

## Location of, and peripheral convergence on, the interneurone in the disynaptic path from the coronal gyrus of the cerebral cortex to the trigeminal motoneurons in the cat

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**Summary.** Primary afferent and descending cortico-bulbar convergence on 186 interneurons located in the intertrigeminal area was investigated. The experiments were performed on cats anaesthetized with chloralose. Nerves from the three trigeminal dermatomes were stimulated electrically at intensities below and above twice the threshold level. Nerves from oral, perioral and periorbital structures, and afferents from the masseteric and digastric muscles were included. The surface of the cerebral cortex was stimulated electrically in systematically selected, maximally receptive points within the trigeminal primary projection fields. The intertrigeminal neurones generally responded to stimulation of low-threshold afferents from periodontal, lingual or perioral cutaneous receptors with a polysynaptic latency. Inputs from 3–5 nerves were common but one afferent input was usually most effective. The neurones were generally discharged from two or more cortical points, as a rule those of the oral and perioral projection fields in areas 3a and 3b of the coronal gyrus. The fastest path from the cerebral cortex to the intertrigeminal area was monosynaptic. However, the median latency was 4–5 ms which indicates an oligosynaptic path. The path went through the pyramide at the pontine level. The discharge pattern of the intertrigeminal neurones was 1–4 spikes in 54% of the neurones and a high frequency train of spikes in 46%. Cortical excitation followed by inhibition of the neurones was observed. The neurones were not discharged by electrical stimulation in the defence-attack area of the hypothalamus. Transsynaptic responses evoked from the mesencephalon were seen in 1/3 of the tested neurones.

**Key words:** Interneurones – Intertrigeminal area – Afferent convergence – Oligosynaptic cortico-trigeminal control – Areas 3a, 3b

### Introduction

Anatomical and neurophysiological evidence has shown that the jaw motoneurons are controlled by paths from peripheral afferents and by descending pathways from the brain (for review see Landgren and Olsson 1980a). In the cat the cortico-trigeminal paths are always transmitted to the motoneurons via interneurons (Walberg 1957). The fastest effects are disynaptic and some of the interneurons have been localized in the gigantocellular reticular nucleus and studied in detail (Nozaki et al. 1983). Many of the pathways, however, are only known in terms of their origin and their effects on the jaw reflexes. This is true for those from the coronal gyrus and from the defence attack area of the hypothalamus to the masseteric and digastric motoneurons as described by Olsson and Landgren (1980) and Landgren and Olsson (1980c). The cortico-trigeminal path from the coronal gyrus to the intertrigeminal area (NintV) was investigated in the present series of experiments, and previous evidence related to the NintV will therefore be reviewed.

The intertrigeminal area is located between the motor (NVmt) and the main sensory trigeminal nuclei (NVsnpr). The area is a part of the borderzone around NVmt, which is referred to as Regio h by Meessen and Olszewski (1949). The motor axons leaving the NVmt travel through the region as do bundles of other myelinated axons running rostro-caudally. The neurones are found in groups between the axons, and the region appears to be poor in cells

and reticulated as compared with the adjacent NVmt and NVsnpr. It was therefore considered as an extension of the lateral parvocellular reticular formation by Torvik (1956), Kuypers (1958), Mizuno (1970) and Gobel (1971). Lorente de N6 (1933) refers to the region as a part of the "reticular nuclei of the trigeminal system", but he points to the fact that this region is "composed of several anatomically perfectly delimited nuclei". The group of cells named the *intertrigeminal nucleus* by Lorente de N6 (1922) is one of the subdivisions of the intertrigeminal region in the rat and Meessen and Olszewski (1949) recognize three other subdivisions in the rabbit (cell groups i and k, and region m).

Kuypers and Tuerk (1964) describe the configuration of cellbodies and dendrites in the NVsnpr. They divide the nucleus into two parts, a lateral zone including clusters of "round cells with bushy dendrites" and a medial zone with "triangular, multipolar and fusiform cells with radiating dendrites". The latter zone includes the intertrigeminal nucleus of Lorente de N6 and is adjacent to the NVmt. According to the morphological observations it is thus reasonable to consider the NintV as a region distinct from the neighbouring nuclei. The distinction is supported by the unit analysis presented in this report. However, it should be remembered that the region includes anatomical subdivisions of neurones which may differ in function.

Walberg (1957) has shown that cortico-bulbar axons do not end in the NVmt of the cat. A considerable amount of preterminal degeneration was, however, found in the adjacent main sensory trigeminal nucleus by Brodal et al. (1956). The observations were confirmed by Kuypers (1958), who also found that the termination was "confined to a zone of the reticular formation interposed between the main sensory nucleus and the motor root of the trigeminus". The degenerations were traced to the ipsilateral and to the contralateral nuclei. The preferential distribution of cortico-bulbar terminals in the intertrigeminal area was further emphasized by Kuypers and Tuerk (1964).

Wold and Brodal (1973, 1974) made small lesions in the coronal and orbital gyri of the cat's cerebral cortex. The preterminal degenerations caused by the coronal lesions were located in the medial and central parts of the main sensory nucleus, whereas those of the posterior orbital lesions were found further caudally in the interpolar nucleus of the spinal trigeminal tract.

Electron microscope evidence of synapses between cortico-bulbar axons and peripheral dendrites of the neurones in the NVsnpr was provided by Gobel (1971). His study focused on the

primary afferent and the cortical inputs to relay cells in the lateral part of the NVsnpr. However, the synapses of cortical origin were sparse. This may be compatible with the degeneration experiments indicating a more dense termination in the NintV than in the NVsnpr.

Olsson and Landgren (1980) described facilitation and inhibition of trigeminal reflexes which were disynaptically evoked from the coronal gyrus of the cat's cerebral cortex. Summarizing the anatomical studies it may be concluded that cortico-bulbar axons from this gyrus terminate in the intertrigeminal area. We therefore decided to look for the interneurone in the disynaptic path from the coronal gyrus in this region.

The present investigation provides evidence for a population of neurones in the intertrigeminal area which were monosynaptically discharged by electrical stimulation of the coronal gyrus of the cerebral cortex. Peripheral convergence from more than one trigeminal dermatome onto these interneurones was also observed. A preliminary report was published by Olsson et al. (1984).

## Methods

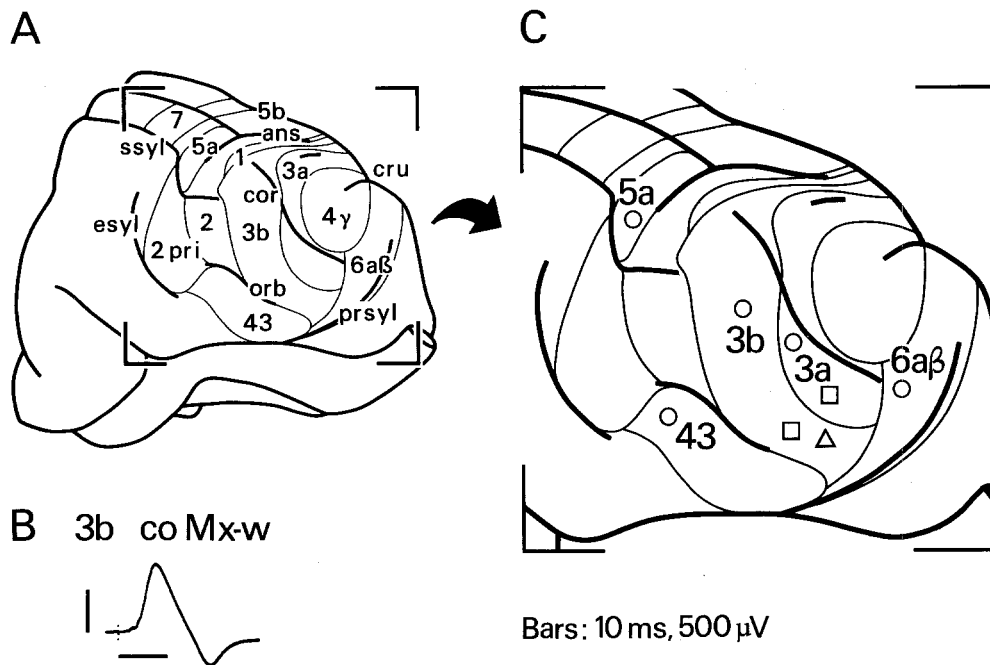
### *Anaesthesia and surgical procedures*

Twenty-seven adult cats (3.0–4.5 kg) of either sex were used for the experiments.

