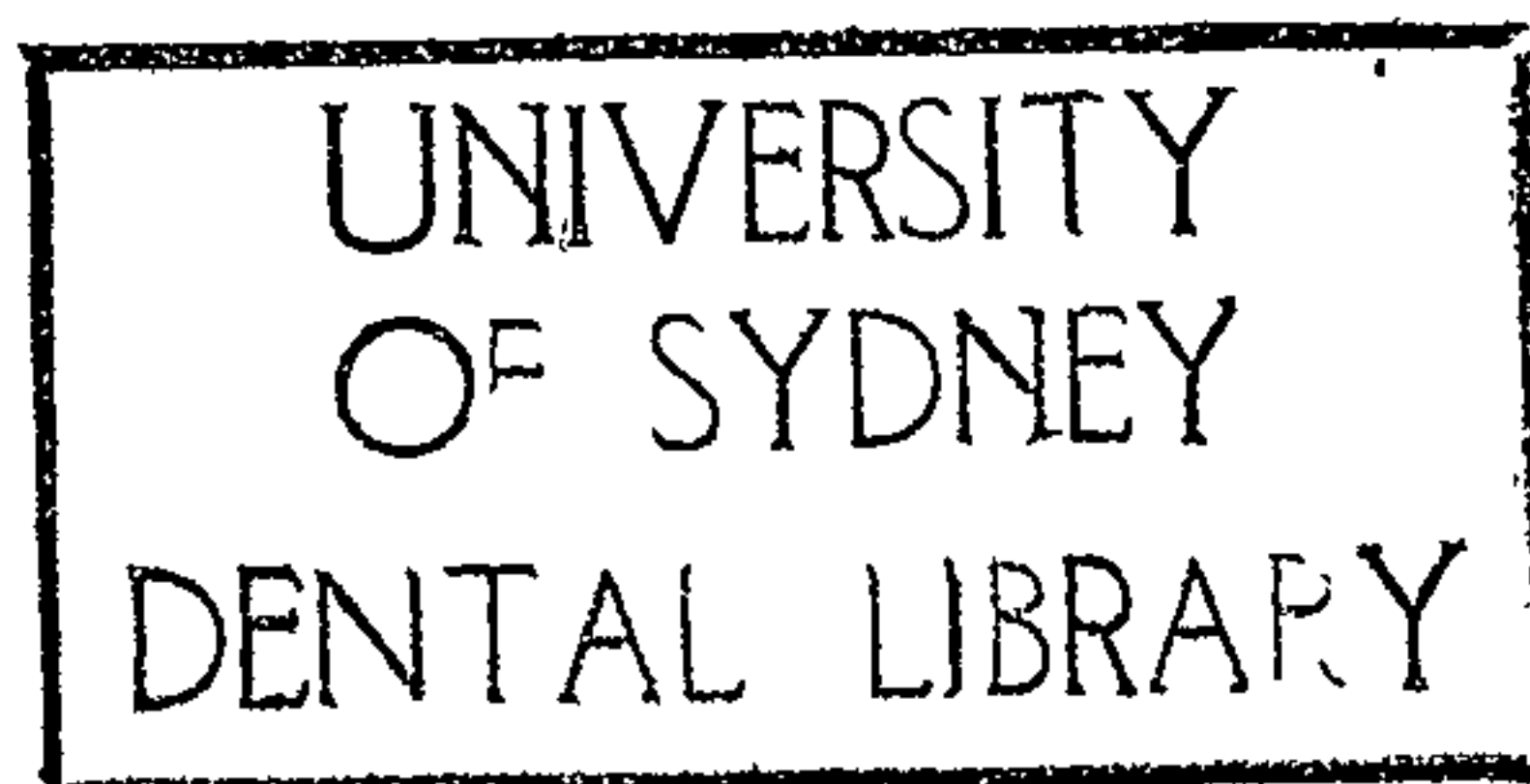


AN ELECTROMYOGRAPHIC STUDY
OF THE
HUMAN JAW-CLOSING REFLEX

Thesis submitted for the degree of
Master of Dental Surgery
to the University of Sydney



by

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STATEMENT OF AUTHORSHIP

The work submitted for examination in this thesis is the original work of the candidate alone. The original investigation was conducted in the Clinical Research Unit of the Department of Prosthetic Dentistry of the University of Sydney between 1981 and 1983 (inclusive). No portion of this work has been submitted by the candidate to this or any other university, either in part or in full, for the award of any other degree.

