A comparison of conditioned and unconditioned neuronal responses in the inferior colliculus of cats¹

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Multiple-unit neuronal responses were recorded from the inferior colliculus of four cats during classical and instrumental conditioning. For three cats, the CS elicited a neuronal inhibition (unconditioned response) that was not modified by various training procedures. For the fourth cat, a conditioned neuronal response was observed during instrumental, but not during classical, conditioning.

In an earlier paper by Halas & Beardsley (1969), it was reported that different neuronal responses appeared in the cochlear nucleus of a cat during classical and instrumental conditioning. The conditioned neuronal response for classical conditioning was a sustained increase in neuronal activity that remained essentially unchanged throughout acquisition. For instrumental avoidance conditioning, there were three different patterns of neuronal responses. The first pattern to appear was a sustained increase similar to the response observed during classical conditioning. During the middle stages of training, a second pattern consisting of a brief onset response appeared. In the final phase of training, the pattern consisted of an initial positive onset followed by a marked decrease in neuronal activity. These results demonstrated the neural involvement of the cochlear nucleus during classical and instrumental conditioning.

The present study examines the complexity of neuronal responses in the

inferior colliculus during classical and instrumental conditioning.

METHOD

The Ss were four adult male cats with chronically implanted electrodes. The procedure for implanting an electrode in the inferior colliculus has been described elsewhere (Buchwald, Halas, & Schramm, 1966; Halas & Beardsley, 1968). The multiple-unit neuronal activity was displayed on a Tektronix 565 oscilloscope and was photographed with a Grass C4 camera. A modified version of the Weber & Buchwald (1965) electronic integrator was used to count the frequency of the multiple-unit activity. The integration of the frequency count was displayed on the scope and was photographed simultaneously with the neuronal activity. Pin lights mounted on the scope recorded the duration of the CS and US, which consisted of a 1,500-Hz tone paired with a mild electric shock to the hindpaw of the cat. The CS lasted 1.5 sec, and the US lasted 0.5 sec. The US overlapped the last third of the CS.

The Ss were given 500 habituation trials to the tone at the rate of 39 trials per day (32 trials on the last day) followed by 800 trials of paired tone and shock during classical conditioning. The Ss were then given 500 extinction trials followed by a 6-week rest period. After a second habituation of 500 trials, the Ss were given 1,000 instrumental avoidance trials. If the S lifted its hindpaw during the first 1.0 sec of the tone, shock was not given. Five hundred extinction trials followed the avoidance training. Intertrial intervals ranged randomly from 20 to 50 sec.

RESULTS

For three of the four cats, there was a marked inhibition of neuronal activity during the tone period that was not modified during any of the training procedures. Records from one of these cats are shown in Fig. 1. This inhibition of neuronal activity was observed in 92% to 96% of all trials (i.e., habituation, classical conditioning, extinction, habituation, instrumental conditioning, extinction) for the three Ss. Although a conditioned neuronal response did not develop, conditioned behavioral responses did develop in all three Ss during classical and instrumental conditioning. On the average, there were conditioned behavioral responses on 15% of the trials during the first 200 trials of classical conditioning and 59% on the remaining 600 trials. For instrumental conditioning, conditioned behavioral responses were observed on 35% of the first 200 trials and on 73% of the remaining 800 trials.

For the fourth cat, there was no neuronal response to the tone during habituation, classical conditioning, or extinction (Fig. 2). However, a change in neuronal activity did appear during instrumental conditioning. Starting with Trial 287 (Trace J), a brief onset response followed by an inhibition of activity appeared. As training progressed, the onset response became stronger and the inhibition more pronounced (Trace K). The brief onset combined with the inhibition is very similar to the conditioned neuronal response observed in the cochlear nucleus during the final phase of instrumental conditioning (Halas & Beardsley, 1969). From Trial 287 onward, the conditioned neuronal response was observed in this study in 87% of the trials. Thus, the data indicated a difference in neuronal activity in the inferior colliculus between classical and instrumental conditioning. Conditioned behavioral responses occurred during 42% of the trials up to Trial 286. From Trial 287 through Trial 1,000, conditioned behavioral responses were recorded in 79% of the trials. The conditioned neuronal response was then extinguished (Trace L).

DISCUSSION

Although a conditioned neuronal response was established in one cat (Fig. 2), there was no conditioned neuronal

Fig. 1. A comparison of neuronal inhibition during classical and instrumental conditioning. The CS denotes the time period of the 1,500-Hz-tone stimulus, while the US denotes the duration of the electric shock to the right hindpaw. The large vertical lines during the US period are due to shock artifact.

Fig. 2. A comparison of neuronal activity during classical and instrumental conditioning. No neuronal responses occurred to the CS during classical conditioning, but during instrumental conditioning a brief onset followed by inhibition was elicited by the CS (Traces J and K).

response observed in the other three Ss (Fig. 1). This lack of a conditioned neuronal response in the three Ss may be related to the fact that the US did not elicit a neuronal response in the CS pathway of these Ss. In the previous paper by Halas & Beardsley (1969) and in the present paper, a conditioned neuronal response was established in those Ss in which the US was capable of eliciting a neuronal response in the CS pathway. This observation raises several questions. How does the US modify the firing pattern of neurons in the CS pathway? What is the contribution of the CS pathway to the neural control of conditioning? Does the same population of neurons in an auditory nucleus have one or two functions?

There are various facts that suggest that the US modifies the firing pattern of the CS pathway by an indirect route rather than directly. To begin with, there is no known direct anatomical collateral going from the US pathway to the CS pathway. However, collaterals are sent to the reticular formation from both the CS and the US pathways, and feedback loops go from the reticular formation to the CS and US pathways. In addition, an

unconditioned neuronal response to the US was not observed during classical conditioning (Fig. 2) until after several hundred trials. Similar results were observed in the cochlear nucleus (Halas & Beardsley, 1969). This again suggests that the US affects the CS pathway by some intermediate route or structure.

The exact contribution of the CS pathway to conditioning is rather confused, but several facts are apparent. Although three of the cats did not show any unconditioned neuronal response to the US (Fig. 1), one cat did exhibit a UNR to the US and eventually developed a conditioned neuronal response to the CS during instrumental conditioning (Fig. 2). When this cat successfully avoided the shock, a marked inhibition of neuronal activity was observed, as seen in Traces J and K. When the cat did not avoid the shock, inhibition of activity was frequently not seen during the tone period, but the US would produce a substantial increase in neuronal activity. The absence of a conditioned neuronal response in the CS pathway on those trials when the S failed to avoid the shock would indicate that the CS pathway is probably a part of the

neural complex that mediates conditioning. It should be reaffirmed, however, that no conditioned neuronal response was observed in this S during classical conditioning; this suggests that the neural mechanisms mediating classical and instrumental conditioning are different.

Since three Ss exhibited only unconditioned neuronal responses to the CS, while the other S developed a conditioned neuronal response to the CS, this suggests that various parts of the inferior colliculus have different functions. One function would be the transmission of sensory information, while the second function would be correlated with the development of a conditioned neuronal response. These changes in the inferior colliculus during conditioning support the earlier paper (Halas & Beardsley, 1969) that subcortical auditory nuclei have not only a role in the transmission of sensory information but are also a part of the neural complex that mediates learning.

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NOTES

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