Secondary Projections from Trigeminal Nucleus Caudalis in Cat Rendered Overreactive to Tactile Facial Stimulation*

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Noxious stimuli applied to the fields of the peripheral receptor of the trigeminal nerve are relayed in nucleus caudalis of the trigeminal spinal complex.8,48 Clinical observations incident to spinal V tractotomy14,18,47,51,56,58–60,68,74 have affirmed consistently the participation of this relay in the appreciation of painful stimuli in man. However, studies utilizing single-unit techniques of recording have failed to establish the presence of neurons in nucleus caudalis that respond specifically to noxious stimuli.17,32–34,1 This dichotomy of clinical and experimental observation serves to emphasize the complexity of the neuronal mechanism subserving noci-perception.

It has been suggested that the primary neurons of relay are not specific in modality but rather act as “common carrier cells”4,70 which relay and encode a pattern of peripherally evoked activity which is decoded and integrated centrally. Recent anatomic and physiologic studies suggest that the trigeminal input to certain regions of the midbrain and thalamus is relayed primarily through nucleus caudalis.67–69 These regions are the centrum medianum-intralaminar nuclear complex, portions of the substantia reticularis mesencephalicus, and pars magnocellularis of the corpus geniculatum medial. To consider further characteristics of the trigeminal input to these loci, strychnine was applied to the surface of the medulla at the level of the trigeminal nucleus caudalis has been reported to induce marked behavioral overreaction to light mechanical deformation of facial hair and skin of cat.25 This preparation of strychnine was utilized to compare evoked responses in midbrain and thalamic loci dependent upon a nucleus-caudalis relay and those responses evoked by impulses relayed at all other levels of the trigeminal nuclear complex.

Methods

Fifty-two adult cats weighing 2 to 4 kg. were anesthetized with ether. After tracheostomy they were placed in a Johnson “210” stereotaxic frame. The infraorbital nerve, gasserian ganglion, lower medulla, and contralateral cerebral cortex were exposed. Rectal temperature was monitored and was maintained between 36–38°C. with external heat. Bipolar silver-hook electrodes were placed on the infraorbital nerve for stimulation. Bipolar steel needles (½ mm. apart, 1 mm. offset and with exposed tips measuring 60–100 μ) were inserted with a micromanipulator into the ipsilateral trigeminal nucleus caudalis for stimulation or recording. Similar bipolar electrodes were used for recording at the ipsilateral gasserian ganglion and selected regions of the mesencephalon and diencephalon contralateral to the side of stimulation. Recording electrodes were positioned in subcortical regions using stereotaxic measurements adapted from the atlas published by Jasper and Ajmone-Marsan.26 The electrical activity led from as many as three subcortical regions was observed in each preparation at approximately 0.2 mm. intervals during descent of the electrodes.

In establishing the adequacy of each preparation for study, the evoked response in nucleus caudalis and the gasserian ganglion incident to stimulation of the infraorbital nerve, and the evoked response at the gasserian ganglion incident to stimulation of nucleus caudalis were examined. The primary neuronal “spike” and a delayed centrifugally conducted potential at the
gasserian ganglion* in each instance were identified. These responses confirmed that the stimulating electrodes at nucleus caudalis and the infraorbital nerve were positioned appropriately and that the preparation had sustained adequate blood pressure and respiration and little trauma to neural elements involved. With mild anoxia, deep anesthesia, lowered blood pressure or trauma the delayed activity recorded at the gasserian ganglion diminished rapidly in amplitude and duration. Monitoring of these elements was repeated throughout and at the end of each experiment to consider further the reliability of evoked neural activity in the midbrain and thalamus.

Monophasic stimuli (Grass stimulator Model S4D), 0.01 msec. in duration, were delivered through an isolation transformer and raised slowly in intensity to establish the voltage required to evoke a threshold and a maximum evoked response at each site of recording. The intensity of stimulus required to evoke a maximum response was used in this study.

When responsive sites were located in the mesencephalon and diencephalon and records had been obtained incident to stimulation of the infraorbital nerve and nucleus caudalis, a tiny collection of powdered strychnine on a moist 1 mm. cottonoid pledget was applied over the surface of nucleus caudalis caudal to the electrode which was positioned below the obex. As the preparation gradually developed overreaction to tactile facial stimulation and the delayed activity recorded at the gasserian ganglion increased, recordings of evoked potentials from the upper brain stem were again obtained for comparison with the responses obtained before the application of strychnine. Only one position of the recording electrodes could be studied in any one preparation as it occasionally required as long as 1 to 2 hours for changes incident to strychnine to subside even with copious irrigation of the posterior fossa.