PART 1 - REVIEW OF LITERATURE

1. INTRODUCTION

A mechanical stimulus producing stretch in human or animal muscle may evoke a reflex response in the muscle that tends to oppose the length change. In decerebrate preparations, limb flexion generates a tonic stretch reflex that manifests as a sustained increase in resistance (Liddell and Sherrington, 1924; Widmalm, 1976b). This tonic response is not readily apparent in the conscious human subject, however, the phasic response may be observed as a burst of action potentials produced by the synchronous firing of several motor units, and as such represents the classic tendon reflex. The analogous compound action potential in the jaw musculature may be demonstrated following a sudden downward mechanical impulse to the mandible in the human or animal subject (Goodwill, 1968; Matthews, 1976) and has been termed the jaw-closing reflex or the jaw jerk reflex, the latter so named in view of its similarity to the knee-jerk and other tendon reflexes induced by sudden stretch (Goodwill, 1968; Munro and Griffin, 1971; Tardieu, Tabary and Tardieu, 1973). The use of the term "jaw jerk" to describe this reflex may be inappropriate as it has been used to describe a sudden opening movement (Riblet and Mitchell, 1971). It would appear preferable therefore to avoid the term "jaw jerk" in favour of less ambiguous terminology such as "jaw-closing"

reflex, or monosynaptic myotatic reflex potential (MSP; Widmalm, 1976a and b).

The jaw-closing reflex is considered a fundamental phenomenon of the facial and oropharyngeal areas (Dubner, Sessle and Storey, 1978) as it utilises afferent and efferent components involved in the generation, learning and modulation of programmed jaw movement sequences. Thus the reflex would appear to form the basis of more complex functions such as mastication and swallowing (Sessle, 1981), although the response itself probably appears only infrequently in normal function.

A downwards tap delivered to the chin in a relaxed human subject causes muscle stretch and this produces an afferent projection along group Ia and group II pathways (Figure: 1) which in turn exert monosynaptic and polysynaptic influences on motoneurons in the trigeminal motor nucleus. Inter-segmental and suprasegmental projections onto alpha and fusimotoneurons located in this motor nucleus (Greenwood and Sessle, 1976; Sessle, 1977a and b) modulate ongoing motoneurone excitability thus influencing the manifestation of evoked monosynaptic reflexes.

Being analogous to the knee-jerk reflex, which usually generates perceptible limb movement, the jaw-closing reflex was believed capable of a similar mechanical phenomenon,

