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Influence of Motor Activity on Click-Evoked Responses in the Auditory Pathway of Waking Cats

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Click evoked responses were recorded from waking cats by means of electrodes chronically implanted along the auditory pathway. The animals were studied in three different situations: sitting still, during bodily movements, and during presentations of novel stimuli. The responses recorded from the round window cochlear nucleus, superior olive, inferior colliculus, medial geniculate body, and auditory cortex were of smaller amplitude during movements than responses recorded in the same animals while sitting still. They were attenuated during the initial moments following the presentation of a novel stimulus at a time when the animal was engaged in orienting movements. However, when animals were sitting still and merely staring at the novel stimulus, click evoked responses were of control amplitudes. A dual regulatory system consisting of both peripheral neuromuscular as well as of central mechanisms is active in modifying click evoked responses during movements. In animals with the tendons of the middle ear muscles sectioned bilaterally, responses recorded from subcortical stations along the auditory pathway did not decrease in amplitude during movements, whereas cortical evoked responses were still attenuated. Thus, modifications of evoked responses in subcortical stations along the auditory pathway are a passive reflection of middle ear muscle induced modifications of sound input. Changes in cortical evoked responses during movements depend, in addition, upon central mechanisms. These mechanisms do not appear to act on the cortex itself but, rather, on pathways connecting brainstem stations of the auditory pathway with auditory cortex.

Introduction

In unanesthetized animals, unchanging sound stimuli elicit evoked responses which fluctuate in amplitude. This noncorrespondence between

¹ I am grateful to Dr. Peter Carmel for performing the bilateral sections of the tendons of the middle ear muscles. This work was carried out with the support and encouragement of Dr. Robert B. Livingston. My current address is: Stanford Medical School, Palo Alto, California.

the constancy of the sound stimulus and the variability of nervous system responses has been related to the duration of sound exposure (2, 19, 29, 39), the nature of events associated with the sound stimuli (11, 16), and the animal's level of arousal (3, 23). We recently reported (4, 39) that evoked responses to steady sounds decreased in amplitude whenever animals moved and suggested that motor activities may also contribute to the evoked response variability. The present experiments examine systematically the modifications of evoked responses to brief sound stimuli appearing during movements. Acoustic response modifications apparently depend upon a dual regulatory system involving the middle ear muscle as well as central neuronal processes. This system provides for integration of sensory and motor events at both input and relay stations along the auditory pathway.

Materials and Methods

Evoked responses to clicks were analyzed in ten waking cats, eight of which had been exposed in earlier experiments to white noise for several hours at an intensity of 85 db re 0.0002 dynes/cm² (39). Under Nembutal anesthesia, four bipolar stainless steel electrodes were implanted stereotactically in each animal into stations along the right auditory pathway according to the techniques of Sheatz (37). Electrode pairs were made of two 125 μ enamel insulated stainless steel wires twisted tightly together having tips separated vertically by about 1 mm. The tips of the cortical recording electrodes were separated by about 2 mm in a horizontal direction and were placed subdurally at the upper end of the posterior ectosylvian sulcus. In three of the animals round window recordings were made according to the technique of Galambos and Ruppert (10). In two of the animals the tendons of the stapedius and tensor tympani muscles were sectioned bilaterally at the time of electrode implantation. Successful auditory pathway recordings were obtained from round window (three cats), cochlear nucleus (five), superior olive (two), inferior colliculus (seven), medial geniculate body (five), and auditory cortex (five). Nonauditory pathway placements included superior colliculus, spinal tract of the trigeminus, midbrain reticular formation, and somatosensory cortex (one cat each).