Recording electrodes were led to capacity-coupled amplifiers. The evoked responses were photographed from a dual-beam oscilloscope.

Ether anesthesia was administered at intervals throughout recording periods without interfering with the overreaction to tactile stimulation or the amplitude of evoked responses.

Spinal V tractotomies rostral to the electrode in nucleus caudalis and midline medullotomies from the obex to C2 were performed in selected circumstances to isolate the peripheral trigeminal afferents from central projections arising from nucleus caudalis and to interrupt projections from nucleus caudalis to higher relays. Decerebration was accomplished in some preparations by transection at the intercollicular level.

Recording sites were marked by the technique described by Hess. Frozen serial sections of the medulla and upper brain stem were stained by a Nissl method and examined microscopically to establish the extent of the tractotomies and medullotomies and to relate the recording sites to anatomic structures.

We have employed the nomenclature used in the atlas of Jasper and Ajmone-Marsan. 

Observations

Many regions of the midbrain and thalamus have shown an evoked response incident to stimulation of the trigeminal nerve. Our observations relate primarily to those portions of the upper brain stem that are altered by the application of strychnine to nucleus caudalis.

In this circumstance the animal characteristically developed overreaction* to tactile facial stimulation and an increase in amplitude and duration of the delayed potential recorded at the gasserian ganglion.

The overreaction to tactile facial stimulation was abolished by a dorsolateral tractotomy across spinal V. It was diminished markedly by contralateral hemidecerebration and was abolished by a total decerebration. We have therefore considered that projections from nucleus caudalis to the thalamus that were interrupted by decerebration may have relayed at the thalamus and been essential to sustaining the behavioral change described as overreaction to tactile facial stimulation. Further, we have attempted to determine whether under this circumstance a change in the evoked re-

* A quick ipsilateral squint, a twitch of the corner of the mouth and occasionally of the ear, pupillary dilatation and occasional mild movement of the ipsilateral forepaw occur in response to light mechanical displacement of vibrissae, hair or skin with a light rigid probe.
response may occur in some regions of the thalamus but not in others.

**Regions With No Characteristic Response Incident to Trigeminal Stimulation.** No evoked response following stimulation of either the infraorbital nerve or nucleus caudalis was identified in the pulvinar, nucleus lateralis posterior, nucleus commissurae posterioris, nucleus medialis dorsalis, nucleus habenularis lateralis, nucleus lateralis dorsalis, nucleus interventricularis, nucleus ventralis anterior, nucleus ventralis lateralis, nucleus centralis lateralis, or nucleus paracentralis. Recordings were not attempted in this study from nucleus reticularis, nucleus centralis medialis, griseum centrale at the level of centrum medianum or nucleus parafascicularis.

Occasional evoked responses of low amplitude (~0-40 gV.) were noted in recordings from the nucleus ruber, nucleus subthalamicus, nucleus subparafascicularis, Forel's field H1, zona incerta, nucleus ventralis medialis and nucleus suprageniculatus. Evoked responses from these regions showed no change in amplitude or duration after the application of strychnine to trigeminal nucleus caudalis.

**Regions in the Midbrain and Thalamus Showing Characteristic Features for Each Anatomic Zone.** The evoked response at nucleus ventralis posteromedialis (Fig. 7c) was characterized by a short latency (~8 msec.), a high amplitude (130-200 gV.), and a moderate duration of 15-20 msec. (Fig. 1a, c). The response remained essentially unchanged when evoked by stimulation of either the infraorbital nerve or nucleus caudalis. Spinal V tractotomy did not abolish the response incident to stimulation of either the infraorbital nerve or nucleus caudalis although occasionally it was reduced in amplitude in either circumstance. A midline medullotomy from the obex to C2 following the tractotomy of spinal V abolished the response incident to stimulation of nucleus caudalis. The application of strychnine to nucleus caudalis in no instance was followed by an increase in the amplitude or duration of the evoked response (Fig. 1b, d) at nucleus ventralis posteromedialis resulting from stimulation of either the infraorbital nerve or nucleus caudalis.