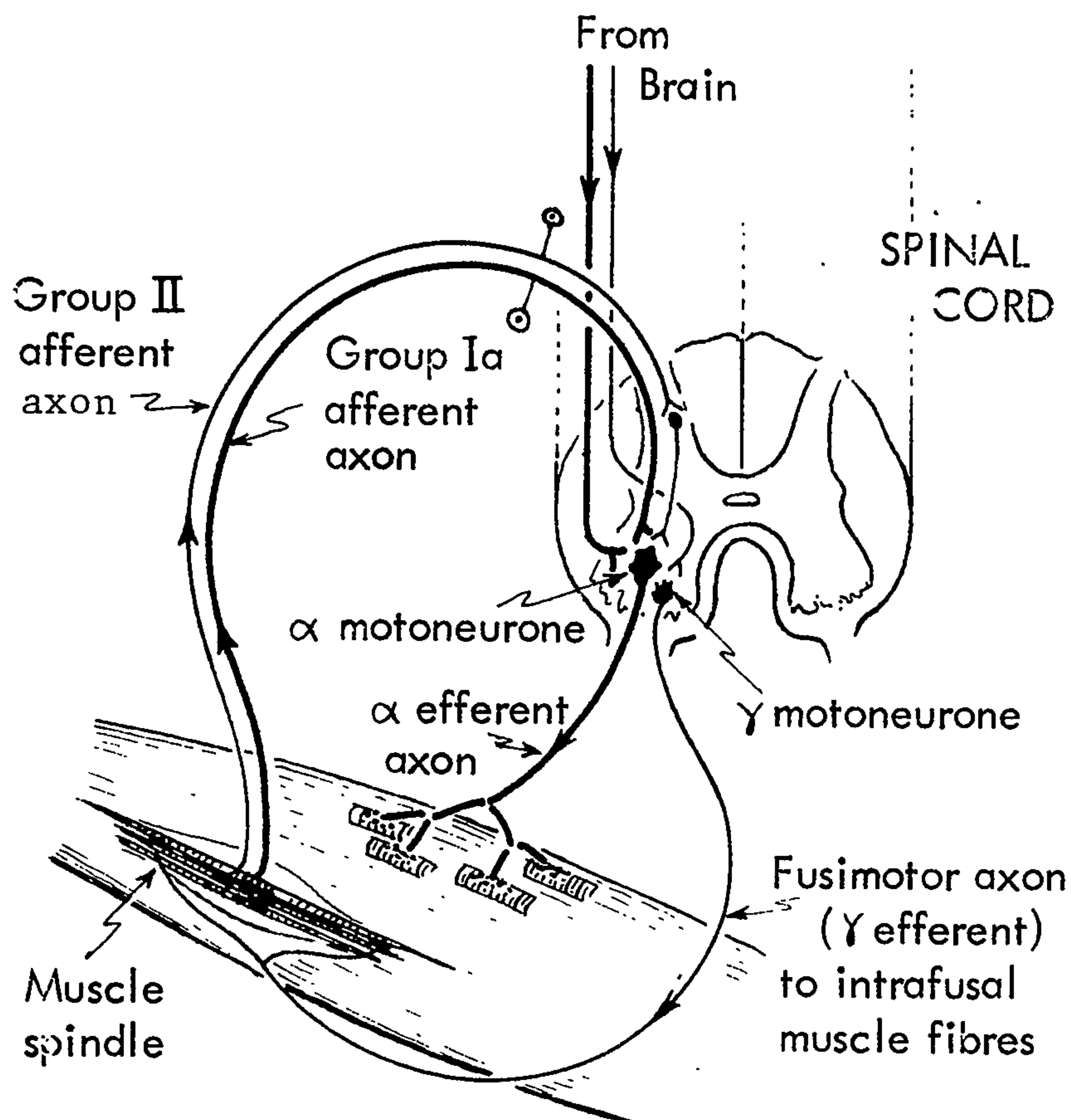


FIGURE: 1

Group Ia primary spindle afferent effecting excitatory monosynaptic junctions with alpha motoneurons of the same muscle. Also shown is a group II afferent effecting excitatory and inhibitory polysynaptic junctions (represented by interneurone) with alpha motoneurons. Descending influences from higher centres modulate ongoing levels of excitability of alpha and fusimotoneurons. This illustration of the monosynaptic pathway in the spinal system may be readily transposed to the cranial system by locating pseudounipolar cytons within the trigeminal mesencephalic nucleus and alpha and fusimotoneurons within the trigeminal motor nucleus (from Boyd, 1980).

that is jaw closure (Hannam, 1972). However, this may not be so for several reasons: firstly, the duration of the jaw-closing reflex appears to be much shorter than the duration of electromyographic activity that has been considered necessary to overcome mandibular inertia and initiate jaw displacement (Widmalm and Hedegård, 1977; Widmalm, 1982). In addition, the latency of the reflex is probably too short to generate movement that would be distinct from a passive recoil of the jaw as part of the visco-elastic nature of the muscle-protein and fibro-elastic connective tissues (Wyke, 1974), or b those passive jaw opening movements directly related to stimulus delivery. Although Jerge (1964) postulated a peripheral interaction of jaw-closing and jaw opening reflexes as the neurologic basis of cyclical jaw movements, it is now apparent that suprasegmental controls establish a pattern of jaw movement during mastication that can operate quite independent of peripheral influences (Lund and Dellow, 1971; Dellow and Lund, 1971). In addition, the "jaw-closing reflex" that has been described during swallowing (Sherrington, 1917) does not refer to a monosynaptic response derived from spindle stretch, but rather a reflex jaw closure generated as part of the central programme coordinating muscle activity to produce swallowing. Therefore, although the jaw-closing reflex does not produce jaw movement per se, segmental systems do provide continuous afferent projection as a mechanism of feedback in the

