that the islands had been denervated to a considerable extent by undercutting. There was no obvious correlation between the presence of these cortical islands and the behavior of the cats. None of the cats in Group AC showed serious bilateral abnormalities in visually evoked responses. The most severely affected AC case suffered a

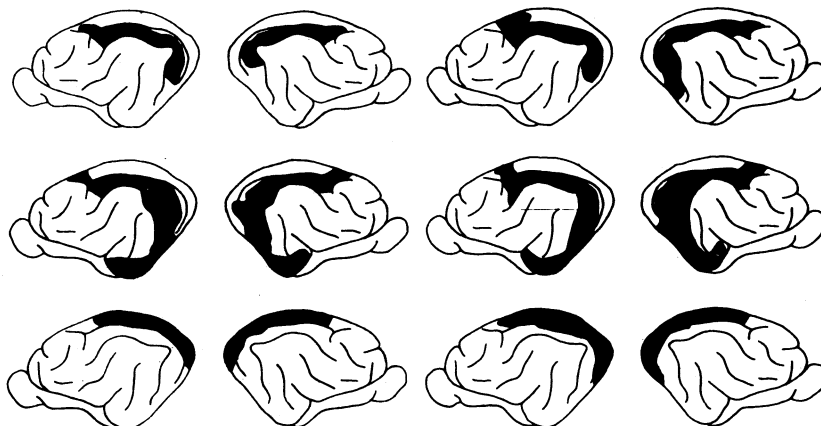


Figure 1. Reconstructions of the smallest (left) and largest (right) lesions in Groups EM2 (top), EM3 (middle), and MS (bottom).

50% reduction in evoked potential amplitude in the posterior lateral sulcus on one side. Visual evoked potentials were normal on its contralateral hemisphere.

The reconstruction of the cortical lesion and coronal sections through the thalamus for a representative case from Group AC are presented in Figure 2. Severe bilateral degeneration was apparent in the main body of the medial geniculate nucleus (MGN) in all of the AC cats, and all suffered mild to moderate degenerative changes in posterior MGN on one or both sides; there was variable, subtotal in some cases, degeneration elsewhere in MGN. Moderate degeneration in pulvinar and lateralis posterior was seen in all cats.

Behavior

One's clearest impression on inspecting the results summarized in Table 1 is that Groups EM2, EM3, and MS differed very little from the controls, whereas Group AC's performance deviated sharply from the other four groups.

An analysis of variance on the number of trials needed to learn the initial discrimination with two cues revealed a significant Groups effect, $F(4,69) = 2.72$, $p < .05$. Subsequent paired-comparisons showed that this effect was caused by the relatively poor performance of the group with the largest extramarginal lesion. Group EM3 required significantly more trials than Group C, the intact controls, $t(48) = 2.19$, $p < .05$. No other paired-comparisons reached statistical significance.

An analysis of variance on the probe test scores showed that the effect of modality (auditory vs. visual) was significant, $F(1,138) = 25.17$, $p < .01$, as was the Modality by Groups interaction, $F(4,138) = 3.17$, $p < .05$. The Groups effect was not significant. A series of paired-comparisons provides an explanation both for the significant Modality main effect and the Modality by Groups interaction. None of the groups differed from one another in number of approaches to light, but Group AC responded significantly less often to noise than any other group [AC vs. C, $t(45) = 3.57$, $p < .01$; AC vs. EM2, $t(17) = 2.91$, $p < .05$; AC vs. EM3, $t(19) = 2.35$, $p < .05$; AC vs. MS, $t(17) = 2.76$, $p < .05$].

Since the total number of responses was necessarily the same for all subjects on the opposition tests (i.e., responses to noise and light were not independent), the data was evaluated by analysis of the number of responses to the acoustic signal. Analysis of variance revealed a significant Groups effect, $F(4,69) = 5.62$, $p < .01$. This effect resulted primarily from the fact that Group AC chose noise significantly less often (and light more often) than any other group [AC vs. C, $t(45) = 4.44$, $p < .01$; AC vs. EM2, $t(17) = 5.11$, $p < .01$; AC vs. EM3, $t(19) = 5.03$, $p < .01$; AC vs. MS, $t(17) = 3.62$, $p < .01$]. There were no other significant intergroup comparisons.

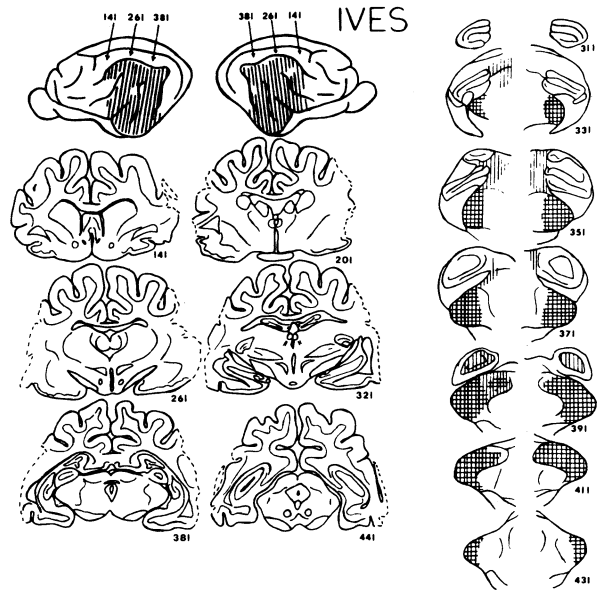


Figure 2. Reconstruction of auditory cortex lesion for a representative subject from Group AC. Upper left: Location and surface extent of cortical lesion is indicated by striations. Angle of striations and arrows indicates plane of section. Numbered arrows indicate level of three of the coronal sections drawn at lower left. Right: Drawings of retrograde degeneration in thalamus of left and right hemispheres. Vertical striations indicate moderate degeneration, whereas vertical and horizontal crosshatching indicates total or nearly total degeneration.