Anaesthesia was induced by 4% halothane (Hoechst) in a mixture of oxygen and nitrous oxide (2 : 1) and was maintained with chloralose (60–70 mg/kg i.v.). Supplementary doses of sodium pentobarbital (Mebumal, ACO) were given when necessary during the experiments. The femoral vein and artery and the trachea were cannulated. Blood pressure, pCO<sub>2</sub> and body temperature were monitored.

Nerves from the three trigeminal dermatomes of the right side (ipsilateral) were dissected for electrical stimulation. The following nerves were prepared: the inferior alveolar, lingual, infraorbital (branch to whiskers and lip), ophthalmic, masseteric, and digastric nerves (Landgren and Olsson 1980b). The left (contralateral) whisker nerve was stimulated with needle electrodes through the skin.

The inferior alveolar nerve carries low-threshold afferents from periodontal mechanoreceptors and from cutaneous afferents of the chin and the lower lip (via the mental nerve). This nerve also receives high-threshold afferents from pain receptors in the pulp of the mandibular teeth. The infraorbital branch contributes low-threshold cutaneous afferents from the mechanoreceptors of the maxillary whiskers and the upper lip. Similar types of cutaneous mechanoreceptors in the orbital region send afferents via the ophthalmic nerve. Both cutaneous nerves include high-threshold afferents from pain receptors. The lingual nerve carries low-threshold afferents from mechanoreceptors and high-threshold afferents from the thermoreceptors and tastereceptors of the tongue. The masseteric and digastric nerves are muscle nerves and include low- and high-threshold muscle afferents. The low-threshold component in the masseteric nerve includes the primary muscle spindle afferents, which evoke the monosynaptic jaw-closing reflex.



**Fig. 1A–C.** Localization of the cortical stimulation sites in relation to cytoarchitecture and response maxima of the projection fields. **A** Tracing of right frontal hemisphere with nomenclature of sulci and gyri according to Hassler and Muhs-Clement (1964). Cytoarchitectonic areas (thin lines) according to Landgren and Olsson (1980b). **B** Evoked potential recorded in a maximum projection point of area 3b in response to low-threshold stimulation of the contralateral maxillary whisker nerve (Co Mx-w). **C** Enlargement of the area framed in **A** with indication of the typical location of the functionally localized stimulation sites in the different cytoarchitectonic areas (○ = maximum projection points of Co Mx-w; □ = Alv inf maximum points in areas 3a and 3b; △ = Ling maximum point in area 3b)

The rostral part of the right (ipsilateral) cerebral hemisphere was exposed after enucleation of the right eye. A caudal extension of the craniectomy allowed the penetration of electrode grids into the hypothalamus and the ascending trigeminal tracts. The dura was cut and reflected and a photograph was taken (cf. Figs. 5, 6). A plexiglass window replacing the eye completed the wall of the paraffin pool, which protected the brain. The animals were mounted in a stereotaxic apparatus.

Dorsal parts of the cerebellum and the medulla were exposed for unit recording and stimulation of the pyramid. The caudal part of the occipital cerebral hemisphere and parts of the bony tentorium were removed. The exposed brain was covered by liquid paraffin and the temperature of the pool was kept at 37–39°C by a radiating heat lamp.

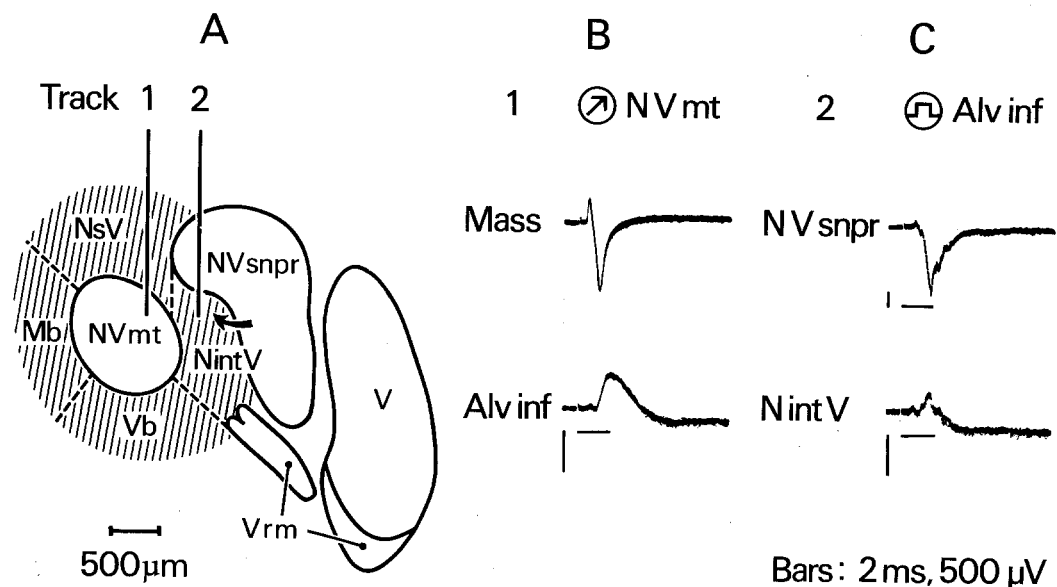
#### Stimulation and recording

Graded electrical stimulation was used for activation of the peripheral nerves, the cerebral cortex and the pyramidal tract. Nerves were stimulated with single pulses (0.2 ms) from 1 to 10 times threshold (T). Thresholds were defined as the minimal stimulus strengths required to evoke a cortical response (Landgren and Olsson 1980b) or antidromic response in the masseteric or digastric motor nuclei. For stimulation in the right hypothalamus and the ascending trigeminal tracts a holder with three grids of glass-coated PtIr electrodes was introduced stereotaxically. The electrodes were placed 1.5 mm apart and had a trip resistance of 15–50 kΩ at 1 kHz. The medial electrode of the rostral grid was placed in the hypothalamic area evoking agonistic behaviour and strong effects on the jaw-closing and jaw-opening reflexes (Land-

gren and Olsson 1980c). Monopolar and/or bipolar stimulation between electrodes with 1–4 pulses, 0.5 ms pulse duration, 500 Hz, 0.1–1.0 mA was used. The caudal grids had two electrodes ipsi- and three contralaterally. They were placed in the region of the ascending trigeminal tracts at the mesencephalic level (Eisenman et al. 1964). By a ventral approach two electrodes were placed in the pyramidal tract at the pontine level.

Spring mounted AgCl-coated silver ball electrodes used for stimulation of the cortical surface (1–4 pulses, 0.5 ms pulse dur, 500–1000 Hz, 0.1–2.0 mA) were placed in the maximum projection points. They were made anodal or cathodal with reference to an AgCl-coated silver plate, which was enclosed in gauze and sewn to a denervated skin area on the left side of the paraffin pool. A roving stimulating electrode was used for final determination of the best point for evoking unitary responses. Monopolar stimulation was used in 18 experiments yielding 137 NintV units. A bipolar stimulation was used in 9 experiments yielding 49 units. In the latter case two silver ball electrodes were placed 5 mm apart in the maximum projection points of the inferior alveolar (Alv inf) and the lingual (Ling) nerves in areas 3a and 3b of the rostral coronal gyrus.