The evoked response in the dorsal half of the contralateral lemniscus medialis at the level of the superior colliculus had a delay of ~3 msec., an amplitude of 35-40 gV., and a duration of 35-40 msec. Recordings at this level of the brain stem for the dorsolateral portion of the griseum centrale and the adjacent commissura posterior as well as medial substantia reticularis mesencephalicus had a delay of ~3.5 msec., an amplitude of 40-50 gV., and a duration of 35-45 msec. There was no change in amplitude or duration following the application of strychnine to nucleus caudalis in any of these regions. Spinal V tractotomy did not characteristically alter these responses until a midline medullotomy was also accomplished. Thereafter the response incident to stimulation of the infraorbital nerve persisted, but there was no evoked response following stimulation of nucleus caudalis.

Evoked responses recorded at the ventral
FIG. 2. The evoked response as recorded at pars magnocellularis of the corpus geniculatum mediale (locus in Fig. 7a) incident to stimulation of nucleus caudalis before the application of strychnine is seen in (a). The unaltered response following application of strychnine is seen in (b). Similarly the response recorded from the midbrain ventral tegmental area (locus seen in Fig. 6b) before (c) and after (d) application of strychnine to nucleus caudalis is unchanged.

tegmental area (Fig. 6b) dorsomedial to the nucleus ruber had a latency of 10–12 msec., an amplitude of 60–125 μV., and a duration of 30–50 msec. (Fig. 2c). There was no change in this potential (Fig. 2d) following the application of strychnine to nucleus caudalis. The response persisted after spinal V tractotomy when the nucleus caudalis was stimulated but was greatly diminished or absent incident to stimulation of the infraorbital nerve. Midline medullotomy from the obex to C2 totally abolished the response.

The evoked response recorded from pars magnocellularis of the corpus geniculatum mediale (Fig. 7a) had a delay of 3–7 msec., an amplitude of 35–50 μV. and a duration of 40–60 msec. (Fig. 2a). The response was unaltered (Fig. 2b) when strychnine was applied to nucleus caudalis. Spinal V tractotomy interrupted the response incident to stimulation of the infraorbital nerve indicating a trigeminal relay caudal to the tractotomy. The evoked activity persisted after the tractotomy when the nucleus caudalis was stimulated but disappeared when a midline medullotomy (obex to C2) was performed.

Regions With a Characteristic Response Incident to Trigeminal Stimulation but With a Change Following the Application of Strychnine to Nucleus Caudalis. The evoked response recorded from the dorsal substantia reticularis mesencephalicus (Fig. 6a) lateral to the griseum centrale and medial to the lemniscus medialis at the level of the superior colliculus demonstrated potentials with a latency of 7–12 msec., an amplitude of 45–50 μV., and a duration of 60–110 msec. (Fig. 3a, d). The application of strychnine to nucleus caudalis resulted, in most instances, in a marked (100 per cent) increase in amplitude of the response (Fig. 3b, e). Spinal V tractotomy at the level of the obex in this circumstance abolished the response to stimulation of infraorbital nerve (Fig. 3c). There was no significant change (Fig. 3f) following stimulation of nucleus caudalis until after a midline medullotomy. The increase in amplitude of both the positive and negative elements of this diphasic potential was a char-

FIG. 3. The response recorded in the dorsal substantia reticularis mesencephalicus seen in Fig. 6a, incident to stimulation of contralateral infraorbital nerve (a, b, c) and nucleus caudalis (d, e, f) was increased in amplitude following the application of strychnine to nucleus caudalis (b) and (e). Spinal V tractotomy at the level of the obex resulted in a loss of the response following stimulation of the infraorbital nerve (c) but no significant change incident to stimulation of nucleus caudalis (f). This observation suggests that the response of dorsal substantia reticularis mesencephalicus was dependent upon a relay of peripheral stimuli at nucleus caudalis.
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FIG. 4. Stimulation of nucleus caudalis evoked these responses seen on slow- (a,b) and fast- (c,d) sweep speeds in nucleus centrum medianum (locus Fig. 7b). Traces (a) and (c) were recorded prior to application of strychnine to nucleus caudalis. After application of strychnine to nucleus caudalis there was a minimal increase in the amplitude of the early peak and a marked increase in that of the late peak of the centrum medianum response as seen in (b) and (d).

The characteristic feature of the response at this locus.