learning and modulation of ongoing movement sequences necessitated by current intraoral constraints (Klineberg, 1980).

Longer latency reflex components have been described following monosynaptic activations in the orbicularis oculi (Shahani and Young, 1973; Widmalm, 1982) and jaw elevator and limb muscles (Evarts, 1973; Merton, 1974). Jaw closure, commencing at about 100msec, was demonstrable only in those subjects for which these longer latency responses, commencing at about 30msec, were evident; mechanical movement was never associated with a jaw-closing reflex alone irrespective of size. Eyelid movement during the blink reflex was closely associated with those reflex components occurring after the short latency response. From this research, Widmalm (1982) concluded that "the electromyographic counterparts of the mechanical contraction during jaw closure after chin tap are not the result of a monosynaptic compound action potential but are late responses with long duration and of true contraction character". However, Lamarre and Lund (1975) described monosynaptic load compensation in human masseter muscle. A loading pulse, which retarded jaw closure without causing jaw opening caused an increased velocity of jaw movement attributed to an evoked jaw-closing reflex. These two interpretations, however, are not necessarily conflicting. The monosynaptic reflex is a mechanism whereby ongoing

pre-programmed cyclical jaw movement sequences may be modulated to assist accommodation of motoneurone activity to alterations in intra-oral constraints, for example, variations in food consistency, and changes in tooth and cusp angulation. Thus, although the reflex may be inadequate to overcome mandibular inertia and generate macroscopically evident jaw movement, small differences in food bolus resistance and texture are able to be accommodated directly at the segmental level; whilst more permanent changes in tooth form are encoded as modulations in afferent return from muscle spindles.

1.1 Electrodes (Ahlgren, Lewis and Yemm, 1980; Yemm, 1977)

Electromyography is the study of the electrical activity of muscle (Pruzansky, 1952). The jaw-closing reflex may be recorded electromyographically as single or compound action potentials employing one of various types of electrode: for example, intramuscular needle, surface disc and subdermal hook electrode types have been described (Ahlgren et al., 1980). Needle electrodes consist of fine insulated wires inserted into the body of a muscle using a modified disposable needle (Yemm, 1977). They are capable of sampling activity from one or a small number of motor units and as such they do not

provide an overall assessment of muscle activity. In addition, needle electrodes may interfere with and become dislodged during function although discomfort from the needle once in place is often minimal (Ahlgren, 1967; Ahlgren et al., 1980).

Surface electrodes sample activity from a large number of motor units in superficial muscles and provide a signal more representative of whole muscle activity (Yemm, 1977). Thus surface electrodes may be inappropriate for detection of low levels of activity. For example, close proximity of small, active motor units to surface location may incorrectly suggest the presence of large units; in addition, some units may produce surface potentials too small to be discriminated above background noise. Despite these limitations, surface electrodes are commonly used which reflects their ease of application and subjective comfort.

