Transfer of learned discrimination from peripheral to central auditory stimulation in cats*

FRANCIS B. COLAVITA
Psychobiology Program, University of Pittsburgh
Pittsburgh, Pa. 15260

Cats were implanted with chronic bipolar electrodes either in the inferior colliculus (IC) or in the lateral tegmental nucleus (LTN). The animals were then trained in a Y-maze to make a differential response to an 800-Hz and a 1,000-Hz tone. On a series of test trials, electrical brain stimulation at either 800 or 1,000 pulses/sec was substituted for the tonal stimuli used during original training. Cats with IC electrodes tended to behave as though they were responding to the tonal stimuli, while LTN animals did not. These data suggest that direct electical brain stimulation can be a useful technique in the study of sensory coding.

Several experiments using animal Ss have noted some degree of gross behavioral equivalence between direct electrical brain stimulation and peripheral stimulation of sensory end organs in the usual fashion. Such equivalence has been reported in the auditory modality by Doty & Rutledge (1959), Nieder & Neff (1961), and Nielson, Knight, & Porter (1962), and in the visual modality by Kitai (1965, 1966) and Miller & Glickstein (1961). For the most part, these experiments have involved training an animal to make some behavioral response in the presence of an auditory or visual stimulus, and then measuring the animal's tendency to perform the response when electrical stimulation of auditory or visual brain regions is substituted for the original training stimulus. This tendency to show response transfer is smaller or absent when the electrical stimulation is delivered to nonsensory brain regions. Thus, direct electrical stimulation of auditory or visual centers and pathways is probably producing a sensory experience that is in some way equivalent to the original training stimulus. Experiments such as the above represent a potential contribution to the understanding of sensory coding.

The present study was designed to do more than demonstrate once again some level of gross behavioral equivalence between central and peripheral auditory stimulation. Rather, an attempt was made to define with more precision the qualities of the auditory sensations produced by direct electrical brain stimulation. This was accomplished by establishing in experimental animals a differential response to two different tones during original training, and then testing for response transfer with two different pulse repetition rates of electrical brain stimulation.

METHOD

Subjects

The Ss for this experiment were four adult cats obtained from a local supplier. The animals were housed in individual cages and were given access to food only for the hour immediately following a daily training session. Water was continuously available.

Surgery

Surgery was performed under pentobarbital anesthesia, with routine sterile precautions being observed. Two animals were prepared with a chronic bipolar electrode in the apex of the left inferior colliculus (IC), while the remaining two animals were implanted in the lateral tegmental nucleus (LTN). The electrodes were constructed from .0067-in. stainless steel wires, insulated with Teflon except for the cross section at the tip. Tip separation was 1 mm. An indifferent lead was fastened to the skull over the frontal sinuses. The IC electrodes were implanted under visual guidance, while the LTN electrodes were implanted by using stereotaxic coordinates, P 1.5, R 1.5, H −2, from the Snider & Niemer (1961) atlas of the cat brain. Leads from all electrodes were attached to an Amphenol plug (No. 54-40140) that was permanently fixed to the cat's skull with acrylic cement and stainless steel screws.

Behavioral Training

Following a 2-week postsurgery recovery period, the animals were placed in a Y-maze with three identical alleys of 54 x 9 x 12 in. At the end of each alley was a goal box, 20 x 9 x 12 in., which could be sealed off by a sliding door. The top of the Y-maze consisted of pieces of clear Plexiglas, hinged at the two sides of the maze, leaving a 5/8-in. open space down the middle of each alley and goalbox. This open space permitted the cat to traverse the maze with a flexible cable for delivering brain stimulation attached to its head. When brain stimulation was used, it was produced by a Grass Model S4 electronic stimulator. Current could be continuously monitored oscilloscopically by observing the voltage drop across a known resistor in series with the animal. Acoustic stimuli could be presented to cats in the maze over a KLH Model 14 B loudspeaker positioned over the choice point in the maze. Tonal stimuli were generated by a Hewlett-Packard Model 200 AB audio oscillator.

Procedure

On the day preceding the start of behavioral training, each cat was placed in the maze and permitted to explore all the alleys. The flexible cable was attached to the animal's head plug, although no electrical stimulation was administered at this time. Only when the animal had finished exploring and had assumed a relaxed, reclining position was brain stimulation presented. The electrical stimulation consisted of .1-msec biphasic pulses, at a repetition rate of 800/sec for two animals and at 1,000/sec for the remaining two cats. Stimulation was initiated at a subthreshold intensity. The current level was then gradually raised until the animal showed a clear sign of behavioral alerting, such as standing up and looking around. The current value was noted at which behavioral alerting first occured. At a second session on the same day, a similar procedure was followed with those animals originally stimulated with 800/sec now experiencing 1,000/sec, and vice versa.

On the day following the determination of the alerting threshold, behavioral training was initiated. All behavioral training was carried out with the overhead cable attached to the animal's headplug, even when brain stimulation was not being used. This was done to accustom the animal to the cable and to prevent behavioral disruption in a later part of the experiment when brain stimulation was administered.