Evoked responses to clicks were recorded from within a wire mesh cage situated in a sound attenuating room. Clicks were produced by square wave pulses, 0.01 msec in duration, generated by a Tektronix type 161 pulse generator and projected as a free field stimulus from a

speaker mounted 77 cm above the animal's head. The click intensity was adjusted to produce a deflection of a General Radio sound level meter (type 1551 B) with scale C set at 70 db. Figure 1 shows the configuration and amplitude of clicks recorded by a condenser microphone located in different parts of the cage. Note that the maximal intensity difference (as measured by peak-peak amplitudes of the initial two deflections) was

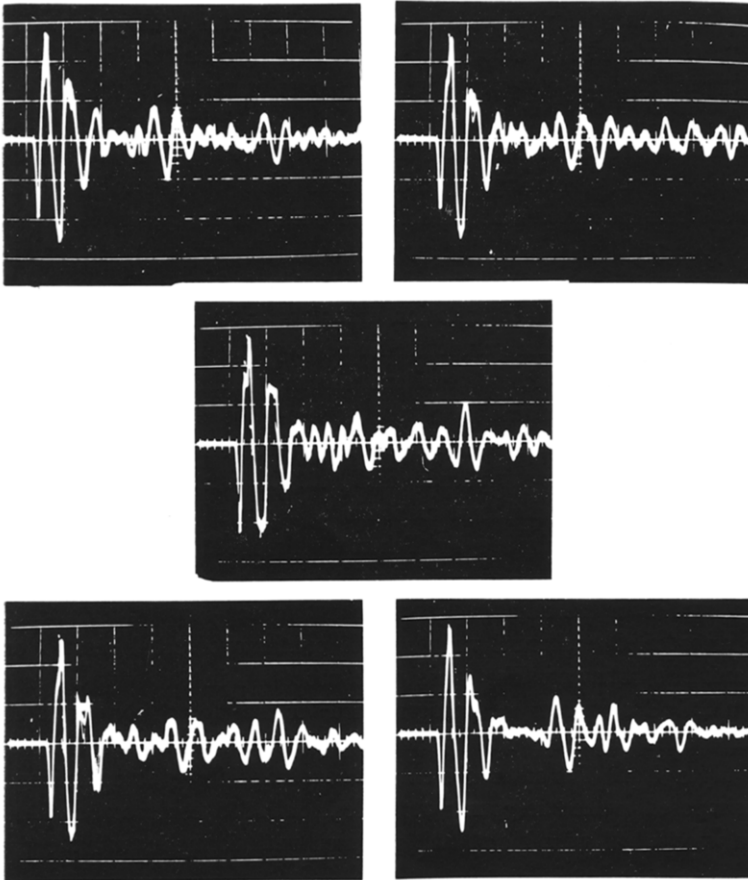


FIG. 1. Physical characteristics of the click stimuli. Each photograph represents superimposed clicks recorded by a condenser microphone placed in the corners and the center of the cage. The onset of the sweep in this and in all subsequent figures except for Fig. 4 was simultaneous with the delivery of the square wave pulse to the loud speaker. Time scale is 2 msec per division. Amplitude calibration is 3 db per division.

only 1.5 db, and that the configuration of the sound waves was quite constant. Animals were observed through a one-way mirror from an adjacent dark recording room. A series of thirty-two clicks was presented at a regular rate of one every 2 sec and evoked responses were recorded in three different situations: first, when the animals were awake, sitting still, and after all orienting reactions to the clicks had disappeared. This condition was achieved within 30 min after the animals had been placed in the cage and before the tenth series of clicks had been presented. Secondly, click evoked responses were recorded when the animals were moving in the cage, either spontaneously or in response to a person entering the room and walking in front of the cage. Thirdly, click evoked responses were recorded when the animals were sitting still and looking at a slowly moving, flashing light presented from the adjacent recording room. Visual attention was assumed to occur when eye movements followed the path of the slowly moving light. Following such procedures, the clicks were discontinued and electrical stimuli from a Grass stimulator were applied through an isolation transformer to the subcortical electrodes for testing evoked responses in auditory cortex. The responses were recorded during the three situations similar to those used with clicks. The amplitude and duration of the square-wave electrical pulses were adjusted to elicit clearly defined cortical evoked responses and ranged between 3–8 volts in amplitude and 0.02–0.2 msec in duration. The animals showed no behavioral response to these stimuli.

Responses were amplified by Tektronix type 122 preamplifiers (band pass set 0.2 c/sec to 10 kc/sec), monitored on a four beam oscilloscope, and recorded in the adjacent room on a Sanborn–Ampex seven channel tape recorder. One channel was used for continuous verbal description of the animal's behavior. The tapes were processed in two ways. For four cats a LINC computer was programmed² to average thirty-two click or shock evoked responses during each of the three experimental situations. The tapes from the other six cats were studied by photographing ten superimposed evoked responses on a Tektronix 535 oscilloscope. The animals were killed with Nembutal, perfused with formalin and the brains serially sectioned at 25 μ and stained with Cresyl Violet to determine electrode location. Middle ears were examined with a Zeiss dissecting microscope to determine that the middle ear muscle tendons had been completely transected.