Cortical surface potentials evoked by a low threshold nerve stimulation were recorded with a small spring-mounted silver ball electrode. The maximum points of the different projection fields of the contralateral whisker nerve (Mx-w) in areas 3a, 3b, 5a, 6aβ and 43 were mapped (cf. Fig. 1 and Landgren and Olsson 1980b) and marked on the photograph of the individual brain (cf. Figs. 5A and 6A). In addition, the maximum projection points of the ipsilateral Alv inf and Ling in the rostral coronal gyrus (areas 3a and 3b) were localized and noted. Focal potentials and unit responses were recorded in the right trigeminal nuclei with glass



**Fig. 2A-C.** Diagrams illustrating the functional definition of the intertrigeminal area. **A** Enlarged tracing of a transversal histological section at the rostrocaudal level of the middle  $\frac{1}{3}$  of the NVmt. Medial is to the left, dorsal up in **A**. The hatched area indicates the borderzone of the NVmt. It is divided into four areas (NintV, NsV, Mb and Vb) as described in the text. **B** Typical focal potentials recorded in the masseteric subnucleus of the NVmt (track 1 in part **A**) and evoked by stimulation of the Mass (upper record) and the Alv inf (lower record). **C** Typical focal potentials recorded in the NVsnpr (upper record) and in the NintV (lower record) in response to stimulation of the Alv inf. Note, the phase reversal seen when the recording electrode advanced into the intertrigeminal area (track 2 in part **A**, arrow). Positivity is recorded upwards in this and subsequent figures

pipette microelectrodes. The electrodes were filled with 4.5 M NaCl, had a tip diameter of 1–1.5  $\mu\text{m}$ , and a resistance of 2–4 M $\Omega$ . They were carried by a manipulator with the axis tilted 30° in the sagittal plane.

#### Functional definition of the intertrigeminal area (NintV)

Recording positions in the lateral borderzone of the NVmt were localized during the actual experiment as illustrated in Fig. 2. The method made use of the characteristics and distribution of functional landmarks in terms of focal potentials evoked by stimulation of the Alv inf and the Masseteric (Mass) nerves. These signals were described and related to the cytoarchitecture by Landgren and Olsson (1976). Typical potentials recorded from the level of the middle and rostral thirds of the NVmt are illustrated in Figs. 2B, C. As can be seen in 2C (from track 2 in **A**), the short latency focal potential evoked in the NVsnpr by the stimulation of the Alv inf, was reduced in amplitude and shifted polarity to a positive wave when the electrode entered the intertrigeminal borderzone. This positive wave increased in amplitude in a more medial track as shown in **B** (lower record). The illustrated track (track 1 in **A**) in fact passed between the masseteric motoneurons which are located laterally in the NVmt. The upper record in Fig. 2B shows the maximum antidromic potential evoked by the stimulation of the Mass.

The horizontal coordinate of the polarity shift was noted in all tracks. Units found between 500  $\mu\text{m}$  above and 250  $\mu\text{m}$  below the shift were assumed to be located in the NintV if the track passed through the masseteric subnucleus of the NVmt as judged from the antidromic response. If the track passed lateral to the NVmt, units found 500  $\mu\text{m}$  above and 750  $\mu\text{m}$  below the polarity shift were accepted. By our definition, the NintV is located between the

NVsnpr and the NVmt. The border between the NintV and the supratrigeminal nucleus (NsV) was defined as a sagittal plane parallel to the tracks and passing through the NVmt just medial to the NVsnpr. Both nuclei were defined by their evoked potentials. The ventromedial borders of the NintV and the NsV were drawn parallel to the main direction of the trigeminal motor root through the center of the NVmt. The medial and ventral parts of the borderzone around the NVmt were subdivided by a line normal to the root direction and passing the center of the NVmt (see Fig. 2A).

#### Histology

Eleven cats were perfused and prepared for histological analysis as described previously (Landgren and Olsson 1980b). The analysis included verification of recording positions in the trigeminal nuclei, verification of positions of stimulating electrodes in the hypothalamus, contralateral trigeminal lemniscus, ipsilateral dorsal trigeminal tract, and cytoarchitectural analysis of the cerebral cortex where the best points for driving the units were located.

#### List of abbreviations

Alv inf	Inferior alveolar nerve
Co	Contralateral
Cx	Cortex cerebri
Dig	Digastric nerve
Ip	Ipsilateral
Ling	Lingual nerve
Mass	Masseteric nerve
Mb	Medial borderzone of NVmt

Mx-w	Infraorbital nerve, a branch to whiskers and lip
NintV	Intertrigeminal area
NVmt	Trigeminal motor nucleus
NsV	Supratrigeminal nucleus (area)
NVsnpr-d	Main sensory trigeminal nucleus, dorsal division
NVsnpr-v	Main sensory trigeminal nucleus, ventral division
Opht	Ophthalmic nerve
Vb	Ventral borderzone of NVmt

## Results

### Material

In the present report 316 neurones were analysed. Records from axons were excluded according to the criteria of Gordon et al. (1961). One hundred eighty-six neurones were located in the intertrigeminal area defined as the NintV according to the functional criteria given in Methods. The NintV neurones were distributed along the rostrocaudal extent of the NVmt (1500  $\mu$ m) with 21 units (12%) at the level of the rostral  $\frac{1}{3}$  of the NVmt. 132 units (74%) at middle  $\frac{1}{3}$ , and 25 (14%) at the caudal  $\frac{1}{3}$ . For 80 of these units the functional localization was confirmed in histological serial sections. They were all located within the NintV, 8 were found in the rostral  $\frac{1}{3}$ , 54 in the middle and 18 in the caudal  $\frac{1}{3}$ . The rostro-caudal localization was ambiguous (middle or rostral  $\frac{1}{3}$ ) in 8 units.

### The primary afferent and cortical inputs to the NintV

The NintV neurones were generally discharged by electrical stimulation of low-threshold afferents ( $<2T$ ) from more than one (60%), and sometimes from all of the trigeminal dermatomes (19%). One of the stimulated nerves, generally the Alv inf, Mx-w or Ling, was the most efficient source of input. Efficiency was judged from the lowest threshold, the shortest latency and the largest number of spikes in the response. High-threshold responses to muscle afferents (Mass, Dig) were recorded in 34 NintV units. However, low-threshold muscle afferents discharged a few units ( $n = 7$ ) located dorsally in the NintV near the border of the NsV.

A descending input from the oral or perioral primary projection fields on the coronal gyrus, i.e. areas 3a and 3b of the somatosensory cerebral cortex (SmI), was a typical feature of the NintV neurones (74%). An input from the premotor cortex (area 6a $\beta$ ) was observed (15%), but inputs from the parietal cortex (area 5a, 3%) or from the orbital gyrus (area 43, 8%) were rare. One of the stimulated cortical points was most effective in the majority of the NintV units. We found that a unit with the best response from the cortical Alv inf maximum also

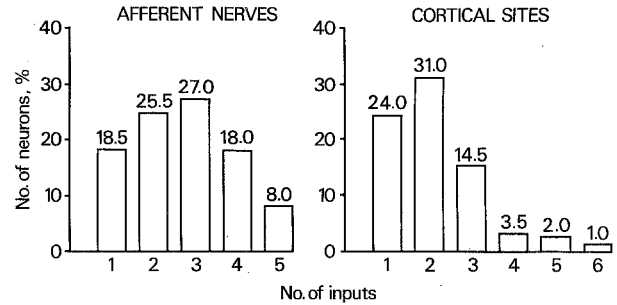


Fig. 3. Histogram summarizing peripheral (left) and cortical (right) convergence on the NintV neurones. The afferent inputs were investigated in 177 units and the cortical inputs in 139 units

