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Research Report

SPINAL MOTOR RESPONSES TO ACOUSTIC STIMULATION *

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SUMMARY PAGE

THE PROBLEM

The phenomenon of direct activation of spinal motor mechanisms by auditory stimulation (startle reaction) is well-known; however, the neural pathways through which this reflex reaction is mediated are not known. This investigation was designed to determine how a volley of impulses set off by auditory stimulation may traverse the brain stem and descend the spinal cord to give rise to a patterned ventral root response.

FINDINGS

Certain aspects of the mechanisms mediating auditory-induced spinal motor activity have been examined by recording within the bulb and from motoneurons at both cervicothoracic and lumbosacral levels. Single auditory click stimulation elicits, in lightly strychninized cats, motor responses appearing along both sides of the spinal cord. In the competition for access to the final common path, the evoked descending acoustic volley of impulses is readily blocked by prior dorsal root stimulation. Since the ventral root responses recorded contralaterally to the side of auditory stimulation have the same appearance, respond identically to higher frequency stimulation, and interact with dorsal root responses in an identical way, as do the ipsilateral ventral root responses, it is assumed that the acousticospinal mechanisms on the two sides of the spinal cord are mirror images of each other, elicited from a common brain stem neuronal pool.

Decerebration and cerebellectomy do not interfere with the transmission of this acousticospinal reflex activity. Auditory projections to the brain stem reticular formation are evidently sufficient to maintain the pattern of the descending reflexes. Partial sections of the spinal cord demonstrate that the descending connections necessary for the transmission of auditory-induced activity are part of a diffusely projecting spinal system. Bilateral motoneuron discharges following unilateral acoustic stimulation are ensured by an abundance of functional crossings in the bulb and along the extent of the spinal cord.

INTRODUCTION

Auditory stimulation may not necessarily activate tracts and nuclei belonging only to the "classical auditory system," but may also trigger neural activity of far reaching systems eventuating finally in the activation of peripheral effectors. The mechanisms for directing neural activity into one or another set of channels, and so focusing attention on one or another input, or selecting an output, are but little understood.

The familiar startle reaction evoked by unexpected auditory stimulation offers a striking example of how sudden recruitment of a larger population of neurons gives rise to complex and variegated motor behavior (2,3,11). In anesthetized or decerebrate cats, the physiologically available neurons of the auditory system appear insufficient for the conduction of a traceable volley of impulses, evoked by natural cochlear stimulation, into the spinal cord. In order to elicit responses from motor neurons along the extent of the cord, it is necessary to mobilize the reserve of anatomically existent connections by establishing a high level of excitability through administration of chloralose (2) or strychnine sulphate in a subtetanic dose.

The present investigation is designed to determine how a volley of impulses set off by auditory stimulation, after entering the lower brain stem, may descend the spinal cord and give rise to a patterned ventral root response involving motoneurons having both large and small amplitude spikes. The study also considers the complex interaction between descending auditory impulses and activity mediated through segmental and intersegmental propriospinal systems as reflected by alterations in spinal motor outflow.

PROCEDURE

Successful experiments were performed on 28 cats of which 6 were anesthetized with intravenously administered chloralose and the rest decerebrated by an intercollicular transection during ether anesthesia. The cats were kept fully immobilized by iterative doses of curare (Syncurine, Burroughs-Wellcome and Co.) and were maintained by artificial respiration. As specified in the Results, a complete cerebellectomy was carried out in certain of the experiments. Following laminectomy the spinal cord was protected by a pool of continually warmed mineral oil. The ventral roots L7 or S$_1$, and, in some cases, the corresponding dorsal roots were divided intradurally, allowing their central portions to span the tips of bipolar silver electrodes for recording and stimulating purposes. In some experiments the deep radial nerve was exposed near the lower end of the humerus and employed in recording. For brain stem recording, the posterior fossa was approached through an occipital craniotomy, the floor of the fourth ventricle was exposed by cerebellectomy, and the medulla was penetrated by a stereotaxically oriented coaxial electrode.

