Contradiction of Auditory and Visual Information by Brain Stimulation

Abstract. *Cats with permanently implanted electrodes were trained to discriminate between trains of flashes or clicks at two different repetition frequencies. After substantial overtraining with these sensory stimuli, high levels of stimulus generalization were obtained to electrical stimulation of the reticular formation. Subsequent stimulation of the reticular formation at either frequency simultaneously with contradictory flicker or click stimulation at the opposite frequency resulted in control of the behavior by the reticular stimulus. Lateral geniculate stimulation failed to show this effect.*

During differential conditioning, electrophysiological responses to auditory or visual conditioned stimuli become anatomically more widespread, appearing prominently in nonsensory specific structures of the brain such as the reticular formation (RF), and responses from different brain regions often display similar features (*1*). In many structures, a late component develops which is absent from the evoked response before conditioning (*2*). The set of brain regions which share this coordinated activity is capable of reproducing a facsimile of the electrical activity characteristically caused by a familiar event when a novel event occurs (*3*). This facsimile, or readout process, most frequently is manifested relatively late in the evoked potential, while exogenous processes primarily determined by the physical characteristics of the stimulus appear at shorter latencies. Exogenous and readout processes have been separated by appropriate computer manipulations, and have been demonstrated to coexist in many brain structures, although the absolute amount varied greatly from region to region (*4*).

Studies with movable microelectrodes revealed that neurons in many regions showed marked differences between the firing patterns elicited by two discriminated signals. The neuronal firing patterns caused by any particular conditioned stimulus were closely correlated with the evoked potential waveshape and were extremely similar as the electrode was moved from region to region. Although single neurons responded with great variability to successive presentations of the same stimulus, poststimulus histograms gradually converged to the characteristic response pattern for that conditioned stimulus (*5*).

These findings suggest that a sensory stimulus influences widespread regions of the brain, which become organized into a representational system integrated by means of the RF and the associated diffuse projection system and storing the information about that experience. We proposed that whether information was entering or being retrieved from the different portions of that system, it was represented by the time sequence of deviations from random or baseline firing averaged across large neuronal ensembles (*6*). Afferent input into these regions caused the exogenous processes, which in turn activated the release of particular readout processes.

This theory, based upon the presumed informational significance of electrophysiological phenomena found to correlate with discriminative behaviors, is amendable to direct test. Specifically, were the meaning of sensory cues indeed encoded as the average firing patterns of anatomically widespread neuronal ensembles rather than by firing in selected synaptic pathways, it should be possible to elicit performance of previously learned discriminative behaviors by using electrical stimulation of the brain to fire large numbers of neurons in the appropriate patterns. If it proved possible to produce differential behaviors by stimulating the brain with different temporal patterns of electrical input, it would be necessary to ascertain whether such electrical signals merely mimicked the sensations caused by peripheral discriminative stimuli or whether they actually simulated the activation of a memory arbitrarily selected by the experimenter. Selective retrieval of a specific memory might be inferred if direct stimulation of a particular brain region could successfully contradict concurrent conditioned stimuli independent of sensory modality. Herein we report the results of experiments designed to test these propositions.

In six cats, approach-approach or avoidance-avoidance discriminations were established to either flicker (V) or click (A) at two different repetition rates, indicated by subscripts 1 and 2. All procedures were carried out in a 2 by 2 by 2 foot (1 foot = 0.3 m) apparatus with a work panel bearing pedals and dippers on the left and right sides and with a shock grid floor, placed inside a soundproof room. Sensory stimuli were delivered from sources in the roof of the apparatus. Training to auditory and visual cues was first carried out by using conventional shaping procedures, with a

Table 1. Transfer to various brain regions after peripheral training. CR, conditioned response.