² The analysis was performed through the courtesy of Mr. Wes Clark and Mr. Charles Molnar at the Lincoln Laboratory, Lincoln, Massachusetts.

Results

Effects of Motor Activity on Click Evoked Responses. Click evoked responses recorded from auditory pathway (round window, cochlear nucleus, inferior colliculus, medial geniculate body, and auditory cortex) as well as from sites remote from this pathway (spinal tract of the trigeminal superior colliculus, midbrain reticular formation, and somato-sensory cortex) were of smaller amplitude while animals were moving than while they were sitting still. Figure 2 shows the effects of motor activity on

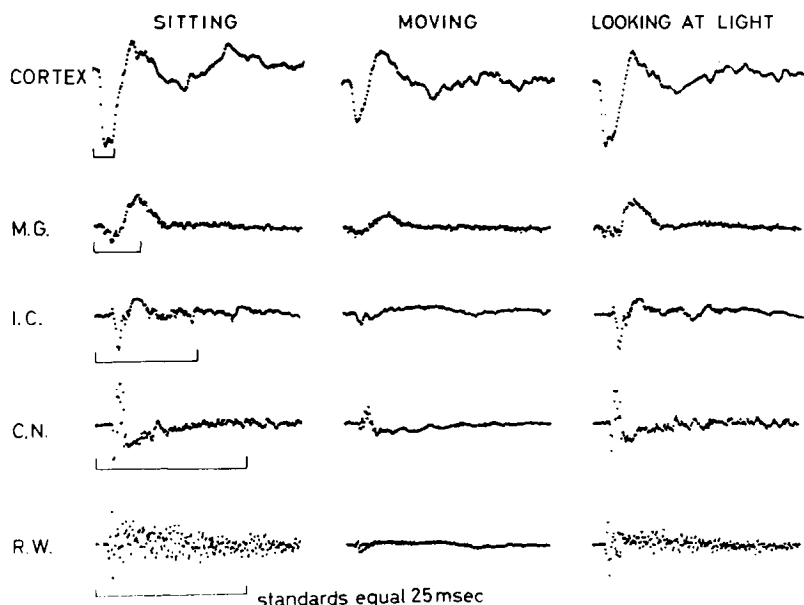


FIG. 2. Averaged evoked responses recorded from auditory pathway of waking cat. In this and in all subsequent figures the abbreviations MG refer to medial geniculate body, IC to inferior colliculus, CN to cochlear nucleus, and RW to round window. In this figure responses recorded from RW, CN, and IC are from one animal and responses recorded from MG, and cortex are from a different animal.

the average of thirty-two evoked responses recorded from several stations along the auditory pathway while Fig. 3 is from different animals and shows the effects of motor activity on ten superimposed click evoked responses. A wide variety of motor activities including those of grooming, eating, scratching, shifting of position, pacing, vocalization, and stretching were associated with an attenuation of click evoked responses. The extent of the attenuation was roughly related to the extent of the

movement; being greater during gross movements as in walking than during movements involving mainly head and neck. Movements of the extraocular muscles alone were accompanied by little or no change in amplitude of click evoked responses.