The intralaminar nuclear responses were striking in the region of nucleus centrum medianum (Figs. 6c, 7b). Following application of strychnine to nucleus caudalis they increased consistently in amplitude and frequently in duration (Figs. 4b, d and 5b, e). The evoked response before strychnine appeared after 4-5 msec., with an amplitude of 75-100 μV., and a duration of 20-30 msec. The characteristic response frequently showed two components (Fig. 4a, c)—an early component with a peak amplitude at 4 msec. and a second with a peak amplitude at 14 msec. Occasionally the two components were not distinct and separate (Fig. 5a, d). The later component in particular increased from 20 per cent to 135 per cent in amplitude and occasionally increased in duration from 30 msec. to 45 msec. The increase in amplitude of the early peak (4 msec.) averaged 20-30 per cent and that at the later peak (14 msec.) averaged 80-100 per cent. The evoked response incident to stimulation of infraorbital nerve was abolished (Fig. 5c) following spinal V tractotomy but was unchanged (Fig. 5f) by stimulation of nucleus caudalis. Obex to C2 midline medullotomy abolished the total response incident to stimulation of nucleus caudalis. Evoked responses from the more caudal portions of centrum medianum were lower in amplitude and showed less change following strychnine than those recorded from the midportion or toward the rostral part of the nucleus. Records from nucleus centralis lateralis and nucleus paracentralis showed no consistent evoked response or change incident to strychnine applied to nucleus caudalis. The evoked response in the region of centrum medianum was characteristically a positive monophasic potential as has been reported by others.

Discussion

Rapidly accumulating data from both clinical and experimental observa-

FIG. 5. Stimulation of the contralateral infraorbital nerve and nucleus caudalis resulted in the response (a) and (d), respectively, at nucleus centrum medianum (locus Fig. 6c). Application of strychnine was followed by a marked increase in amplitude of response with stimulation of the infraorbital nerve (b) and nucleus caudalis (e). Spinal V tractotomy resulted in a loss of the evoked response incident to stimulation of the infraorbital nerve (c) but no significant alteration with stimulation of nucleus caudalis (f), thus indicating a relay of peripheral stimuli at nucleus caudalis.
FIG. 6. Nissl preparations demonstrate the position of recording electrodes in (a) substantia reticularis mesencephalicus, (b) midbrain ventral tegmental area, and (c) nucleus centrum medianum. The responses recorded at each of these loci relate to Figs. 3, c, d and 5, respectively.

Abbreviations in Figs. 6 and 7

BCI = brachium colliculi inferioris
BCS = brachium colliculi superioris
CL = N. centralis lateralis
CM = N. centrum medianum
CP = commissura posterior
CS = colliculus superior
Da = N. of Darkschewitsch
GC = griseum centrale
GL = corpus geniculatum laterale
GM = corpus geniculatum mediale
H₁, H₂ = Forel’s fields
Hb = N. habenularis
Hp = Hypothalamus posterior
IP = N. interpeduncularis
IV = N. interventricularis
LD = N. lateralis dorsalis
LM = lemniscus medialis
LP = N. lateralis posterior
mc = pars magnocellularis
MD = N. medialis dorsalis
Mm = corpus mammillare
NCM = N. centralis medialis
NCP = N. commissurae posterioris
NPL = N. paralemniscalis
NR = N. ruber
P = N. posterior
Pc = N. paracentralis
Ped = pedunculus cerebralis
Pf = N. parafascicularis
Prt = praetectum
Flo. 7. These Nissl sections were obtained from a single cat in which three bipolar electrodes were placed simultaneously in (a) pars magnocellularis of the corpus geniculatum mediale, (b) nucleus centrum medianum, and (c) nucleus ventralis posteromedialis. The evoked responses incident to stimulation of nucleus caudalis are recorded in Figs. 2a, b, 4a, c and 1a, c, respectively. Here in one experimental preparation were seen two loci (mcGM and VPM) apparently unaffected by application of strychnine (Figs. 2b and 1b, d) and one locus (CM) which demonstrated a marked increase in amplitude of the evoked response (Fig. 4b, d).