Item	Cat No. 1	Cat No. 2	Cat No. 3	Cat No. 4	Cat No. 5	Cat No. 6	Average
Initial transfer to RF							
First day (percent)	40	96	28	76	50	80	61.7
First 50 trials							
Percent CR's	80	92	86	92	54	66	78
Percent correct discrimination	85*	87*	47	63	70†	85*	72*
Subsequent transfer to other regions							
First day (percent correct)							
Visual cortex	42	80	44	64	0		46.0
Lateral geniculate	90	0	50	50	0	13	33.8
Medial geniculate	0	13	60	59			33.0
Intralaminar midline thalamus	100	95	0	75	0	60	55.0
First 50 trials (percent CR's)							
Visual cortex	26	88	60	80	33		58
Lateral geniculate	54	90	54	88	56	64	68
Medial geniculate	30	86	60	80			64
Intralaminar midline thalamus	98	94	6	92		58	70
First 50 trials (percent correct)							
Visual cortex	54	80*	63	53	46		63*
Lateral geniculate	48	88*	44	48	68†	41	58†
Medial geniculate	60	58	53	80*			64*
Intralaminar midline thalamus	76*	83*	100	63		62	74*

* $P < .001$. † $P < .05$.

counterbalanced sequence of sensory modalities (*7*).

After substantial overtraining of the discriminations A_1 versus A_2 and V_1 versus V_2, stimulus generalization and transfer to direct electrical stimulation of various brain structures was studied. Brain stimuli were delivered to bipolar electrodes chronically implanted into a wide variety of brain structures, by means of a flexible cable connected to a subminiature plug mounted on the skull (*8, 9*). Complete details about training methods, stimulation procedures, thresholds, stimulus generalization, and transfer between visual, auditory, and central stimuli are available elsewhere (*10*).

By using bursts of electrical pulses delivered at the rates corresponding to the peripheral signals, the effects of the direct reticular formation stimuli RF_1 and RF_2 were first explored. The brain stimuli were occasionally introduced into random sequences of A_1, A_2, V_1, and V_2, in a sequence counterbalanced for modality and frequency of the previous stimulus. High initial levels of stimulus generalization were displayed by all six cats, with a mean discrimination accuracy of 61.7 percent on the first day, as seen in Table 1.

Of the 300 initial trials of stimulus generalization to reticular input performed by this group of six cats (first 50 trials for each cat), 235 resulted in performance of one or another conditioned response (78 percent). Seventy-two percent of the conditioned responses were correct discriminations. For three of these animals the probability of obtaining the observed discrimination levels by chance was below the .001 level, a level achieved by the group as a whole. This confirms previous reports of rapid transfer of training from peripheral to RF stimuli (*11*) and extends those results to differentiated behavior, providing a control for nonspecific effects.

After criterion performance was achieved in response to differential RF stimulation, requiring 2 to 10 days of further training, peripheral stimuli at either repetition rate were combined with RF stimuli at the other rate (conflict). The various compound conflict stimuli A_1RF_2, A_2RF_1, V_1RF_2, or V_2RF_1 were inserted in counterbalanced fashion into a random sequence of the individual auditory, visual, and electrical signals. Compound concordant stimuli A_1RF_1, A_2RF_2, V_1RF_1, and V_2RF_2 provided controls for unspecific interaction effects. Data were discarded if performance to individual or concordant cues fell below criterion levels.

In each conflict session, RF current was varied parametrically above and below the usual training intensity. At each current level, several conflict trials of each type were presented and sessions usually included an ascending and descending series. Figure 1 shows the results of visual-RF conflict (left) and auditory-RF conflict (right). As stimulus current increased, RF input completely controlled the outcome in six out of eight studies of both kinds of conflict. In the two exceptions, a significant control of behavior by RF stimuli was apparent but limited by disruption of discriminative responses at higher current levels.

After completion of these peripheral versus RF conflict trials, transfer of training was initiated to the visual cortex, lateral geniculate, medial geniculate, and the intralaminar nuclei of the thalamus. The order in which these structures were trained was permuted daily. In spite of the substantial experience with electrical stimuli and further overtraining received during RF training and conflict studies, the transfer to these brain regions was slower than the initial transfer to RF. Nonetheless, good stimulus generalization to stimulation of the intralaminar nuclei of the thalamus was observed in four cats, which confirmed previous reports (*12*), while one or two cats showed high levels of stimulus generalization and discrimination ($P < .001$) to each of the