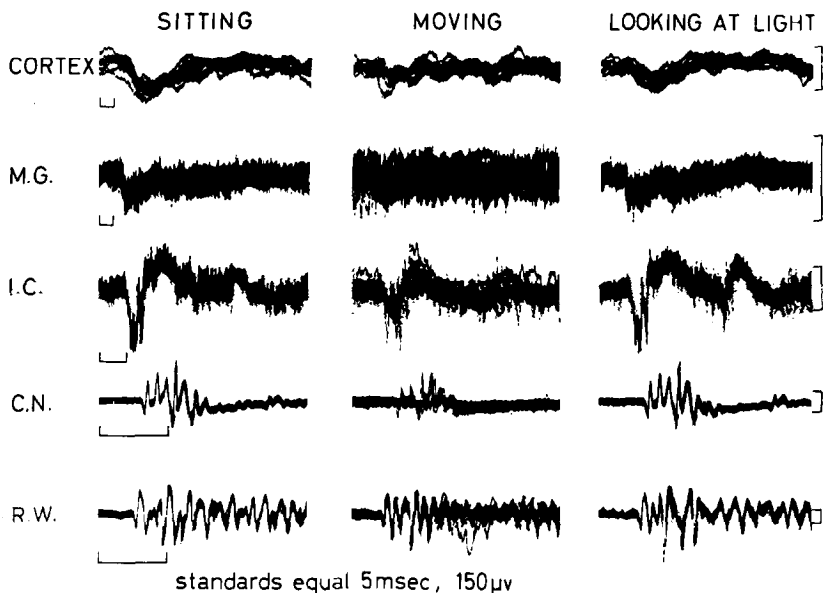


FIG. 3. Superimposition of ten evoked responses recorded from the auditory pathway. All subcortical evoked responses recorded from same animal.

A bright flashing light or a sudden loud sound elicited a turning of the head, neck and body toward the source of these stimuli. Click evoked responses decreased in amplitude during such orienting movements. However, after the animal had completed the orienting movements, and while it was staring in the direction of the novel stimulus, the amplitudes of click evoked responses resembled control responses recorded in the absence of environmental novelty (Figs. 2 and 3). Apparently, "attentive behavior" alone, in the absence of head, neck or bodily movements, is not associated with an attenuation of click evoked responses.

Mechanisms Modifying Click Evoked Responses During Motor Activity. The middle ear muscles contract during motor activity and effect a decrease of sound transmission through the middle ear (4). This modification of acoustic input can account for the attenuation of click evoked

responses recorded from round windows and from subcortical stations along the auditory pathway. Thus, in the animals with severed tendons of both middle ear muscles, the amplitudes of both the microphonic and neural components of round window responses to low intensity clicks did not decrease during bodily movements in contrast to the attenuation observed in intact animals executing similar movements (Fig. 4). More-

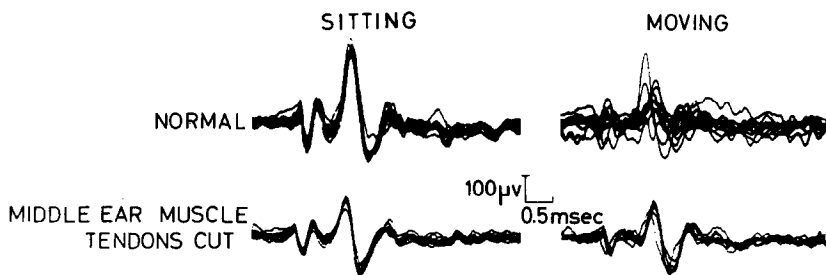


FIG. 4. Effects of sectioning of the tendons of the middle ear muscles on round window responses to clicks. The onset of the sweeps occur after the delivery of the square wave pulse to the loudspeaker.

over, in the animals with severed middle ear muscle tendons, the amplitudes of click evoked responses recorded from subcortical stations along the auditory pathway were similarly unaffected during movements (Fig. 5) whereas cortical evoked responses decreased in amplitude even in the absence of action of these muscles (Figs. 2, 3, 5). Thus, there appear to be at least two distinct mechanisms operating to modify click evoked responses during motor activities. The first involves alterations of sound input as a result of middle ear muscle activity and undoubtedly affects evoked responses recorded from all levels of the auditory pathway. The second mechanism involves central processes which modify cortical evoked responses even in the absence of middle ear muscle activity.