For free field click and/or white noise stimulation, a loudspeaker was placed at the opening of the right external ear. Both types of stimuli were measured by an Altec Type 21BR-180 condenser microphone system set up at 0° incidence with the diaphragm in the plane of the mouth of the loudspeaker and connected to a calibrated oscilloscope. Voltage measurements were converted to sound pressure level in decibels re 2×10^{-4} dynes/cm^2. Auditory stimulation was confined to the right ear. The left cochlea was removed completely or, less often, the left VIIIth nerve was severed in its span between internal auditory meatus and brain stem.

RESULTS

No visible response to click or white noise stimulation of high intensity was obtained by recording from spinal motoneurons of either cervicothoracic or lumbo-sacral levels. It is conceivable, however, that descending impulses evoked by acoustic stimulation may reach all levels of the spinal cord, but not in a sufficiently synchronized fashion to elicit a visible response from spinal motor roots. If so, even slight changes in motor pool excitability would be reflected by amplitude variations of a local segmental reflex discharge, elicited at various intervals following click stimulation or during white noise stimulation. Several trials of even this sensitive method of detection of auditory-induced spinal activity failed to give evidence of such effect in experiments upon chloralose-anesthetized or decerebrate animals.

CHARACTERISTICS OF SPINAL MOTOR REPONSES
TO AUDITORY STIMULATION

Unambiguous ventral root responses followed regularly upon acoustic stimulation when a subtetanic dose of strychnine sulphate of about 0.1 mg per kg body weight was injected intravenously. The appropriate subtetanic dose is difficult to establish since repeated acoustic stimulation may suddenly trigger a vigorous strychnine tetanus.

Figure 1 A shows acoustic responses recorded at equal amplifications from the left and right L_7 ventral roots in a decerebrate cat with only the right ear intact. Single click stimulation of 147 db was applied every four seconds. During strychnine hyperexcitability, the lumbar ventral root responses appeared after a latency of 17-21 msec, had a duration of 10-15 msec, and an amplitude of about 0.5 V. The functional characteristics of the responses of corresponding right and left lumbar roots seemed to be identical even though the sensory input was unilateral. Neither the latencies, the slopes of the ascending limbs, the duration, nor the amplitudes differed significantly. The slight differences in response amplitude between the two sides which were encountered in some experiments can be explained by slight mechanical trauma during preparation of the ventral roots. This assumption is supported by recording the activity during an induced strychnine tetanus. When the responses to acoustic stimulation are of the same size, the spontaneously appearing strychnine waves are always of the same amplitude bilaterally. In those preparations showing haphazard differences in response

Figure 1

Decerebrated, strychninized cat. Left cochlea destroyed. Responses to click stimulation recorded from VRL7 left side (upper beam) and VRL7 right side (lower beam). Frequency of stimulation gradually increased as shown in:

A. One click every 4 seconds.

B. One click every 2 seconds.

C. One click every 1.6 seconds.

D. One click every second.

E. Control response to single shock DRL7 stimulation recorded from corresponding ventral root.

F, G, H. Segmental reflex responses preceded at increasing intervals by responses elicited by click stimulation.

I and J. Paired stimuli applied every 1.6 seconds and 1 second, respectively.

K. Response to click stimulation recorded from VRL7, right side.

L. Same as K., but preceded by local segmental reflex response.

Dots mark moment of click stimulation. Time scales in 1 msec intervals (A – D) and in 10 msec intervals (E – L).

amplitude to click stimulation, the amplitudes of the waves of the rhythmic convulsive neuronal activity evoked by strychnine revealed a similar amplitude discrepancy.

The firing rate of a vigorous strychnine tetanus (20-30 waves/sec) was not influenced by click stimulation, the strychnine activity being in complete command of the motor outflow and thus precluding activation of the motor cells by descending volleys of impulses evoked by acoustic stimulation. During this initial stage the strychnine waves were always of higher amplitude than those evoked by click stimulation before or after a tetanic period. Only when the strychnine tetanus became weak and irregular was it possible to elicit click responses of an amplitude exceeding that of the waning strychnine waves. As a consequence, recording of responses to acoustic stimulation was confined to periods either before the slowly injected dose of strychnine accumulated enough to trigger a tetanus or after the tetanic discharge had completely stopped.