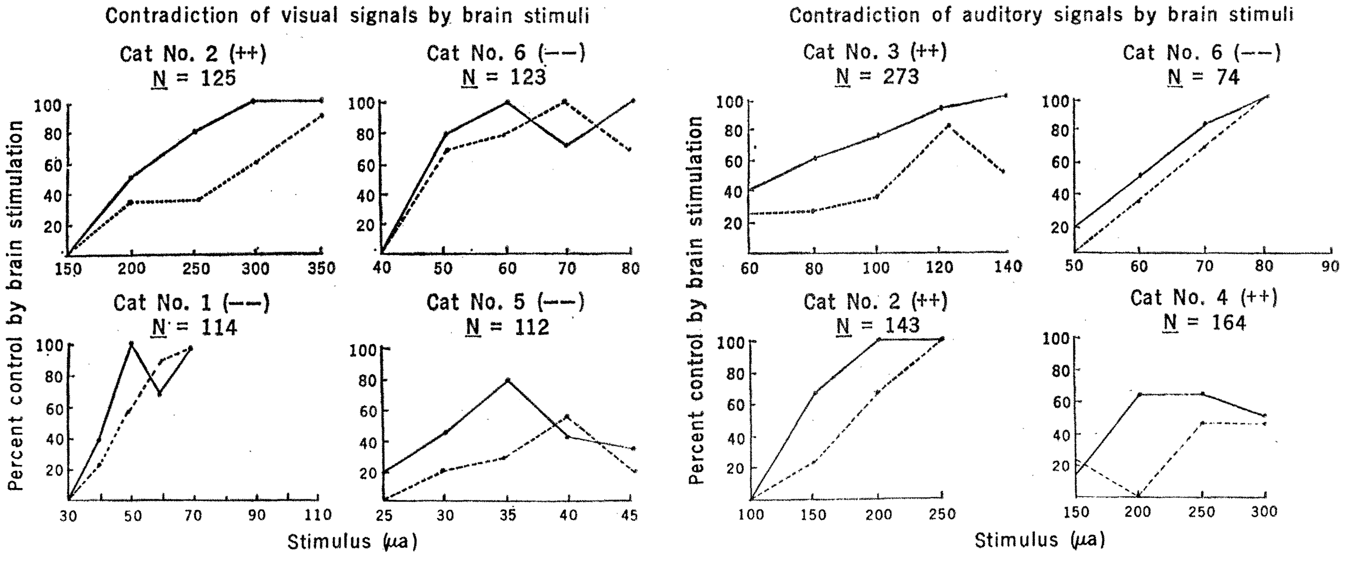

Fig. 1. Each graph shows the effectiveness with which stimulation of the mesencephalic reticular formation at either of two frequencies (RF_1 and RF_2) contradicted simultaneously presented visual stimuli (V_2 and V_1, left) or auditory stimuli (A_2 and A_1, right), plotted as a function of increasing current intensity. For cats 1, 3, and 6, frequency 1 was 4 per second and frequency 2 was 2 per second. For cats 2, 4, and 5, frequency 1 was 5 per second and frequency 2 was 1.8 per second. Solid lines show the outcomes when peripheral stimulation at the higher frequency (V_1 in left graphs, A_1 in right graphs) was pitted against RF stimulation at the lower frequency (RF_2), while the dotted lines show the outcomes when the higher-frequency stimulus was delivered to the RF. Cats 1, 5, and 6 were trained to perform an avoidance-avoidance discrimination (— —), while cats 2, 3, and 4 were trained to perform approach-approach discrimination (+ +). *N* refers to the total number of conflict trials carried out in each cat, accumulated in three sessions for cats 2, 5, and 6 and four sessions for cat 1 (visual-RF conflict), and in three sessions for cat 2, four for cat 6, five for cat 4, and seven for cat 3 (auditory-RF conflict).

other stimulated structures (Table 1).

After achievement of criterion performance to lateral geniculate (LG) stimulation, peripheral versus LG conflict was carried out in three cats. Occasional instances were obtained in which electrical stimulation of the LG at the higher frequency successfully contradicted the flicker cue at the lower frequency, while LG stimuli at the lower frequency seldom prevailed over higher frequency flicker signals. Lateral geniculate stimulation was uniformly ineffective to control behavior in auditory-LG conflict.