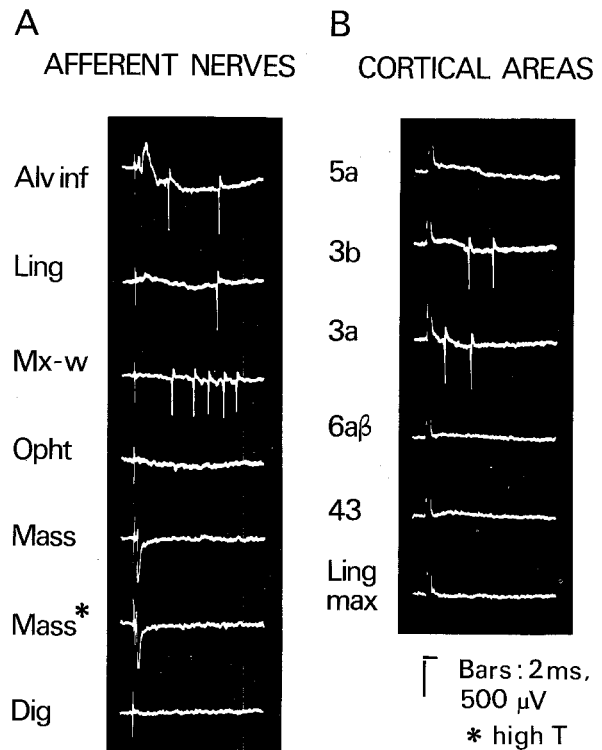
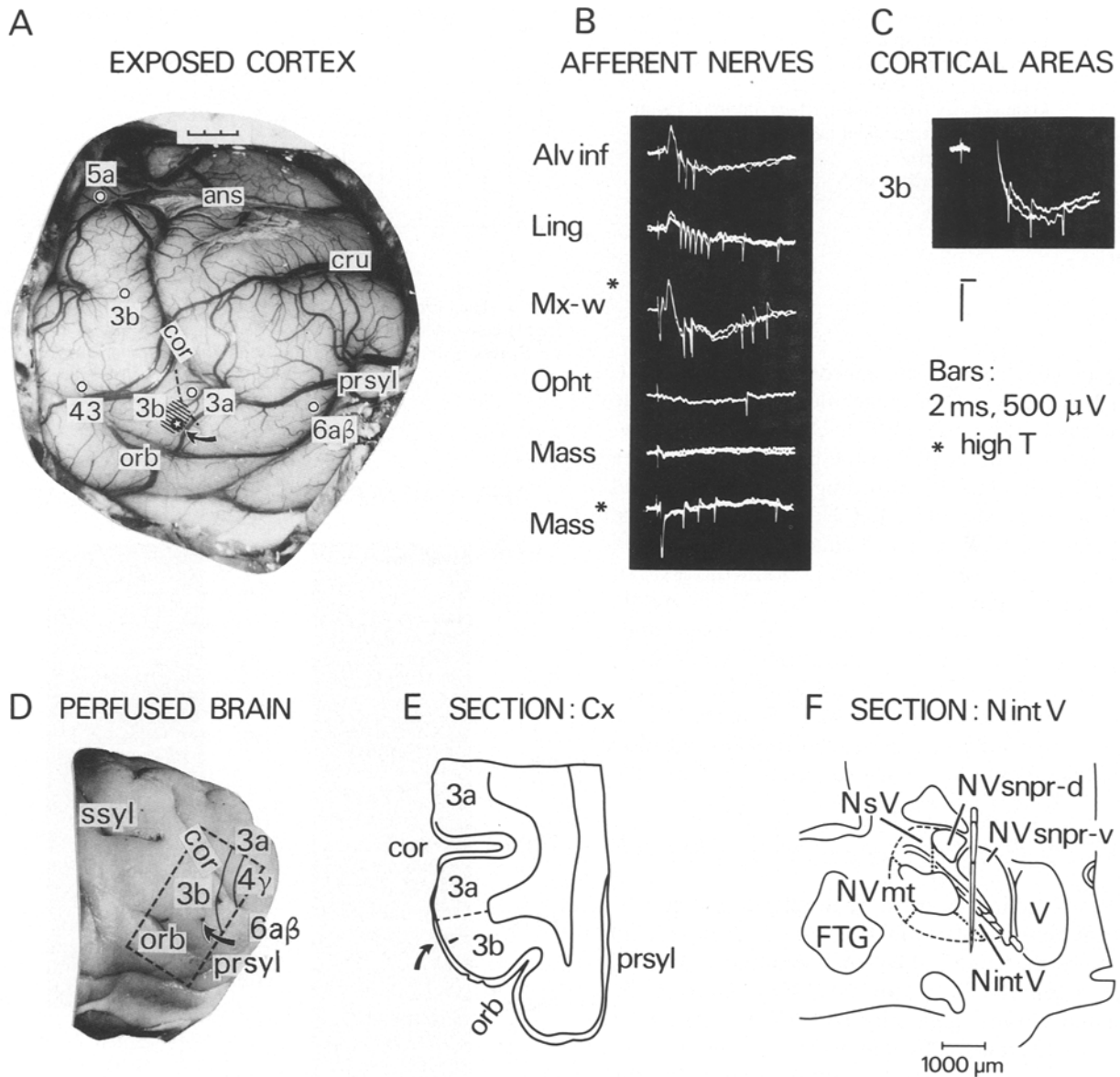


Fig. 4A, B. Records from a neuron recorded in the intertrigeminal area. The unit was recorded 140  $\mu$ m below the Alv inf reversal point at the level of the middle  $\frac{1}{3}$  of the NVmt. A Activation of the unit from two trigeminal dermatomes (Alv inf, Ling, Mx-w). Star (\*) indicates stimulation strength above 2T in this and subsequent figures. B Responses to single pulse stimulation (0.69 mA, 0.5 ms) of the cerebral cortex. Stimulation of areas 3a (latency 2.2 ms) and 3b discharged the unit

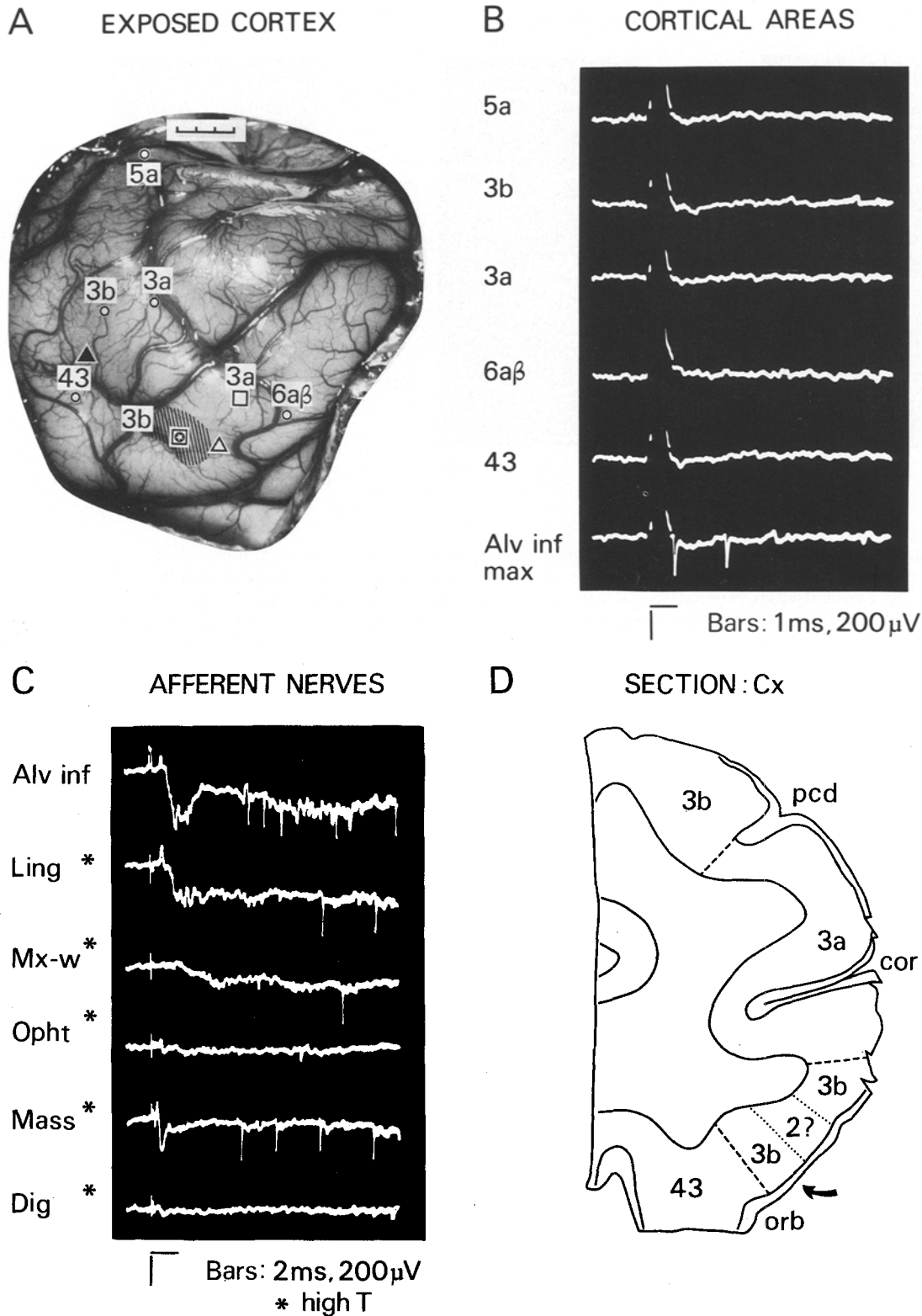
received its most effective input from the Alv inf nerve. The same was true for the units discharged from the cortical Ling max and Ling. The best point on the cortex was carefully determined for 4 units by a roving surface electrode and by a cytoarchitectural analysis of the location (cf. Figs. 5 and 6).