The spinal motor responses to click stimulation were very sensitive to an increased frequency of stimulation (Figure 1 A-D, H-J). When the rate of stimulation was gradually increased from one click every four seconds to one click per second, the motor responses declined in amplitude and eventually disappeared (Figure 1 A-D). Figure 2 depicts graphically the relation between response amplitude and frequency of click stimulation.

INTERACTIONS BETWEEN SPINAL ACOUSTIC RESPONSES AND SEGMENTAL SPINAL REFLEX ACTIVITY

When an evoked segmental reflex response was preceded by a motor root volley elicited by click stimulation, there was a slight but nonetheless clear effect on the segmental reflex response. Following strychninization, and simultaneously with the appearance of the response to click stimulation, both the mono- and polysynaptic components of the local segmental reflex response were augmented. Figure 1 E shows control L7 segmental reflex response in a lightly strychninized cat. In F, this local discharge was preceded at a short interval by a click response. The monosynaptic component of the segmental reflex response may show a slight decline in amplitude, but the polysynaptic activity was markedly influenced and was completely obliterated at this interval between the two stimuli. The same effect of interaction was noticed between spontaneously appearing strychnine waves during a tetanus and the local segmental reflex response (Figure 3 A and B). A gradual increase of the interval between the click and the segmental reflex evocation still shows an effect of interaction (Figure 1 G) until the two responses, measured from stimulus point to stimulus point, are about 70 msec apart at which interval the segmental reflex response returns to control amplitude (Figure 1 E and H). At this setting, the frequency of click and electrical shock stimulation, respectively, was increased from one pair of stimuli every 4 seconds (Figure 1 H) to every 1.6 seconds (Figure 1 I) and every 1 second (Figure 1 J). The click evoked response was unable to follow the higher rate of stimulation and disappeared while the

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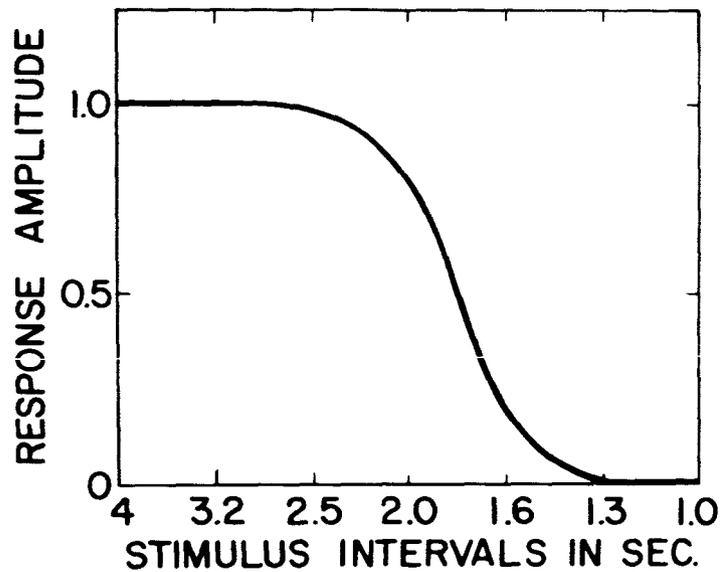
Figure 2