Effects of Motor Activity on Auditory Cortex. A brief electrical pulse applied through bipolar electrodes located along subcortical stations of the auditory pathway (cochlear nucleus, superior olive, inferior colliculus, and medial geniculate body) elicited potentials in auditory cortex which resembled click evoked responses: There was an initial biphasic deflection lasting about 25 msec followed by a series of longer lasting waves. Any prompt modifications of the shock evoked responses appearing during movements must reflect central mechanisms since the shock bypasses the regulatory effects induced by middle ear muscle activity. The present

analysis concerned only the changes in amplitude of the initial response deflection. The amplitude of shock evoked responses in cortex decreased during motor activity depending on the location of the stimulating electrodes. Thus, auditory cortical responses evoked by subthalamic stimula-

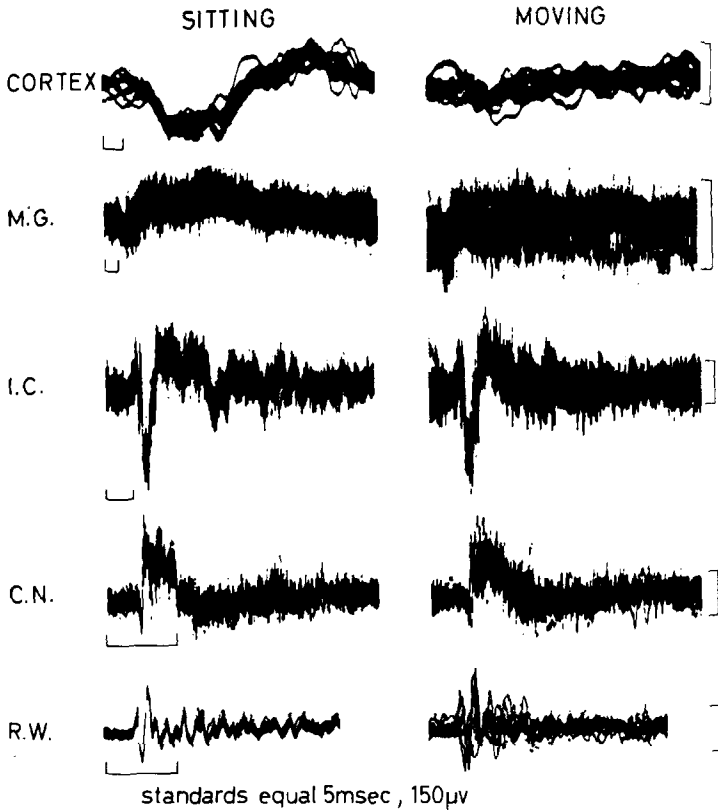


FIG. 5. Effects of bilateral sectioning of the tendons of middle ear muscles on click evoked responses. RW and cortical responses recorded from one animal and other responses recorded from another animal.

tion (cochlear nucleus in three cats, inferior colliculus in three) always decreased in amplitude during movements while responses evoked by medial geniculate stimulation (in five cats) were not attenuated during similar motor activities (Fig. 6). These results suggest that mechanisms modifying auditory cortical responses during motor activity do not in-

fluence the cortex directly but, rather, act at intermediate sites conveying impulses from subthalamic nuclei of the auditory pathway toward the auditory cortex.

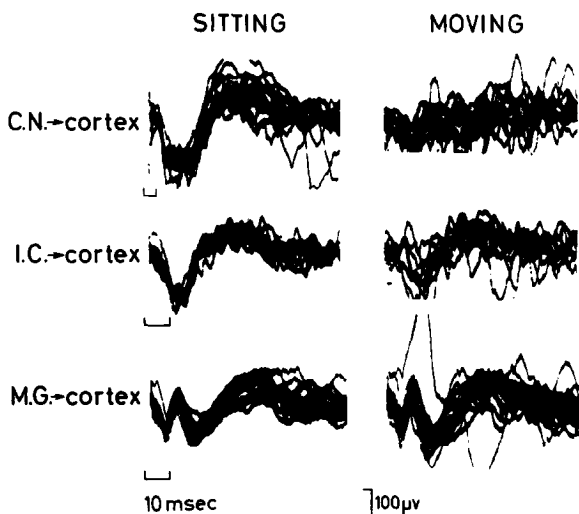


FIG. 6. Effects of movements on cortical responses to electrical stimulation of subcortical stations along the auditory pathway. Cortical responses to cochlear nucleus and inferior colliculus stimulation recorded from the same animal. Cortical responses to medial geniculate stimulation recorded from another animal whose cortical responses to click stimuli are shown in Fig. 2. The onset of sweeps coincide with the stimulus.