Our findings of high levels of differentiated stimulus generalization and rapid transfer to RF stimulation provide strong support for the contention that discriminations such as these are mediated by the average temporal patterns of firing in extensive neuronal ensembles rather than by discharges in particular synaptic pathways representing a specific experience. These RF stimuli cannot conceivably reproduce a unique and intricate topology of synaptic discharges corresponding to those normally excited by particular peripheral signals. Undoubtedly, gross electrical stimuli merely impose a corresponding temporal pattern upon masses of cells. The stability of performance when the fine structure of RF stimuli was altered, as well as the stimulus generalization obtained so readily when other brain regions were stimulated, provides further proof that these discriminations do not depend upon activation of specific synapses or pathways. These results cannot be attributed to nonspecific factors because they require correct discrimination between two different patterns of stimulation applied to the same site.

Lateral geniculate stimulation successfully contradicted visual cues only when the rate of central stimulation was more rapid than the flicker. Lateral geniculate stimuli completely failed to contradict auditory cues at either rate. Visual cues were hardly ever found successful in contradicting auditory cues. These results suggest that LG stimulation simulates visual sensation. The ability of RF stimuli to preempt control of behavior whether in conflict with visual or auditory cues shows that RF input does not merely simulate the sensations caused by ordinary sensory events, but seems to provide unique access to the brain mechanism which interprets sensory events of whatever modality. These findings suggest that the organized firing of anatomically extensive neuronal ensembles accomplished by patterned RF stimulation simulates the activation of specific memories.

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7. Some animals learned first to discriminate between the two auditory cues, A_1 and A_2, and then received transfer of training to the two visual cues, V_1 and V_2. Other animals first learned the visual and then the auditory discrimination. The two stimulus repetition rates were 5 versus 1.8 hertz in three cats and 4 versus 2 hertz in the other three. For three cats, the differential responses consisted of pressing either the left- or the right-side pedal on a work panel to avoid foot shock (conditioned avoidance response). For the other three cats, the same differential response was motivated by food reinforcement. Food-motivated animals received food only in the training situation, except on weekends. Sessions were usually 1 day apart and consisted of 40 to 200 trials.
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9. All brain stimuli were trains of 30 biphasic constant-current pulses 200 μsec wide at a frequency of 200 pulses per second, repeated at rates corresponding to the discriminated flicker and click signals. Stimulus intensity was selected by ascertaining the current threshold to elicit motor responses or to interfere with ongoing behavior, and then reducing to approximately one-half that value for training. Brain stimuli were specified by Nuclear-Chicago stimulators (model 7150) photically coupled to the brain by Tektronix stimulus isolation units (model 2620). Phase locking of peripheral and central stimulation and system timing was accomplished by a control unit of our own design. Electrophysiological responses were amplified with a Grass model 7 polygraph, stored on a 14-channel model 1000 Mnemotron tape transport, and analyzed with a PDP-12 computer.
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Origin of Martian Channels: Clathrates and Water

The similarity of many large martian channels to terrestrial ones has led to speculation that at some time in the past there was sufficient water on the surface of Mars to erode the observed channels (*1*). Some of these channels are so large, however, that flow rates many times that of the Amazon River are suggested. The fact that these channels frequently begin in "chaotic terrain" and lack tributaries implies an underground source capable of supplying the large flows.

The most obvious underground sources would seem to be either the rapid melting of an ice permafrost or the release of liquid water trapped beneath such a permafrost. Milton (*2*), noting that there is a considerable heat problem associated with the rapid melting of a permafrost, proposes that the liquid water might come from the depressurization of CO_2 hydrate, which could exist at depths where the pressure exceeded 10 bars and the temperature exceeded 0°C. This explanation ignores the obvious alternative that *liquid* water could already exist under those conditions. In fact, with the molecular ratio of H_2O/CO_2 of 15/1, cited by Milton, only about one-third of the available water can be tied up in the clathrate compound. Thus, a far larger volume of water would already