Curve showing amplitude of acoustically-induced motoneuron discharge plotted against stimulus interval. Control amplitude is represented by the arbitrary value of 1.0; stimulus intervals are given in seconds.
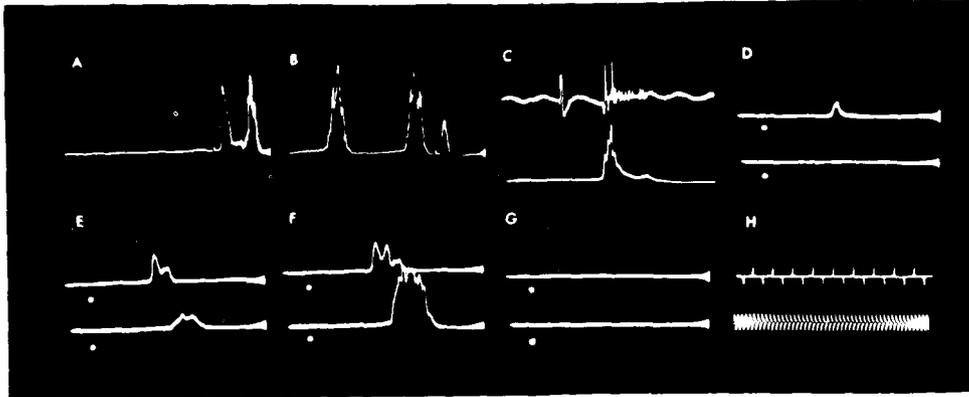
Figure 3

Decerebrated, strychninized cats.

A. DRL_7 - VRL_7 control response.

B. DRL_7 - VRL_7 control response during strychnine tetanus.

C. Click responses recorded simultaneously from L_7 ventral root filament showing individual unit responses (upper beam) and parent L_7 ventral root (lower beam).

D - G: Responses to single click stimulation recorded simultaneously from ipsilateral radial nerve (upper beam) and L_7 ventral root (lower beam). Threshold determination obtained by gradually increasing the click intensity:

D. 137 db intensity.

E. 145 db intensity.

F. 146 db intensity.

G. Acoustic responses to 146 db click stimulation (122 db).

H. Time scales in 10 msec intervals (upper beam) for records A, B, and C and in 1 msec intervals (lower beam) for records D - G.

White dots mark the moment of click stimulation.

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polysynaptic component of the segmental reflex response showed the usual increase in size (Figure 1 J) seen in both strychninized and nonstrychninized animals during higher rate of stimulation.

When two stimuli were delivered in reverse order, i.e., the click evoked response preceded by the local reflex response at gradually increasing intervals, the former was completely obliterated over an interval of about 300 msec before it began to return to control level (Figure 1 K and L). Thus, in the competition for access to the final common path, the local segmental reflex response was in more powerful and long-lasting control of the motor pool.

SEGMENTAL ANALYSIS OF SPINAL ACOUSTIC RESPONSES

Figure 3 C shows responses to supramaximal click stimulation recorded simultaneously from a thin filament of the VRL_7 (upper beam) and the parent root itself (lower beam). The motor outflow consists of both gamma and alpha impulses. Filament recordings show that the threshold response to acoustic stimulation is lower for the gamma fibers than for the alpha. In Figure 3, D–G, the acoustic responses were recorded simultaneously from the deep radial nerve (upper beam) and the VRL_7 of the right side. At a sound pressure level of 137 db, the first response appears in the radial nerve recording (Figure 3 D). At 145 db, responses are seen in both recordings (Figure 3 E). The radial nerve response appears after a latency of 15 msec, the VRL_7 response after 19 msec. The difference in latency between responses at the two levels is small compared with the over-all latency, suggesting that the relatively long latencies for the acoustically evoked responses, recorded at both cervicothoracic and lumbosacral levels, are due to delays at some higher level rather than to slowly conducting spinal pathways or to exceptional spinal nuclear delay. On the contrary, the small difference of 4 msec indicates rapid spinal conduction. A further increase in acoustic stimulus intensity (146 db) evoked maximal responses (Figure 3 F). These maximal spinal motor responses following click stimulation were completely obliterated when white noise stimulation was applied simultaneously. This masking effect is demonstrated in Figure 3 F (control) and G where the responses to 146 db click stimulation were abolished by applying white noise stimulation at a sound pressure level of 122 db.