As might be inferred from Table 1, all of the groups responded at significantly greater than chance levels on auditory probes, and all groups except MS responded at greater than chance levels on light probe trials. On opposition test trials, Groups C, EM2, and MS significantly preferred noise, and Group AC preferred light over the alternative cue. However, a small number of cats (10%-20%) in Groups C, EM2, EM3, and MS also showed a statistically significant preference for light over noise (binomial test, $p < .05$).

DISCUSSION

Although Group EM3 showed a mild deficit on initial learning with the noise-light compound, it showed significant control by both cues on probe tests. The behavior of Group EM3 differed from that of the other groups primarily on the opposition tests. These animals responded equally often to noise and to light, with neither cue overshadowing the other. This loss of overshadowing of light by noise was probably caused by the partial damage to the auditory system produced by the inclusion of inferior temporal cortex and the posterior bank of the posterior ectosylvian gyrus in the EM3 lesion. There was no apparent difference in the amount of posterior association cortex removed in EM2 and

Table 1
Mean Learning and Test Scores

	C	EM2	EM3	MS	AC
Number of Cases	37	9	11	9	8
Mean Trials to Learn	60	83	141	39	25
Percent Responses on Probe Tests:					
To Noise	84*	85*	79*	86*	68*
To Light	69*	65**	76*	63	76*
Percent Responses on Opposition Tests:					
To Noise	71*	75*	59	67**	26
To Light	29	24	41	27	73*

* $p < .01$ vs. chance by t test

** $p < .05$ vs. chance by t test

EM3 lesions, since both lesions destroyed all of the association areas described by Thompson, Johnson, and Hoopes (1963). Moreover, Groups EM2 and C performed in an almost identical manner throughout the experiment. Therefore, the notion the lesions in the posterior association cortex produce a general disruption of intermodal learning was not supported. The prediction that cats with lesions in primary sensory projection cortex would ignore perceptible cues in the affected modality was partially confirmed.

Cats deprived of the auditory cortex localize widely separated, continuous sounds, like those used in this experiment, with considerable accuracy (Neff & Diamond, 1958), as demonstrated by the significant responsiveness of Group AC to auditory probes. Yet, despite the availability of discriminable auditory cues, Group AC responded more frequently to light than to noise on both the probe and opposition tests, reversing the preference for noise over light seen in the controls and the other operated groups. This change in the control of Group AC's behavior by visual and auditory stimuli, without a change in sensitivity sufficient to account for the shift, is the kind of alteration in selective attention predicted in the introduction.

There is no evidence of a complementary change in Group MS. Extensive injuries to the visual cortex did not markedly increase responses to noise, or decrease responses to light much below the controls' level. This failure may well be due to the strong bias toward auditory over visual stimuli that characterizes normal cats. It is apparently harder to increase the strength of the preference for noise than it is to decrease it by ablations of sensory cortex, at least under the experimental conditions used in this study.

Diamond (1967) conducted several overshadowing studies on cats with lesions in the auditory cortex similar to those of our Group AC. His results differed from ours in one major respect. He observed a marked overshadowing effect on single-cue probe trials as well as opposition trials. On probe trials, normal cats responded to a buzzer but not to the light with which it had been combined in a compound stimulus. Cats with ablations of the auditory cortex responded to light, but not to the

buzzer. Table 1 shows that both our Group C and Group AC were moderately successful with both single stimuli in probe trials. However, multiple differences between Diamond's experiments and ours preclude a direct comparison of results. Of greatest importance is the fact that Diamond did not determine the discriminability of his auditory and visual cues by testing the rate at which normal cats would learn the initial discrimination with either cue alone. It is possible that his cues were not equally salient initially, and this may account for the difference in results between our studies.

In general, our results on opposition tests do support the idea that noise overshadows light for most normal cats. However, the demonstration that most cats can effectively use either cue of the compound in single stimulus probes is of some theoretical and methodological importance. It suggests that the examination of potential controlling stimuli should not be limited to a single experimental test.

Finally, the existence of a small number of normal cats (15%) for which light overshadowed noise makes it clear that the predisposition to respond preferentially to noise is not an immutable species characteristic even in cats without brain lesions. At least this seems to be true for lab-reared cats. Aside from natural variation within the population, there is no ready explanation for this tendency of different cats to respond preferentially to different stimulus modalities. The experimental histories of the cats in this study were virtually identical and there were no obvious differences in rearing conditions between those animals that showed significant preferences for light or for noise on the opposition tests.

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