Two main forms of surface electrode have been described: a surface disc, and b subdermal hook. Surface disc electrodes are secured to skin with adhesive collars or tape and a conduction pathway between skin and electrode is provided using a form of saline jelly. Subdermal hook electrodes (Ahlgren, 1967) are short (5mm long; 0.18 mm diameter) platinum wires inserted 45° into the subcutaneous tissues overlying the muscle belly. Subdermal hooks have

been considered superior in performance to disc electrodes (Yemm, 1977). This might be expected based on the reduced impedance characteristic of these electrodes and also the greater control possible over other variables such as thickness of keratin and subcutaneous tissues. However, a recent study specifically devoted to these two types of surface electrode concluded that there was no advantage for either type other than convenience in placement (Ahlgren et al., 1980). Small differences in motor-unit amplitude were described when comparing hook and disc signals but these were apparently random, and neither electrode was superior at the extremes of motor-unit potential (Ahlgren et al., 1980). Hook electrodes appear to be appropriate for recordings from hair-covered regions such as the temporal region. However, as discomfort and apprehension accompanying insertion may influence the evoked reflex response and as they are more liable to dislodge than surface electrodes, Widmalm and Hedegård (1976a and b) considered surface disc types to be the electrode of choice whenever possible.

Although electrode location might influence the amplitude of an evoked jaw-closing reflex it does not appear to modify latency in those muscles having their efferent innervation localised in a transverse plane (Gassel and Ott, 1973) as has been reported for the masseter muscle (Karlsen, 1965). Nevertheless, the

ability to record reproducible reflexes in one subject on different days appears to depend on, inter alia, accurate relocation of surface electrodes (Frame, Rothwell and Duxbury, 1973). Nouri, Rothwell and Duxbury (1976) achieved reproducibility within a subject on different days which was attributed to careful attention to replacement positions for electrodes.

1.2 Clinical Application of the Jaw-Closing Reflex

The monosynaptic jaw-closing reflex may be observed in the temporalis and masseter electromyogram (emg) following a light mechanical tap to the menton region of human subjects (Goodwill, 1968; Munro and Griffin, 1971; Goldberg, 1972c; Ongerboer de Visser and Goor, 1974; Yamada and Ash, 1982). To date, however, there have been no reports of a similar reflex response in the associated musculature such as the pterygoid or digastric muscles (Bratzlavsky, 1976), despite the reported presence of at least a few spindles in these muscles (Freiman, 1954; Voss, 1956). Nevertheless, longer latency excitatory responses appear to exist in the digastric muscle (mean latency: 31msec, Hellsing and Klineberg, 1982a and b).

Although a hand-held reflex hammer is often used to evoke the response, a high degree of variability in the

magnitude, rate and direction of force application both within and between operators is likely to be associated with this instrumentation. Despite this limitation, previous workers have established a range of "normal" values for jaw-closing reflex parameters, a selection of which have been tabulated (Table: 1). Electromyography has been applied in the evaluation of patients with various systemic disorders and the observations indicated that the masticatory muscles are susceptible to the same disorders affecting muscles elsewhere (Pruzansky, 1952). Clinically undetectable abnormalities of trigeminal reflex transmission have been identified employing jaw-closing reflex parameters (Goodwill and O'Tauma, 1969; Ongerboer de Visser and Goor, 1974). For example, a delay or absence of the reflex on one or both sides has been associated with multiple sclerosis (Goodwill and O'Tauma, 1969) and trigeminal neuralgia (Ongerboer de Visser and Goor, 1974). However, Goodwill's differentiation of a jaw-closing reflex into 'brisk' and 'normal' categories in the diagnosis of upper motoneurone lesions (Goodwill, 1968) seems obscure as no elaboration as to the meaning of this terminology is given.

Nevertheless, the monitoring of jaw reflexes does allow an insight into the status of the trigeminal motoneurone pool by providing clues to the patency of afferent and efferent pathways involved in jaw muscle control. This

Table 1. A selection of jaw jerk latency, duration and amplitude values recorded from the masseter muscle by various authors.