SIMULTANEOUS RECORDINGS OF ACOUSTICALLY EVOKED RESPONSES FROM BULBAR AND SPINAL REGIONS

The assumption that descending impulses of cochlear origin may pass down each side of the spinal cord in a symmetrical fashion is based on the observation that ventral root responses on each side of both cervicothoracic and lumbosacral levels were similar in appearance, responded in a like manner to repetitive stimulation, and interacted identically with peripheral nerve evoked responses. The crossover from the side of auditory input to the contralateral side must be accomplished without much delay since there was no measurable latency difference between the two opposite ventral root responses. In an endeavor to understand how cochlear influences are projected onto

spinal mechanisms we sought to observe directly the influx of acoustically evoked responses as they invade the brain stem. Since this series of experiments was performed upon decerebrate cats after a complete cerebellectomy, several central connections of the auditory system were eliminated from the outset (1, 10). Figure 4 A shows the response to single click stimulation obtained from the ipsilateral cochlear nuclei (upper beam) in a nonstrychninized cat. No response is visible in the VRL7 recording (lower beam)of the corresponding side. As usual, this response first appeared after strychnine was injected in a subtetanic dose (Figure 4 B). The responses were completely abolished by the application of continuous white noise stimulation (Figure 4 C). The breaking up of a previously synchronized volley of impulses evoked by click stimulation, and consequent elimination of a visible spinal motor response, does not necessarily rule out any subtle excitability changes within the motor pools elicited by the more continuous stream of descending auditory impulses evoked by white noise stimulation. In order to test this possibility, a lumbar segmental reflex response was evoked before (Figure 4 D) and during white noise stimulation (Figure 4 E). In addition to the conventional local reflex response, there appears the delayed (spino-bulbo-spinal) activity, now enhanced by strychnine. This delayed activity is channeled through supraspinal connections bracketed somewhere between the inferior colliculi and the obex before re-entering the spinal cord from above downward (8, 9, 12). As seen in Figure 4, D and E, both the local segmental reflex response and the delayed activity were uninfluenced by the application of white noise stimulation. Figure 4 F (upper beam) shows the lack of click stimulation effect upon the cochlear nuclei response during a vigorous strychnine tetanus which, however, prevents the evoked descending volley of impulses from activating the ventral horn cells (lower beam).

Figure 4 G demonstrates control responses to single click stimulation, recorded from the cochlear nuclei (upper beam) and VRL7 (lower beam). In Figure 4, H and I, these responses were preceded, at two different intervals, by the local segmental reflex response and by the delayed activity elicited by DRL7 single shock stimulation. As expected, no effect was revealed in the cochlear nuclei recording, but the ventral root response to acoustic stimulation was extinguished. When the two stimuli were delivered in reverse order, i.e., the click stimulation preceded the shock to the dorsal root, the monosynaptic component of the segmental reflex response was slightly decreased in amplitude while the polysynaptic and delayed responses were abolished (Figure 4 J and K). With this same experimental arrangement, a simultaneous application of white noise stimulation immediately prevented the click responses from appearing as motor responses whereas the local and delayed reflex responses to dorsal root activation again became visible (Figure 4 L).

The convergence of impulses from a multitude of different sensory receptors and central structures onto the reticular formation has been abundantly demonstrated. When auditory click stimulation was applied and recordings were made from the bulb of decerebrate-decerebellate cats, large responses were recorded bilaterally throughout both the medial and the lateral reticular formation. The latency of these responses, about