**Fig. 5A–F.** Illustration of the original data from one experiment. The unit was recorded in the NintV, 100  $\mu\text{m}$  ventral to the reversal point of the focal potential evoked by the Alv inf stimulation (cf. Fig. 2). **A** Photograph of the exposed right hemisphere with 3 mm scale in place (top). The stimulation points (O) were functionally localized (cf. Fig. 1). The border line (dashed) between cytoarchitectonic areas 3a and 3b was localized on histological serial sections of the brain (cf. E). **B, C** Records of the unit showing trigeminal (**B**) and cortical (**C**; 4 pulses, 1000 Hz, 1 mA) convergent inputs; two sweeps superposed in all but the Opht record. Afferents from three dermatomes are effective. The effective cortical field (oblique hatching) and the best point (star) are indicated in **A**. **D** Photograph of the perfused hemisphere. Dashed lines indicate the block of tissue, which was serially sectioned for identification of the cytoarchitectonic area of the most effective point (india ink puncture at the arrow) for activating the neurone. **E** Outline of a section from the level of the india ink puncture and with classified cytoarchitecture. The marked best point (arrow) belonged to area 3b (cf. A). **F** Tracing of a section at the level of the middle third of the NVmt. The canal left by the recording electrode is seen in the NintV

Of 158 tested NintV neurones, 122 (77%) responded to cortical stimulation. In 3 units the cerebral cortex was the only effective stimulus, but 98% of the cortically-discharged units received peripheral convergence. A group of 36 units (23%) were discharged from the periphery only. The degree

of the peripheral and cortical convergence on the NintV neurones is summarized in Fig. 3. It can be seen that three inputs from the periphery and two from the cortex were the most common observation. Thus, the typical NintV interneurone receives a considerable convergence of afferent impulses from



**Fig. 6A–D.** Illustration of the original data from a NintV unit recorded 270  $\mu$ m dorsal to the Ling reversal point at the level of the rostral half of NVmt. **A** Photograph of the exposed cortex. Maximum projection points:  $\circ$  = Co Mx-w,  $\square$  = Alv inf in 3a,  $\boxtimes$  = Alv inf in 3b,  $\triangle$  = Ling,  $\blacktriangle$  = Ment. The hatched area gives the 20% border of the Alv inf field in area 3b. **B** Records of responses from tested cortical input sites (single pulse stim, 1 mA). **C** Records of afferent nerve inputs. **D** Tracing of a section through the effective point (arrow; cf star in **A**), which belonged to cytoarchitectonic area 3b of the coronal gyrus

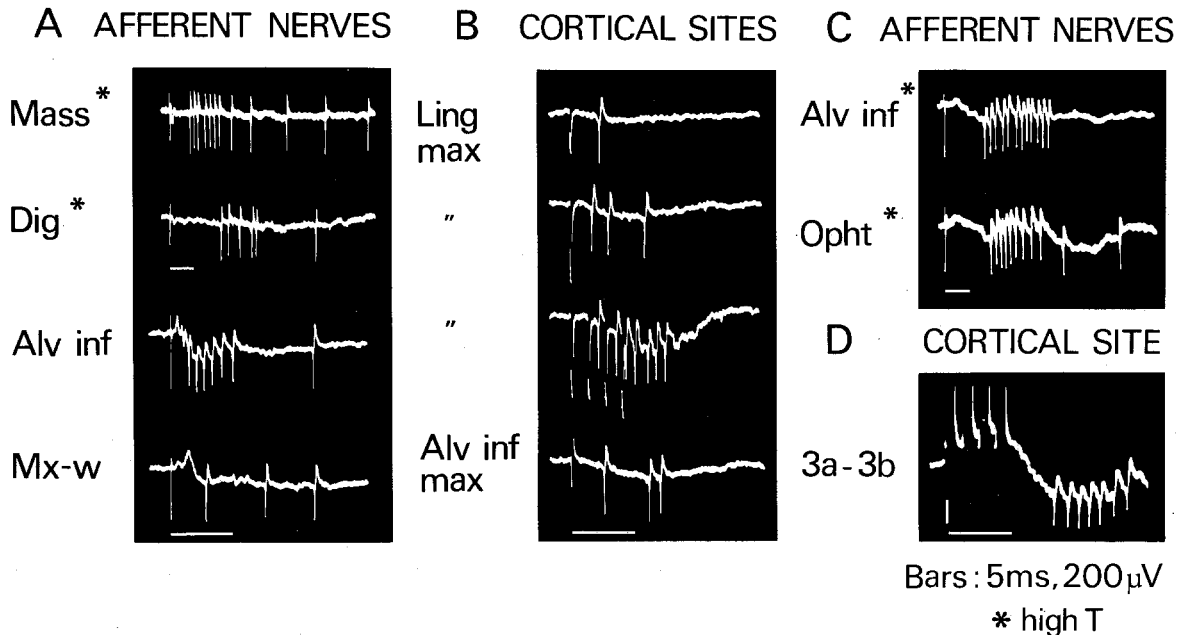


Fig. 7A–D. Examples of typical burst discharge patterns of two NintV units, A, B and C, D, respectively. A, B Low-threshold stimulation of the Alv inf and high-threshold stimulation of the Mass and Dig evoked burst discharges of the unit. Stimulation of the cortical Ling max point evoked a burst after a train of pulses. Stimulation in B from top record; 1 pulse, 1 mA; 1 pulse, 2 mA; 4 pulses, 2 mA; 1 pulse, 2 mA. C, D Examples of high frequency burst firing elicited by high-threshold stimulation of the Alv inf and the Opht. A train of pulses evoked a burst from the cortex

the oral and perioral receptors, and from the somatosensory projections of these receptors on the cerebral cortex, as illustrated in Fig. 4. Evidence obtained from the analysis of two other NintV neurones is given in Figs. 5 and 6. The unit in Fig. 5 showed a wide convergence from the three trigeminal dermatomes and from high-threshold masseteric muscle afferents. It was also discharged from the cerebral cortex with the best point located in area 3b near the border between the Mx-w and the Alv inf projection fields on the coronal gyrus. The area from which the cortical response was evoked overlapped slightly with area 3a.