Pul = pulvinar
R = N. reticularis
Ret. Mes. = substantia reticularis mesencephalica
SG = N. suprageniculatus
SN = substantia nigra
Sth = N. subthalamicus

THP = tractus habenulo-peduncularis
TO = tractus opticus
VPL = N. ventralis postero-lateralis
VPM = N. ventralis postero-medialis
ZI = zona incerta
III = third nerve
tions have suggested that the centrum medianum-intralaminar complex is an integral part of the neural mechanism involved in the appreciation of noxious stimuli. Recent anatomic and physiologic studies of the trigeminal system in cat have indicated that the trigeminal input to the centrum medianum-intralaminar complex is relayed primarily through nucleus caudalis of the spinal trigeminal nuclear complex.

This investigation of evoked potentials recorded from nucleus centrum medianum and other "nucleus caudalis dependent loci," i.e., loci receiving their trigeminal input primarily through nucleus caudalis, in the "strychnine preparation" was designed to obtain further information relating to these structures in an animal with overreaction to tactile facial stimulation.

Our observations were comparable to those of Stewart et al. with respect to the loci and wave-form characteristics of midbrain and thalamic evoked responses incident to stimulation of peripheral trigeminal and nucleus caudalis. The effects of spinal V tractotomy and a medullotomy between the obex and C upon these evoked responses were also similar.

Centrum medianum has been described in carnivores as a sparse cluster of cells related to the internal medullary lamina. In contrast to some of the other thalamic nuclei, it becomes more pronounced in higher phylogenetic forms. In cat it remains a poorly delineated area occupying the region of the caudal thalamus lateral to the habenulopeduncular tract, ventral to nucleus dorsalis medialis, and dorsomedial to the caudal portion of nucleus ventralis posteromedialis. In man, nucleus centrum medianum has been described as a prominent nuclear mass lying more rostral and lateral with respect to adjacent thalamic structures than in cat.10,15,38 This same anatomic area first described by Luys has been variously named medialis b, medialis c, centre median, nucleus centrum medianum, central nucleus, nucleus centralis centralis, and nucleus centromedianus (centromedian nucleus).7

Nissl and Weil preparations have indicated that this region contains dense nerve-fiber elements with at least two scattered types of cells, particularly in primates. It is connected with the analogous contralateral region by a fiber commissure which has been demonstrated by both anatomic and physiologic studies. Afferent connections from the cerebellum and cortex (gyrus proreus) have been described as have projection pathways from nucleus centrum medianum to the caudate nucleus, putamen and globus pallidus.

Many of our centrum medianum responses were similar to those of other investigators in that they were composed of a single, long-duration positive wave form (Fig. 5). Others had two positive components (Fig. 4) with similar thresholds. The latter potentials usually were recorded from the more central and medial portion of nucleus centrum medianum. The earlier brief component of the response may represent activity recorded from preterminals or afferent pathways passing through centrum medianum. The late component of longer duration may reflect postsynaptic activity in the cellular mass of centrum medianum. In this event the two components of the response of centrum medianum seen in this study may relate to different neuronal elements within this region. Evaluation of these two possibilities using microelectrode techniques may further clarify this observation. It has been suggested that multiple neural elements in centrum medianum may be activated by trigeminal stimulation since responses not dependent exclusively on a relay at nucleus caudalis occasionally were recorded in this region. These responses did not have a longer delay when evoked by peripheral stimulation as compared to stimulation of nucleus caudalis.

We have not been able to differentiate morphologically or physiologically a clear division between the medial elements of nucleus centrum medianum and lateral components of nucleus parafascicularis, although others have made a distinction between these nuclei. However, there was an apparent rapid drop off of evoked responses at the
dorsal, lateral, ventral, caudal and rostral borders of nucleus centrum medianum. Reasonable correlation could be established between the morphologic margins of this area and the disappearance of an appropriate evoked response at these margins.

The ventral midbrain tegmental area of Collins and O'Leary was considered in this study because evoked responses in this region were reported as being "similar to the centre median potential" and have been related to a mechanism subserving the projection of noxious stimuli to the thalamus. Responses recorded in this ventral tegmental area (Fig. 2c, d) following single stimuli to nucleus caudalis were similar to the response described by Collins and O'Leary although they were using monopolar rather than bipolar recording electrodes. This response occasionally was abolished incident to stimulation of infraorbital nerve following spinal V tractotomy although it persisted with stimulation of nucleus caudalis. It may therefore represent an additional pathway dependent upon a relay at nucleus caudalis when activated by peripheral trigeminal stimulation. It demonstrated no change following application of strychnine to nucleus caudalis in our study.