Author(s)	Jaw Jerk Latency (msec)	Jaw Jerk Duration (msec)	Jaw Jerk Amplitude (mV)
Bratzlavsky, de Boever and van der Eecken, 1976	-	-	0.2 - 4
Godaux and Desmedt, 1975a	7.5 ± 0.43* ^{††}	-	-
Goldberg, 1971 and 1972c	9.9 ± 0.9 (8-12), R [†] 9.9 ± 0.6 (8-12), L [†]	-	-
Goodwill, 1968	8.4 ± 1 (6-10.5)	6.2 ± 1.1 (4-9), R 6.1 ± 1.1 (4-9), L	0.07 - 3.7
Griffin and Munro, 1971	6.6 ± 2.0	8.7 ± 2.1	-
Hamada, 1981	5.8 ± 0.4	-	-
Hannam, 1972	8 (approx.)	-	-
Haraldson and Ingervall, 1979	6.3	6.7	-
Klineberg and Murray, 1982	9.39 ± 1.01, R 8.97 ± 0.83, L	4.94 ± 1.08, R 5.14 ± 0.93, L	0.36±0.23, R 0.42±0.22, L
Kugelberg, 1952	7.3	-	-
Lennartsson, 1980	7.8	6.0	-
Matthews, 1976	8 (approx.)	-	-
McIntyre and Robinson, 1959	7.4 (6.1 -8.2)	-	-
Munro, 1972a and b	6.5 ± 1.7	9.0 ± 2.1	-
Munro and Griffin, 1971	6.5 ± 1.7	9.0 ± 2.0	-
Ongerbeor de Visser and Goor,1974	7.6 ± 1.3 (6.4-9.2)	-	-
Orchardson and Sime, 1981	8.21 ± 0.73	-	0.12 - 2.75
Vural, Mohl and McCall, 1982	10.9 ± 1.7	-	-
Widmalm, 1976b	6 (approx.)	-	-
Widmalm, Gill and Widmalm,1979	6 (approx.)	-	-
Widmalm, et al., 1979	-	-	0.26 - 2.11
Widmalm and Hedegard, 1976a and b	6.3	5.9	-
Yamada and Ash, 1982	(8-10)δ	-	-
Overall mean value (widest range for amplitude)	7.8 ± 1.4	6.8 ± 1.6	0.07 - 4

* ± standard deviation value † range of values in parentheses ††R: right masseter; L: left masseter
δ not included in calculation of overall mean value - no value reported

patency reflects the level of excitability from central and peripheral inputs, which themselves may be modified by various oro-facial functional and dysfunctional states. Thus compound action potential measurement parameters (e.g. jaw-closing reflex latency) recorded from the jaw muscles have been suggested useful in clinical diagnosis (Goodwill and O'Tauma, 1969; Ongerboer de Visser and Goor, 1974; Widmalm, Gill and Widmalm, 1979).

1.3 Motor Unit Physiology

A motor unit consists of a single alpha motoneurone and the muscle fibres that are innervated by it. The innervation ratio is the number of muscle fibres supplied by each axon and is about 640 for the human masseter muscle (Carlsöö, 1958-59). Rather than forming a discrete aggregation, component fibres of individual motor units are distributed throughout a large portion of the entire muscle volume. The considerable overlap of muscle fibres from different motor units implies that a small circumscribed area of muscle tissue will contain fibres derived from many units (Brandstater and Lambert, 1973; Burke and Tsairis, 1973). The sarcomere, composed of overlapping actin and myosin protein strands, is the contractile unit of a skeletal muscle fibre (Bloom and

Fawcett, 1975) and when arranged in series, they form a long strand called a myofibril. Action potentials arriving at motor end plates generate potentials in the postsynaptic sarcolemma via an exclusively chemical transmission (Shapovalov, 1980), and which releases Ca^{2+} from sarcoplasmic reticulum enveloping individual myofibrils. The ensuing ATPase-enzyme activation produces sarcomere shortening by the sliding of actin and myosin cross-bridges.

Skeletal muscle fibres have been classified on the basis of histochemical characteristics into Type I and Type II fibres (Barnard, Edgerton, Furukawa and Peter, 1971; Taylor, 1973; Eriksson, 1982). The small, slow motor units of the Type I category are myosin ATPase poor, whilst the fast contraction speeds of the Type II fibre reflect high levels of this enzyme. The Type II fibre may be further subdivided into oxidative-rich units which are fatigue resistant (Type IIA fibres) and oxidative poor which are fast fatiguable (Type IIB fibres). Although the masseter muscle exhibits considerable heterogeneity as regards muscle fibre type, the majority of fibres are Type I (62-72%) which are able to be recruited at low force levels and are therefore likely to tonically fire at postural jaw position. The Type IIB fibres constituting most of the remaining motor unit fibre types are adapted to rapid acceleration and high speed of

contraction (Taylor, Cody and Bosley, 1973; Eriksson, 1982).