Each cat was placed in one of the three goalboxes, and trained, when the restraining door was opened, to approach and

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enter the left goalbox in the presence of an 800-Hz tone and to approach and enter the right goalbox in the presence of a 1,000-Hz tone. Tonal intensity was varied over a 10-dB range around 70 dB SPL in order to insure that tonal intensity was an irrelevant cue. The tone was turned on several seconds before the sliding door was opened, and was left on until the animal had entered either the left or right goalbox. Choosing the correct arm of the maze gained the cat access to a teaspoon of Puss-N-Boots fish-flavored cat food. Then the next trial would be initiated in 20 sec. Entering an incorrect goalbox resulted in the animal's being trapped in the empty goalbox for 2 min before the next trial was initiated. A small portion of the cat food was smeared over all three food cups in the goalboxes at the start of a daily session to prevent the animal from making use of olfactory cues.

On each trial, the choice of tonal frequency was determined randomly, with the constraint that each frequency occur an equal number of times. Animals were given 20 trials per day and were trained to a criterion of 19 out of 20 correct responses.

On the day after criterion had been reached with the tone stimuli, the animals were placed in the maze and given 10 trials with brain stimulation, with either 800 pulses/sec or 1,000 pulses/sec being substituted for the 800- and 1,000-Hz tones. The current intensities used were slightly higher than those that had been found earlier to produce behavioral alerting.

Ten trials involving the original training stimuli were interspersed with the 10 brain-stimulation trials. No food reward was available on brain-stimulation trials, but food reward was available on tone trials. It was hoped that this procedure would (a) rule out rapid new learning as the basis for any "correct" responses seen on brain stimulation trials, and (b) protect the learned discrimination from the effects of extinction long enough to obtain a measure of response transfer.

RESULTS

The intensities of brain stimulation used in this experiment ranged from .3 to .8 mA. These levels were high enough to produce behavioral alerting, but not intense enough to have any obvious aversive qualities.

All four cats eventually reached criterion on original training with tonal stimuli. The number of trials required ranged from 200 to 400.

Table 1 summarizes the transfer data obtained when brain stimulation was substituted for the tonal stimuli. Animals with electrodes in IC showed a significant ($p < .01$) tendency to turn left when stimulated with 800 pulses/sec and to turn right when stimulated with 1,000 pulses/sec. Those animals stimulated in LTN showed no such tendency, performing essentially at a chance level.

Table 1
Transfer Shown by Cats Trained With Tones and Tested With Brain Stimulation

Cat	Placement	Percent Transfer
S-104	IC	100
MH-1	LTN	50
FC-1	LTN	30
FC-2	IC	90

DISCUSSION

The present study is clearly in line with the findings of Colavita (1969), Doty (1961), and Nielson, Knight, & Porter (1961), that subcortical electrical brain stimulation can readily serve as a conditioned cue in a learning task. Moreover, the data provide a further indication that direct electrical brain stimulation may serve as a useful tool in the study of sensory coding. Cats trained to make a behavioral response to tonal stimuli showed a strong tendency to transfer this training to the situation where stimulation of IC with electrical pulses was substituted for the tonal stimuli.

The present data suggest not only that there was some degree of behavioral equivalence between central and peripheral stimulation of the auditory system, but also that it is possible to specify with more precision the perceptual properties of auditory sensations produced by electrical brain stimulation. In some way, stimulation of IC with 800 pulses/sec was perceived by the cats as being more similar to an 800-Hz tone than to a 1,000-Hz tone, while stimulation with 1,000 pulses/sec was perceived as being more similar to a 1,000-Hz tone than to an 800-Hz tone. No such tendency was seen when stimulation was delivered to LTN, a nonauditory area.

Previous work strongly suggests the participation of IC in the coding of frequency information. Rose et al (1963) have found clear evidence of tonotopic organization in IC, while behavioral studies involving selective lesions (Goldberg & Neff, 1961) have implicated IC in frequency discrimination. Nevertheless, it is unlikely that electrical stimulation of IC with pulse rates of 800 and 1,000/sec could produce the sensation of 800- and 1,000-Hz tones. While frequency following has been implicated as a pitch coding mechanism at lower levels of the auditory system for low frequencies, Whitfield (1967) has pointed out that even the operation of a volley principle is unlikely to maintain good synchrony as high up in the auditory system as IC. This is due to the time variations necessarily introduced by the number of synapses that occur between the cochlea and IC.

Possibly, the behavioral correspondence seen between 800 and 1,000 pulses/sec and 800- and 1,000-Hz tones resulted from the spread of electrical current downstream to regions of the auditory system below the level of IC, where frequency following is still a possible mechanism for pitch coding.

While it is clear that many questions remain to be answered, the present data suggest that, when combined with appropriate behavioral training and testing, electrical stimulation of auditory centers and pathways can provide insights into the neural mechanisms of auditory discrimination.

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