Strychnine neuronography has been considered extensively by Dusser de Barenne. Strychnine in such studies was applied to the surface of cortex or spinal cord, injected into neural tissue or administered through the intravenous route and the changes in “spontaneous” neural discharge were examined. The interpretation of observations based on strychnine neuronography have been considered recently by Wall et al. and by Fuortes and Nelson who suggested that “the activity of interneurons becomes abnormally homogenous under the influence of strychnine, as may happen with more effective coupling among the different units.” They were unable to find evidence that indicated a change in potential, threshold, after potentials or refractoriness of the membrane of spinal motoneurons following the administration of intravenous strychnine.

These deductions suggest that in our study a hypersynchronous central excitatory state in small neurons of trigeminal nucleus caudalis may have been established by the local application of strychnine. An additional brief electrical stimulus of the infraorbital nerve or nucleus caudalis may then discharge increased numbers of these neural elements in synchrony. Electrical recording of evoked responses at remote loci, which are dependent upon a relay of these hypersynchronous elements, may also reflect a synchronous discharge of increased numbers of units incident to the single stimulus. Such a thesis may account for the increase in amplitude of the evoked response in some portions of the thalamus after the addition of strychnine to nucleus caudalis.

However, one might then consider that all such remotely recorded electrical signs of neural activity of nucleus caudalis might be increased in a similar fashion. Our inability to record such an increase in amplitude of the evoked response at some relays of midbrain and thalamus while consistently recording such an increase in others seems a dichotomy. Some loci (pars magnocellularis of the corpus geniculatum mediale and the ventral tegmental area) seem dependent upon a relay at nucleus caudalis but do not show this increase while others (centrum medianum, dorsal substantia reticularis mesencephalicus) show it quite consistently.

In most instances, loci that show no increase in their evoked response following application of strychnine to nucleus caudalis and that do not relay exclusively at nucleus caudalis receive their trigeminal input through relays at all levels of the medullopontine trigeminal complex. Strychnine applied to nucleus caudalis in this circumstance may not influence relay neurons to these higher centers. A hypersynchronous discharge of neurons of nucleus caudalis presumably was inadequate to increase the amplitude of the evoked response in the loci of midbrain or thalamus.

Regions of the midbrain that are dependent upon a relay of nucleus caudalis (pars magnocellularis of the corpus geniculatum mediale and ventral tegmental tract) but
which showed no change after application of strychnine to nucleus caudalis presumably require a greater synchronous input than they received from nucleus caudalis under the experimental conditions employed in this study to show a change in the evoked response.

We would consider then that centrum medianum and some elements of the substantia reticularis mesencephalicus receive a major portion of their trigeminal input from nucleus caudalis and that a hypersynchronous discharge from nucleus caudalis is an adequate circumstance in which to evoke an increase in the amplitude of the recorded evoked response in these two regions although not in others.

It may be that such a phenomenon then reflects a major primary projection from nucleus caudalis to these two loci. It may also imply for them a primary role as terminal relays for projections from nucleus caudalis related to the transmission of noxious trigeminal stimuli.

Nucleus centrum medianum has been implicated clinically as a relay area essential for the appreciation of some, although not all, forms of noxious stimuli. Thalamotomy has been attempted for the relief of pain refractory to other conservative medical and surgical therapy. In the few instances in which such lesions have been studied in serial sections the area of nucleus centrum medianum has been the primary region of ablation.

A reciprocal corollary to ablation of nucleus centrum medianum with consequent relief of pain from diverse origins has been a case of thalamic pain in which subsequent anatomic study demonstrated sparing of nucleus centrum medianum in the face of an extensive thalamic lesion.

Summary

Strychnine preparations were utilized to investigate central projections from nucleus caudalis to the mesencephalon and diencephalon in cat.

A portion of the dorsal substantia reticularis mesencephalicus and nucleus centrum medianum were the only two loci which demonstrated a consistent increase in amplitude of the evoked response following application of strychnine to nucleus caudalis. These loci are dependent upon a primary relay of peripheral stimuli at nucleus caudalis.

Regions of the thalamus and midbrain in which evoked responses may be recorded without a change incident to application of strychnine at nucleus caudalis have been considered as having less dependence upon a dominant relay of peripheral stimuli at nucleus caudalis.

These observations suggest a major relay and projection system for noxious trigeminal stimuli at nucleus caudalis, the dorsal substantia reticularis mesencephalicus and nucleus centrum medianum.

References


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