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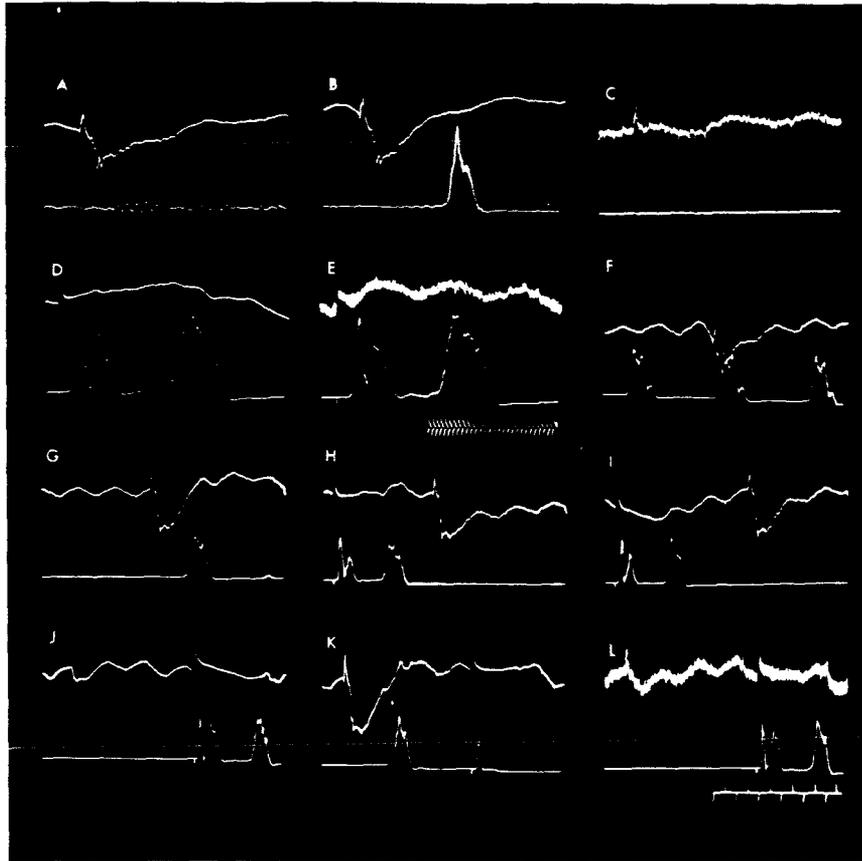
Figure 4

Decerebrate, decerebellate cat.

Simultaneous recordings from right cochlear nuclei (upper beam) and right VRL$_7$ (lower beam). Recording A illustrates single click auditory stimulation before strychnine injection; B, after strychnine injection; and C, during simultaneous white noise stimulation.

D. Single shock DRL$_7$ activation.

E. Single shock DRL$_7$ activation during white noise stimulation.

F. Single click stimulation during strychnine tetanus.

G. Single click stimulation.

H and I. Responses to single click stimulation preceded at two different intervals by activity evoked by DRL$_7$ single shock stimulation.

J. Responses to DRL$_7$ stimulation.

K. Same as J, but preceded by click evoked response.

L. Same as K, but during white noise stimulation.

Time scales in 1 msec intervals for A – E and 10 msec intervals for F – L.

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3 msec, was not altered by strychnine administration. Figure 5 shows the responses to single click (A) and DRL_7 single shock stimulation (B), recorded from the reticular formation (upper beam) and VRL_7 (lower beam) in a nonstrychninized cat. The site of brain stem recording was midway between obex and the entrance of the VIIIth nerve, 1 mm right of the midline, and about 4 mm beneath the floor of the fourth ventricle. Figure 5 C depicts the responses to DRL_7 stimulation obtained from the same recording site in a strychninized cat. In Figure 5 D, these responses are preceded by activity evoked by single click stimulation. In addition to the interaction between the two responses (lower beams) evident at the spinal segmental level, there is clear-cut evidence that strong interactions also take place within the reticular formation.

ANATOMICAL CONSIDERATIONS

Ventral root responses to acoustic stimulation do not depend upon integrity of the local dorsal roots or upon nervous centers above the intercollicular decerebration level. Nor does the cerebellum provide a way-station of any significance in the conduction of descending auditory impulses, as judged by the lack of effect of a complete cerebellectomy upon the bilaterally recorded ventral root responses.

When a hemisection of the cervical cord at the C_1 level was performed on the right side, i.e., ipsilateral to the side of acoustic stimulation, in a cat with the left cochlea destroyed, no interference could be observed affecting the ipsilateral acoustically evoked lumbar root response. This demonstrates that, whatever excitations cross from the cochlear nuclei on one side to the contralateral bulbar reticular formation on the other side, fibers from this latter region re-project back in sufficient quantity to ensure bilateral responses in strychninized cats. Hemisection at the level of entrance of the most cranial rootlet of the seventh lumbar root on the right side, thereby cutting all descending uncrossed pathways and eliminating any conduction through tracts recrossing along the extent of the cord above the level of that cut, left a right sided VRL_7 response markedly reduced in amplitude and with a latency increased by about 2 msec (Figure 5 E and F).