Motor units are recruited in an orderly linear fashion as a function of voluntary force levels. Thus with light contractions, small low threshold motor units are activated before the larger higher threshold units (Milner-Brown, Stein and Yemm, 1973a; Yemm, 1976; Goldberg and Derfler, 1977; Clark, Luschei and Hoffman, 1978). Alterations in force levels during a voluntary contraction relate to changes in the number of active units and also changes in the discharge frequency of those units currently active (Yemm, 1976). However, the relative contribution from each of these varies depending on force level; thus at low forces, increased tension is produced principally by way of recruitment of additional units whereas at higher forces, alterations in firing rate appear to become more important (Milner-Brown et al., 1973a; Milner-Brown, Stein and Yemm, 1973b). Nevertheless, with progressively increasing voluntary effort, higher threshold, faster contracting motor units will be recruited thus producing action potential components of higher amplitude (Milner-Brown et al., 1973a; Clark et al., 1978). However, a certain flexibility exists in the ordering of motor unit recruitment depending on prevailing conditions (Grimby and Hannerz, 1968, 1970, 1973). Thus, in phasic muscle activity, as during reflex activation, motor units appear

to be recruited in a different order than in tonic activity. In addition, the recruitment order in phasic activity is somewhat variable even under standardised conditions in contrast to the stable recruitment order characteristic of tonic discharge (Grimby and Hannerz, 1973). Variations in recruitment order in a series of identically elicited phasic activities reflect variations in the relative importance of two factors: firstly, the pre-existing state of facilitation from higher centres tending to activate motor units in a stable tonic order; and secondly, the short duration stimulus that tends to activate motor units in a different 'phasic' order. In addition, programming of the motoneurone pool in advance can modify this recruitment order. Thus, subliminal facilitation of the motoneurone pool during the anticipation of a stimulus delivery will tend to activate motoneurones in a stable recruitment order. If the subject does not expect the stimulus then the first motor unit to be recruited varies unexpectedly from stimulus to stimulus (Hannerz and Grimby, 1973). Recruitment of motor units during reflex activation may therefore not necessarily be in the same order as during a voluntary contraction - larger faster motor units may not necessarily be recruited after smaller slower units. Despite this variable recruitment order, the net resultant reflex potential may nevertheless still be the same.

1.4 Artefact and Interference in the EMG Recording

1.4.1 Interference arising from alternating current (AC) fields.

Both magnetic and electric forms of interference may arise from nearby AC fields (Huhta and Webster, 1973). Thus a changing magnetic field is capable of inducing an electromotive force in nearby conductive loops; a changing electric field may produce interference by causing alternating currents to flow to ground through the system. These nearby AC fields include room lighting, AC wiring and outlets and associated operating equipment. Radio stations are a source of high frequency interference. The use of a highly conductive surface such as copper or aluminium will shield electric fields from emg circuitry, however control of magnetic interference requires shielding with some form of ferromagnetic material.

Huhta and Webster (1973) have identified four ways in which interference may enter a system:

- 1.4.1.1. magnetic induction;
- 1.4.1.2. electric fields inducing currents in electrode leads;
- 1.4.1.3. electric fields inducing displacement currents within the body; and
- 1.4.1.4. equipment interconnection and imperfections.

1.4.1.1. Magnetic Induction.

A changing magnetic flux density is capable of inducing a potential in any conductive loop in the vicinity proportional to the area of the loop, its orientation and the size of the flux density. Bipolar electrodes are subject to induction of magnetic fields within the leads and this may be minimised by reducing the size of the loop, i.e. twisting the wires together.