The unit analyzed in Fig. 6 was discharged from the oral and perioral afferents and from the high-threshold muscle afferents. The Alv inf was the most effective peripheral input. This unit was discharged with monosynaptic latency (0.8 ms) from the best point in the Alv inf projection in area 3b of the coronal gyrus near the rostral end of the orbital sulcus. No response was evoked from the other tested areas of the cerebral cortex as shown in Fig. 6B.

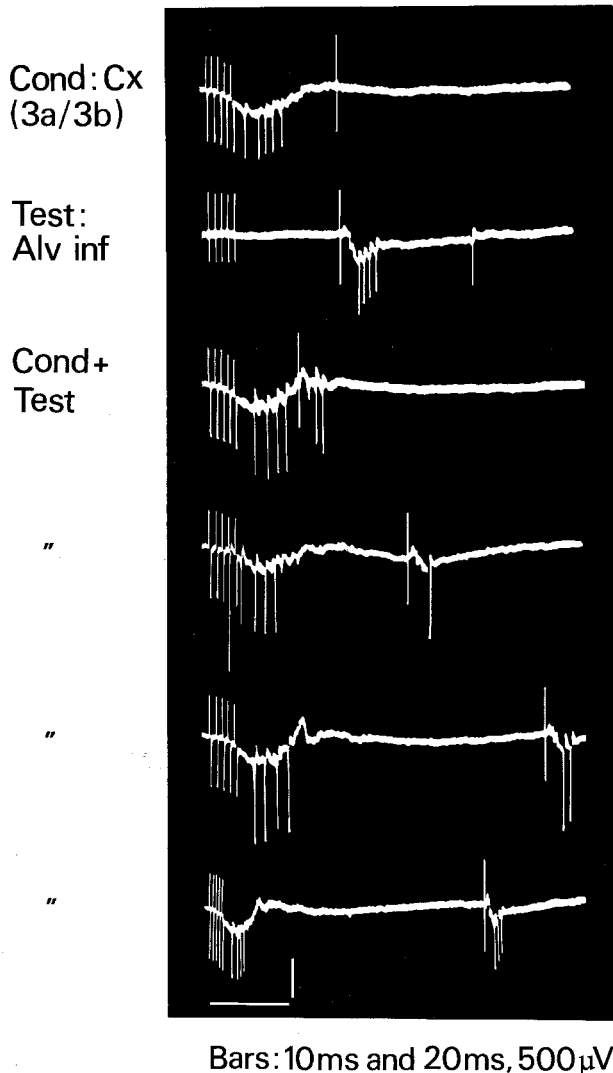
#### *The pattern of discharge*

The pattern of discharge was investigated in 140 NintV units. Seventy-six (54%) of these units dis-

charged a small number of spikes (not exceeding 4), in response to peripheral and cortical stimulation. However, 64 units (46%) responded with a burst discharge ( $\geq 5$  spikes) generally consisting of a short high frequency burst followed by a train of spikes with decreasing frequency. Examples of typical burst discharges are given in Fig. 7.

Bursts were discharged by peripheral and by cortical inputs in 22 units, only by the peripheral inputs in 36 and only by cortical inputs in 6 units. The number of spikes in the bursts varied between 5 and 15. The duration of the bursts varied from 3 to 32 ms. The frequency, computed as an inverse of spike intervals within the bursts was 125–2,000 Hz for stimulation from the peripheral afferents and 50–1,250 Hz from the cerebral cortex. The burst discharge generally was evoked only from one or two of the peripheral inputs, while the other inputs evoked less than 5 spikes. The most efficient inputs were the Alv inf and the Mx-w. However, bursting was observed from all the investigated nerves. Bursting was seen from the muscle afferents only in response to stimuli above 2T. The stimuli within the projection fields of the Mx-w and the Alv inf in areas 3a and 3b of the coronal gyrus were efficient in evoking the bursts. Stimulation of area 43 did not evoke burst discharge and such responses from area 5a were only observed in two units.





**Fig. 8.** Inhibition of a NintV interneurone revealed by cortical conditioning (Cond: Cx) of an Alv inf test response (Test). Cond. stim = 5 shocks, 0.5 ms pulse dur, 1000 Hz, 0.5 mA. Test stim = 2T. Spikes and artefacts retouched

#### *Cortical inhibition of the NintV interneurones*

Inhibition evoked from the cerebral cortex was observed in 5 NintV units. The inhibition was revealed by cortical conditioning of a test response evoked by an afferent volley in the Alv inf. Fig. 8 shows a series of records with increasing intervals between the conditioning and the test volleys. The initial excitation of the NintV neuron evoked by the train of shocks to the cerebral cortex was followed by inhibition which lasted longer than 80 ms. The latency of the inhibition was less than 10 ms from the first stimulus. In all 5 investigated neurones the inhibition was evoked by a pair of surface electrodes with the cathode placed at the maximum point of the

Ling projection field in the rostral coronal gyrus. The anode was placed in the nearby Alv inf projection field in area 3a.

#### *The latency of the NintV discharge*

The latencies of the NintV responses to afferent nerve stimulation are given in Table 1. The measurements were obtained for 183 NintV interneurones. A wide range of latencies was observed. The majority of the units responded with a latency compatible with a polysynaptic activation. However, a monosynaptic latency (1–2 ms) in response to peripheral stimulation was found in 37 (20%) of the units. Monosynaptic latency was computed from records of the afferent volley in the trigeminal tract at the level of the NVmt (Landgren and Olsson 1976) by adding 0.5 ms for one synaptic and spike delay. The latency of the NintV units in response to electrical stimulation in the cerebral cortex was studied for 89 interneurones. Fifteen of them were discharged by a single pulse while 74 required a short train of shocks. The median latency between the single shock and the discharge was 3.2 ms (range 0.8–5.4). Of those 15 units 3 showed a latency < 1.6 ms and 3 showed 1.6–2.0 ms latencies. The effect of repetitive stimulation on the latency was studied for 4 units; three were discharged by one shock with latencies of 3.4, 4.4 and 5.4 ms. One unit was not discharged by the first shock but responded to two shocks with a latency of 2.4 ms. Adding a second or third shock reduced the latency by 2–3 ms. The latencies of the responses to stimulation of the investigated best cortical points of the Mx-w, Alv inf and Ling projections are given in Table 2. Minimum latencies below 2 ms were found from stimulation in the projection fields in areas 3a, 3b and 6a $\beta$ . The minimum latencies from areas 5a and 43 were longer than 3 ms, with the median latencies exceeding 4 ms.

The latency of the direct response ( $N_1$ ) evoked by electrical stimulation of the pyramidal tract and recorded from the cortical surface in area 3a was 1.0 ms. The duration of the antidromic  $N_1$  wave was 1.2 ms. Thus, the antidromic conduction time in the cortico-bulbar axons was 0.8–2.0 ms taking into account a 0.2 ms latent period of spike generation. In 8 NintV units minimum latencies within the range of 0.8 to 1.9 ms (median 1.6 ms) were observed. These units were thus discharged via a monosynaptic cortico-bulbar path.