DISCUSSION

Although the gap between results obtained in animal experiments and neurological findings in man may be difficult to bridge, the described impulse activity evoked by acoustic stimulation and recorded from motoneurons at widely separated levels of the spinal cord may contribute to identifying some essential features of physiological and anatomical organization of Moro's reflex and the startle reaction. Cinematographic and electromyographic studies of the startle reaction distinguish between primary and secondary startle reactions; the primary is supposed to be an acousticomotor reflex descending directly through lower brain stem and spinal cord while the secondary is thought to involve the cerebral cortex and the thalamus or striatum (4, 13). Since, in the present experiments, acousticomotor responses were observed in decerebrate cats, it is evident that these observations may be considered relevant to the primary startle
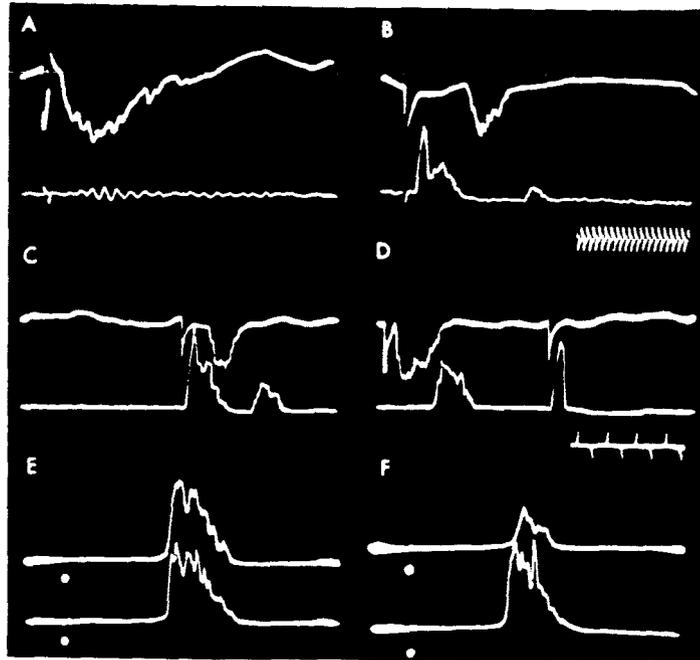
Figure 5

Decerebrate, decerebellate cat. Simultaneous recordings from brain stem formation (upper beam) and right VRL_7 (lower beam):

A. Single click response.
B. Responses to single shock DRL_7 activation.
C. Responses to single shock DRL_7 activation. Cat strychninized.
D. Same as C, but preceded by responses evoked by single click stimulation.

Decerebrated, strychninized cat:

E. Responses to single click stimulation recorded from VRL_7 right side (upper beam) and VRL_7 left side (lower beam).
F. Same as E, but after right side spinal cord hemisection at the level of entrance of the uppermost cranial rootlet of DRL_7.

Dots mark moment of click stimulation. Time scales in 1 msec intervals (upper beam) for recordings A, B, E, and F and in 10 msec intervals for C and D.

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reaction only. Since it is necessary to establish a state of hyperexcitability by the injection of strychnine in order to obtain visible responses, it is not possible to warrant that all connections involved in conducting the descending acoustic influences function in this way under more physiological conditions.