Discussion

Effects of Motor Activity on Click Evoked Responses. These results indicate that something associated with the animal's motor activity significantly affects the amplitude of click evoked responses recorded all along the auditory pathway. This interpretation is supported by observations of a decrease in amplitude of acoustic evoked responses during a wide range of motor activities including vocalization, scratching, and bodily movements (23), eating (12), head and neck movements (42), swallowing (42), lever pressing (16), extreme activity (36) and orienting responses to novel stimuli (24, 31, 33). The present evidence indicates that neurophysiological mechanisms relating to middle ear muscles and central processes underlie the response modifications and that recording artifacts associated with movements, masking of clicks by noises gener-

ated within the animal during movements and variations in sound intensity in different parts of the experimental cage (30) cannot account for the observed response changes. The attenuation of click evoked responses accompanying motor activity might provide an explanation for the report of Hernández-Peón, Scherrer and Jouvet (20) that click evoked responses recorded from cochlear nucleus in cats decreased in amplitude during "attention" to a novel stimulus such as a mouse. Behavioral evidence of "attention" in cats is usually considered to involve turning the head, neck and body in the direction of the novel stimulus. In the present experiments evoked responses decreased in amplitude during such movements but were of control amplitudes, or as in the experiments of Horn (21), even larger than controls when cats simply stared at a novel stimulus. Thus, response attenuation accompanying the presentation of novel stimuli may be due simply to the animal's movements rather than "attention," per se. Moreover, the changes in evoked responses accompanying orienting movements cannot be ascribed to activity in mechanisms specific to the orienting reflex (31), since click evoked responses also decrease in amplitude whenever cats move.

Mechanisms Modifying Click Evoked Responses. At least two distinct mechanisms participate in modifying click evoked responses during movements: Contractions of the middle ear muscles affect evoked responses in subcortical stations along the auditory pathway; and central mechanisms modify cortical evoked responses independently of middle ear muscle action. The middle ear muscles are coordinated with general bodily movements and become active within 5–20 msec following the onset of activity in neck or limb muscles (A. Starr and G. Salomon, in preparation). The middle ear muscle contractions cause an attenuation of sounds reaching the cochlea by as much as 30 db (4, 10). This, in turn, affects the amplitude of sound evoked responses recorded from along the auditory pathway.

A comparable dual regulatory system consisting of both peripheral neuromuscular and central mechanisms affects light evoked responses recorded from along the visual pathway (1, 8, 34). Single units in visual cortex show changes in both spontaneous activity (27) as well as in light evoked activity (6) whenever animals move. Electrical stimulation of areas of the nervous system (cerebellum, reticular formation and somatosensory cortex), known to produce stereotyped movements in unrestrained animals (7, 13, 38), may also effect modifications of visual (18), auditory (5, 22, 25, 40) and somesthetic (14, 15, 41) evoked re-

sponses. In both the acoustic and visual systems the peripheral neuromuscular mechanisms affect evoked response amplitudes by regulating the intensity of environmental stimulus impinging on the receptor organs. The site of action of central mechanisms modifying cortical evoked responses is unknown in both cases. Results from the present experiment imply that the central processes may modify cortical evoked responses by interfering with extralemniscal pathways linking brainstem and cortex rather than by direct effects on the cortex itself. Thus, cortical responses evoked by electrical stimulation of brainstem nuclei along the auditory pathway (cochlear nucleus, superior olive, inferior colliculus) were regularly attenuated whenever animals moved, whereas evoked responses to medial geniculate stimulation were unchanged during similar movements. Galambos, Meyers and Sheatz (9) demonstrated that there are pathways for transmitting acoustic evoked impulses to cortex which bypass the brachium of the inferior colliculus. Such pathways might project from the inferior colliculus to the midbrain reticular formation (32) and thence to cortex. The reticular formation would be particularly suited for the modifications of sensory messages during movements since the reticular formation is itself also intimately involved in regulating motor activity (26, 28).

Thus, the integration of sensory and motor events occurs not only centrally, but peripheral to the receptor, before the environmental stimulus has affected the nervous system, by means of middle ear and pupillary muscle controls. The changes appearing in sensory pathways in animals during movements probably also occur in man, and may be the basis for human perceptual modifications reported to occur as a consequence of motor activity (17, 35).

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