#### *The cortico-bulbar path to the NintV*

The course of the cortico-bulbar path to the NintV was investigated by applying stimuli at different

**Table 1.** Latencies (ms) of NintV unit responses to electrical stimulation of afferent nerves. The data for low threshold (1T =  $\leq$  2T), and high threshold (hT =  $>$  2T) responses are listed separately. n = number of units

Afferent nerve Stimulus intensity	Alv inf		Ling		Mx-w		Opht		Mass		Dig	
	1T	hT	1T	hT	1T	hT	1T	hT	1T	hT	1T	hT
Minimum	1.0	2.0	1.0	1.2	1.7	1.3	1.5	1.8	1.2	1.4	–	2.0
Median	2.6	4.6	2.5	5.2	3.2	4.8	5.8	5.0	1.4	8.4	–	8.0
Maximum	21.0	17.4	19.0	26.0	22.0	14.4	14.0	17.2	5.6	25.0	–	21.0
n	102	22	50	31	38	51	19	25	7	34	–	13

subcortical sites in 3 experiments. The descending axons from the Mx-w, Alv inf and Ling projection fields in areas 3a and 3b of the coronal gyrus travelled ventro-medially in the internal capsule and in the pyramid. Eight NintV units, discharged from the cerebral cortex, were also discharged by electrical stimuli applied in the internal capsule. Seven units were discharged from the cortex and from the pyramid. The positions of the stimulating electrodes were confirmed by histological sectioning, and those in the pyramid were also confirmed by the typical direct response ( $N_1$ ) evoked in the cerebral cortex by the pyramidal stimulation. The shortest pair of latencies from the cortex and the internal capsule to the NintV, or from the cortex and the pyramid to the NintV, were used to calculate the conduction velocity in the cortico-trigeminal path. The distance from cortex to the pyramid at the entrance into the pons was 45 mm, and 10 mm from the pyramid to the NintV. The shortest pair of cortex-internal capsule latencies was 1.4 and 1.0 ms and the cortex-pyramide pair was 1.6 and 0.9 ms. Assuming a synaptic and spike delay of 0.5 ms, the conduction velocity in the Cx-pyramid limb was 64 m/s, and the velocity in the pyramid-NintV limb was 25 m/s, suggesting a slower conduction velocity in the bulbar terminal branches.

*The NintV neurones were not discharged from the hypothalamic defence-attack area*

Electrical stimulation in the hypothalamus (Fr12 L1 H-3) failed to evoke responses in the NintV interneurons: 34 units in 9 experiments were tested.

*NintV neurones discharged by electrical stimulation in the contralateral trigeminal lemniscus and the ipsilateral dorsal trigeminal tract at the mesencephalic level*

The contralateral trigeminal lemniscus and the ipsilateral dorsal trigeminal tract were stimulated in the

**Table 2.** Latencies (ms measured from the first shock) of the NintV unit responses to electrical stimulation of the maximum projection points on the cerebral cortex

Cerebral cortex area	Co Mx-w		Ip Alv inf 3a+3b	Ip Ling 3a+3b	Co Mx-w		
	3a	3b			6a $\beta$	5a	43
Minimum	1.4	1.6	0.8	1.6	1.4	8.2	3.4
Median	5.4	4.8	4.5	4.7	4.8	9.0	5.2
Maximum	28.0	21.0	12.4	9.4	22.0	11.2	11.8
n	55	57	34	22	21	3	9

mesencephalon in an attempt to classify the NintV units as local interneurons or projecting neurones. In 10 experimental animals 33 NintV units were tested with Co trigeminal lemniscus stimulation and 32 units were tested with Ip dorsal trigeminal tract stimulation. Eleven units were discharged from the former and 10 from the latter input. Only one of the Co trigeminal lemniscus responding units showed a minimum latency (0.7 ms) and a frequency following (1,000 Hz) which were compatible with an antidromic discharge. All of the other units responses had longer latencies (1.1–7.4 ms) and did not follow repetitive stimulation. In one of the NintV units stimulation of the region of the Ip dorsal trigeminal tract evoked responses at a latency of 0.8 ms but the response did not follow stimulation at 500 Hz. All other tested units responded with latencies between 1.1 and 4.4 ms and did not follow high-frequency stimulation. Six units were discharged from both the Ip and the Co inputs. The stimulating electrodes were localized on histological sections in the experiments yielding 28 of the Co- and 32 of the Ip-tested units. It may be added that responses of 3 relay cells located in the main sensory trigeminal nucleus all fulfilled the short-latency and frequency-following criteria typical of an antidromic response.

These observations suggest that the majority of the NintV units were local interneurons. Transsynaptic activation from the mesencephalon via axon collaterals of ascending axons or via descending

axons occurred in about  $\frac{1}{3}$  of the tested units. It cannot be excluded that some of the NintV units send axons to the mesencephalic level.

## Discussion

### *A monosynaptic cortico-bulbar path through the pyramid to the intertrigeminal area*

Our report demonstrates the existence of a monosynaptic path from the cerebral cortex to the NintV neurones. Response latencies below 1 ms were observed and the discharge of the NintV units could be evoked by a single shock to the cortical surface. The origin of this path was within the projection areas of the low-threshold afferents from the maxillary whiskers or from the oral receptors in areas 3a or 3b of the coronal gyrus. Some short latency responses were evoked from area 6a $\beta$  in the presylvian gyrus. Area 5a in the suprasylvian gyrus and area 43 in the orbital gyrus were less effective. The mono- and oligosynaptic nature of the connections between the cerebral cortex and the interneurons in the NintV is a new contribution by the present report. In addition, we have analyzed a large population of NintV interneurons and localized the origin of their cortical input with a relatively high degree of precision. The lack of excitation from the agonistic area in the hypothalamus may be valuable for the interpretation of their function.

Olsson and Landgren (1980) described short latency (2.5–3 ms) cortical facilitation and inhibition of the jaw-closing and the jaw-opening reflexes. The origin of these effects was the oral and perioral projection areas in areas 3a and 3b of the coronal gyrus, i.e. the areas discharging the NintV interneurons with monosynaptic latency. Thus, the present findings suggest that the NintV units could be the interneurons in a disynaptic path from the coronal gyrus to the trigeminal motoneurons. This suggestion is supported by the observations of Mizuno et al. (1978) and Landgren et al. (1986), who demonstrated retrograde transport of horseradish peroxidase from small depots in the NVmt to neurones in the contralateral and the ipsilateral NintV. Further investigations using intracellular recording from the motoneurons and spike triggering by discharges of the NintV interneurons will be required for a complete proof of this theory.

### *The response to natural stimulation*

Convergence of primary afferent and descending cortico-bulbar inputs onto neurones in the inter-

trigeminal area was found in the present study. The first evidence of primary afferent input to the NintV units comes from Eisenman et al. (1963). They described units located in the lateral borderzone of the NVmt corresponding to our NintV, and observed four types of responses to natural stimuli. The observed increased discharge was evoked by: 1) gentle pressure or tapping on a tooth or the nearby gingiva, 2) touch or pressure within a wide receptive field exceeding the borders of one trigeminal dermatome, 3) nociceptive mechanical and thermal stimuli, and 4) opening and closing movements of the lower jaw. The units were also tested with non-nociceptive cooling and warming via a thermode applied to the receptive field, with taste solutions applied to the tongue, with light flashes, with loudspeaker clicks and general vibration caused by tapping of the earplugs and stand. No NintV units responded to these latter stimuli.

Dubner (1967) investigated units in a region corresponding to the NintV using mechanical stimuli, light flash, loudspeaker click and electrical stimulation of the cerebral cortex. The units were discharged or inhibited by electrical stimulation of the cerebral cortex. They responded with increased discharge to mechanical stimulation within restricted receptive fields in the orofacial region. Some of them also responded with a long latency to light flash and click. These long-latency responses are interesting because they might suggest a descending input from the superior colliculi to the NintV. However, they should be further tested to exclude the possibility that the responses were due to a lightflash-evoked whisker movement.

The observations of responses to natural stimuli from wide receptive fields suggest that afferents from receptors responding to different modalities, and located in more than one trigeminal dermatome, converge on the NintV interneurons. The present results corroborate those of Eisenman et al. (1963). Dubner's (1967) observation of cortical excitation and inhibition was confirmed.

### *Comparison of responses of the NsV and the NintV interneurons*

The responses of the NsV neurones to natural stimuli were described by Jerge (1963) and by Takata and Kawamura (1970). These interneurons were discharged by afferents from mechanoreceptors in the jaw muscles and in the oral and perioral structures. They were also discharged or inhibited by jaw movements.