The motor responses evoked by single click stimulation and recorded bilaterally from lumbosacral vental roots have a latency of 17-21 msec. Single shock electrical stimulation applied to the peripheral branches of the vestibular nerve elicits bilateral responses from the same roots after a latency of only 5 msec (7). The difference between application of natural stimulation, thus activating the peripheral receptors, and evoking a synchronized volley of impulses by direct electrical stimulation of the nerve filaments just central to the receptor structure cannot explain this large a discrepancy in latencies, as is clearly demonstrated by recording the influx of impulses into the vestibular and cochlear nuclei, respectively. The response to an electrically induced vestibular volley has a latency of 2 msec and that to acoustic stimulation a latency of about 3 msec. The latency of the cochlear nuclei response is the same in nonstrychninized and strychninized cats. The simultaneous recording of the motor outflow from cervicothoracic (deep radial nerve) and lumbar levels shows that the latency difference between the responses is the same, i.e., 4 msec, as when recording the responses to vestibular stimulation from the same outputs (6). Thus, like the descending vestibular impulses, the descending auditory impulses must be conducted along large-diameter fibers of approximately alpha velocity within the spinal cord (7). Since we have a rapid activation of the cochlear nuclei and a fast speed of conduction along the spinal cord, it is necessary to search for some other link in the chain of conduction which might be responsible for the remarkable delay of descending impulse transmission. Central recording of responses to auditory stimulation indicates that rather extensive regions of the reticular formation are activated bilaterally. Conduction within the reticular formation is slow, occurring at a rate of only 1.5 to 3 m/sec. Responses evoked by auditory stimulation require an elapsed time of 16 to 20 msec to traverse the distance from the receptors to the mesencephalic brain stem reticular activating system (5). A 10-12 msec central bulbar delay of the main reticulospinal discharge would account for the latency differences between the responses recorded from the cochlear nuclei and those from the radial nerve. A delay of this order of magnitude is comparable to that of reticular formation latencies to sensory stimulation. It can be assumed that impulses elicited by acoustic stimulation encounter synaptic relays within the lower brain stem reticular formation before they can descend along the spinal cord. Cells in the nucleus reticularis gigantocellularis are known to give rise to reticulospinal fibers which may provide the descending linkage by which auditory impulses can reach all levels of the spinal cord (12).

In a functional sense, it is not surprising that there should be a difference in latency to final common paths of the volleys evoked by auditory and vestibular stimulation, respectively. The vestibular influence on spinal motor neurons is primarily tonic, while the auditory, so far as we are justified in relating it to the startle response, is more phasic. In addition, the vestibular conduction system to spinal motor neurons is

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open and easily activated under the modified physiological conditions of experimental situations, whereas the descending auditory system is notably active only after strychnine administration. Weak, repetitive stimuli are effective in influencing the descending vestibulospinal pathways on a sustained basis. In contrast, the acousticospinal connections have a high threshold and are geared to a pattern of massive, transient, less repetitive reaction. Continuous acoustic stimulation with white noise, even at a high intensity level, fails to evoke spinal motoneuron activity in strychninized animals. This suggests the possibility that, while impulses evoked by a short-lasting stimulus, such as a loud click, may be effectively transmitted, any sustained activity elicited during steady-state stimulation may lead to self-cancellation among the diffuse interconnections of the reticular system.

The spinal motor responses to acoustic stimulation are remarkably frequency sensitive. Simultaneous recording from the cochlear nuclei and lumbar or sacral ventral roots shows that the effect is not entirely a peripheral one since the spinal motor response declines in amplitude and disappears at a frequency of stimulation which still leaves a visible response at the cochlear nuclei. This smaller volley of impulses, however, may now be of subthreshold strength for evoking the descending activity. In order to obtain spinal motor responses, powerful volleys of well-synchronized auditory impulses must enter the brain stem. The relatively high threshold of these responses makes it necessary to apply strong and abrupt acoustic stimuli, i.e., clicks of about 140 db intensity. The marked difference between the acoustic responses and those obtained by activation of the vestibular system allows us to rule out the possibility that we are dealing here with a Tullio effect.

In addition to the decline and disappearance of the responses at higher frequency stimulation, they are under powerful proprioceptive control. Thus, the startle reaction evoked by auditory stimulation will ultimately damp and thereby control itself. The feed-back of proprioceptive impulses, initiated by muscular contraction, will prevent additional descending auditory-evoked impulses from further activating the ventral horn cells. The psychological aspects of alertness, attention, and preparedness will also be involved in the rapid decline of any outward expression of the startle reaction during repetitive, acoustic stimulation.

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