The interneurons mediating disynaptic inhibition from lingual, periodontal and cutaneous affer-

ents to the jaw-closing motoneurons were located in the NsV by Goldberg and Nakamura (1968) and by Kidokoro et al. (1968a,b). Excitation of the NsV interneurons by low- and high-threshold masseteric afferents was reported by Gura et al. (1972). Nakamura et al. (1973) analyzed the effects of group II afferents in the masseteric nerve on the inhibitory interneurons in the NsV. These interneurons were excited ipsilaterally but inhibited contralaterally. However, the group II afferents did not originate in muscle spindles.

Preterminal degeneration in the NsV following lesions in the cerebral cortex was found by Kuypers and Tuerk (1964), although the degeneration was sparse. We have observed excitation of the NsV interneurons evoked by stimulation of the coronal gyrus (unpublished observations). A quantitative analysis of the input to the NsV from the cerebral cortex requires further experiments.

A comparison of the afferent convergence on the NsV and the NintV interneurons reveals certain differences. While low-threshold muscle afferents seem to be an important peripheral input to the NsV, these afferents only discharged a few NintV units located close to the border with the NsV. In contrast, low-threshold afferents in the alveolar, whisker, and perioral cutaneous nerves provide the dominating input to the NintV and the majority of neurons in this area also received a mono- or oligosynaptic descending input from the primary projection fields of these nerves in the somatosensory cortex.

#### *Comparison of our results with observations on interneurons in cortico-spinal paths to the segmental motoneurons*

The segmental interneurons discharged by mono- and oligosynaptic paths from the sensori-motor cerebral cortex were investigated by Lundberg and Voorhoeve (1962) and by Lundberg et al. (1962). Both studies found cortico-spinal facilitation of transmission via interneurons in the disynaptic path of the reciprocal Ia inhibition and facilitation of transmission via interneurons serving disynaptic reflexes from Ib afferents. These interneurons receive a complex convergence but are characterized by input from the low-threshold muscle afferents (Hultborn et al. 1976; Harrison and Jankowska 1985). Therefore they show similarities to the NsV interneurons and to the small group of the NintV population discharged by low-threshold muscle afferents. Another important group of segmental interneurons which was facilitated from the cortex received peripheral input from the flexor reflex afferents

(FRA; Lundberg 1979a). A third group was discharged by cutaneous afferents only. The majority of the NintV interneurons resemble the third segmental group, but 18% of the NintV population were discharged by high-threshold muscle afferents, thus corresponding to the FRA type.

#### *The cortico-trigeminal systems in the cat*

We now have strong evidence for two disynaptic descending paths from the cat's cerebral cortex to the trigeminal motoneurons. One is the path from the coronal gyrus via the NintV to the jaw-closing and jaw-opening motoneurons, and is described in this report. Another disynaptic path was demonstrated by Nakamura et al. (1976) and by Nozaki et al. (1983). That path originates rostrally in the orbital gyrus and the interneurons are located medially in the tegmental field including N reticularis gigantocellularis at the level of the inferior olive. It transmits excitation to the digastric motoneurons and inhibition to the masseteric motoneurons. Two other oligosynaptic cortico-trigeminal paths are less extensively investigated: 1) the cortico-pontine path (Nakamura et al. 1979; Katoh et al. 1982), and 2) the path originating caudally in the orbital gyrus and terminating in the interpolar nucleus of the spinal trigeminal tract (Mizuno et al. 1968; Wold and Brodal 1974).

Previous attempts to interpret the function of the descending cortico-trigeminal systems in behavioural terms concentrated on their role in the control of masticatory movements (Nakamura et al. 1979). Additional models, however, may be suggested on the basis of a comparison between the oligosynaptic cortico-trigeminal and the cortico-spinal descending paths described by Lundberg and Voorhoeve (1962) and Illert et al. (1976a,b; 1977). They have described disynaptic paths from the cerebral cortex of the cat: through the pyramids and via segmental or proprio-spinal interneurons to the motoneurons of the hindlimbs and the forelimbs.

Considering results of the behavioural investigations of Alstermark et al. (1981) on the target-reaching and the food-taking functions of cortico-proprio-spinal and cortico-spinal paths to the cat's forelimb motoneurons, we suggest four different behaviours which might employ the fast descending paths to the trigeminal motoneurons. These behaviours are:

- 1) manipulatory movements of the jaws for holding food, catching prey or carrying young,
- 2) the target-reaching of the head in close cooperation with the forelimbs,

3) orientation of the head in cooperation with vision, and

4) rhythmic chewing and lapping.

At present we can only guess which of these functions is (or are) controlled by the cortico-trigeminal system investigated in the present study. Further experiments may improve this analysis. One suggestion is based on the interpretations from the Lundberg group (for review, see Lundberg 1979b) which demonstrated a convergence of cortico-spinal, rubro-spinal, reticulo-spinal, and tecto-spinal paths on the proprio-spinal interneurone serving target-reaching of the cat's forelimb. Alstermark et al. (1983, 1985) found that medullary reticular neurones are involved in disynaptic paths to the neck muscles from the cerebral cortex and from the mesencephalic tegmentum. Sumino et al. (1981) reported a trigemino-neck reflex. Thus, interneurons in oligosynaptic paths to the neck and jaw muscles could be controlled by descending systems similar to those involved in the target-reaching of the forelimb.

We hypothesize that the disynaptic trigeminal path from the coronal gyrus via the NintV serves manipulative functions. Suggestive support for this assumption is the observation that low-threshold afferents from the teeth and the perioral cutaneous receptors are the most effective peripheral input to the NintV. Furthermore, a descending monosynaptic path to the NintV has its origin in the primary SmI projection fields of these afferents in areas 3a and 3b of the coronal gyrus. Area 3a in turn, is directly connected to the motor cortex and to parietal association areas (areas 4 and 5) as described by Grant et al. (1975), and may serve mechanisms involved in active touch (Landgrén et al. 1984).

The portion of the cat's cerebral cortex where the coronal, presylvian and orbital gyri meet is a small region which has many different functions. It is therefore necessary to carefully localize sites of stimulation or lesion. The design of the experiments and the interpretation of the results should utilize cytoarchitecture, anatomical and histochemical evidence of connections, electrophysiological input-output analysis, and results of behavioural experiments. Somatosensory functions of the perioral region could be related to area 3b of the coronal gyrus, with its large whisker and periodontal projection fields. Sensorimotor functions of the jaws and the tongue could be related to area 3a of the coronal gyrus. Area 6a $\beta$  in the presylvian gyrus should correspond to the premotor area in the primates. The region between the rostral end of the orbital sulcus and the angle between the rhinal and presylvian sulci receives projections from the lingual afferents. Chewing movements and lapping may be evoked by

electrical stimulation in this projection field. Area 43 of the orbital gyrus meets the caudal border of the field. A projection to the interpolar trigeminal nucleus of unknown function originates further caudally in the orbital gyrus. Functions related to swallowing and taste may also be located in the orbital gyrus.

It is obvious that electrical stimulation will spread within this region of the cerebral cortex and will activate several widely different systems. We have tried to define the location of cortical stimulation in terms of cytoarchitectonic areas and maximum points within primary projection fields. In most contemporary reports cortical localization is only crudely related to gyri and sulci. We suggest that the location of cortical stimulation should be more carefully reported. Spread of the stimulating current should be considered, and intracortical microstimulation used for detailed analysis. Also lesions in degeneration studies and experiments with tracing substances ought to be more selective. Careful studies of cortical localization may reveal interesting functions related to the cat's oral behaviour. Differences between rostral and caudal parts of the orbital gyrus should be noted because a path to the interpolar nucleus of the spinal trigeminal tract originates in the caudal part of this gyrus (Wold and Brodal 1974). The gyrus also provides efferents to the insular cortex, anterior amygdaloid area and the medial forebrain bundle (Mizuno et al. 1969).

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