1.4.1.2. Electric Fields Inducing Currents in Electrode Leads.

Changing electric fields may induce displacement currents within electrode leads. With unshielded leads, interference could arise from AC displacement currents if the electrode-tissue interfaces have different impedances. This may result from poor electrode to skin contact such as poor skin preparation and dry electrode paste, or unfavourable electrode lead placement making the displacement currents into the leads unequal. This may be remedied by careful attention to skin preparation and electrode placement and handling procedures.

1.4.1.3. Electric Fields Inducing Displacement Currents Within the Body.

Electric fields may generate displacement currents within the body. Potentials so generated are not uniform throughout the body and thus the difference between the potential at one point on the skin and that at another will be amplified in the emg signal. As bipolar electrodes for facial muscle recording are usually located very close to each other, differences in skin potential between each electrode are likely to be very small. This source of interference is therefore probably not a major problem in emg recordings from these muscles.

1.4.1.4. Equipment.

If the subject is grounded to two instruments supplied by different power outlets then a potential difference between the instruments may appear in the biopotential trace. This is usually not a problem in emg recordings as the subject is not often grounded to other instrumentation.

Electrode impedance imbalance may be minimised by employing high quality amplifiers.

1.4.2 Artefact arising at the electrode metal-to-solution interface (Tam and Webster, 1977).

Recordings utilising polarizable metal plate electrodes may exhibit motion artefact which appears to derive from the electrode metal-to-solution interface. Agitation of the paste during movement changes the half-cell potential generated at the interface by altering the metallic ion gradient. This is an important source of artefact for these flat plate electrode types; however, the modern, recessed "nonpolarizable" metal/metal halide electrode provides a more constant ionic concentration at the interface and motion artefact is markedly reduced employing these electrodes (Tam and Webster, 1977).

1.4.3. Skin artefact (Tam and Webster, 1977; Burbank and Webster, 1978).

Other sources of artefact relate to time variations in the potential from the inside to the outside of the skin. These variations are encountered following mechanical deformation of the skin as during stretch or pressure and with the secretory activity of the sweat glands. The skin potential appears to vary at a maximum rate of around

1mV/sec and to a typical degree of 15mV during sweating and 5mV during stretch deformation. Sweating is unlikely to be a problem in most emg recordings from seated subjects performing chewing or clenching tasks in air-conditioned laboratories. Stretch deformation could be a problem but this may only be so if significant skin stretch occurred as during chewing. However, no study appears to have been attempted of the contribution of skin stretch associated with chin tap to changes in the skin potential. In the study of Tam and Webster (1977) tight stretching of the skin produced an offset potential of between 2.5 and 5mV at a rate of potential change of 1mV/sec. Chin tap would only produce very slight skin stretch and thus any motion artefact deriving from this would probably be too small to be a significant problem and would nevertheless be removed by low-pass filtering.

Abrasion of skin before applying the electrode contributes significantly to reducing skin potential artefacts by stabilising variations in skin potential and minimising skin impedance (Tam and Webster, 1977). Although Tam and Webster did not recommend a particular figure for the number of skin abrasion strokes, they suggested light abrasion with fine sandpaper (SN2, Flint Paper, 3M Company), and from their table (Table: 4; p.136) ten sandpaper strokes might be an appropriate guide to skin abrasion preparation. However, excessively

vigorous abrasion (i.e. exceeding 20 sandpaper strokes) was shown to increase susceptibility to irritants such as electrode paste. An improvement in the skin abrasion technique has been devised by Burbank and Webster (1978) who recommended puncturing the skin atraumatically. This technique was shown to virtually eliminate skin artefact with much less irritation than sandpaper abrasion.

Artefact and interference are significant factors which must be addressed in any biopotential recording system. With careful attention to minimising the various sources, acceptable records may be obtained.

1.5 The Pathway of the Jaw-Closing Reflex.

The monosynaptic nature of the jaw-closing reflex has been well documented since its early description by de Watteville (de Watteville, 1886). The trigeminal mesencephalic nucleus has been shown to be an essential component of the pathway of the jaw-closing reflex (Figure: 2). Histological studies tracing degenerating fibres from lesions placed in the mesencephalic nucleus (Corbin, 1940) and tract (Szentagothai, 1948) have demonstrated

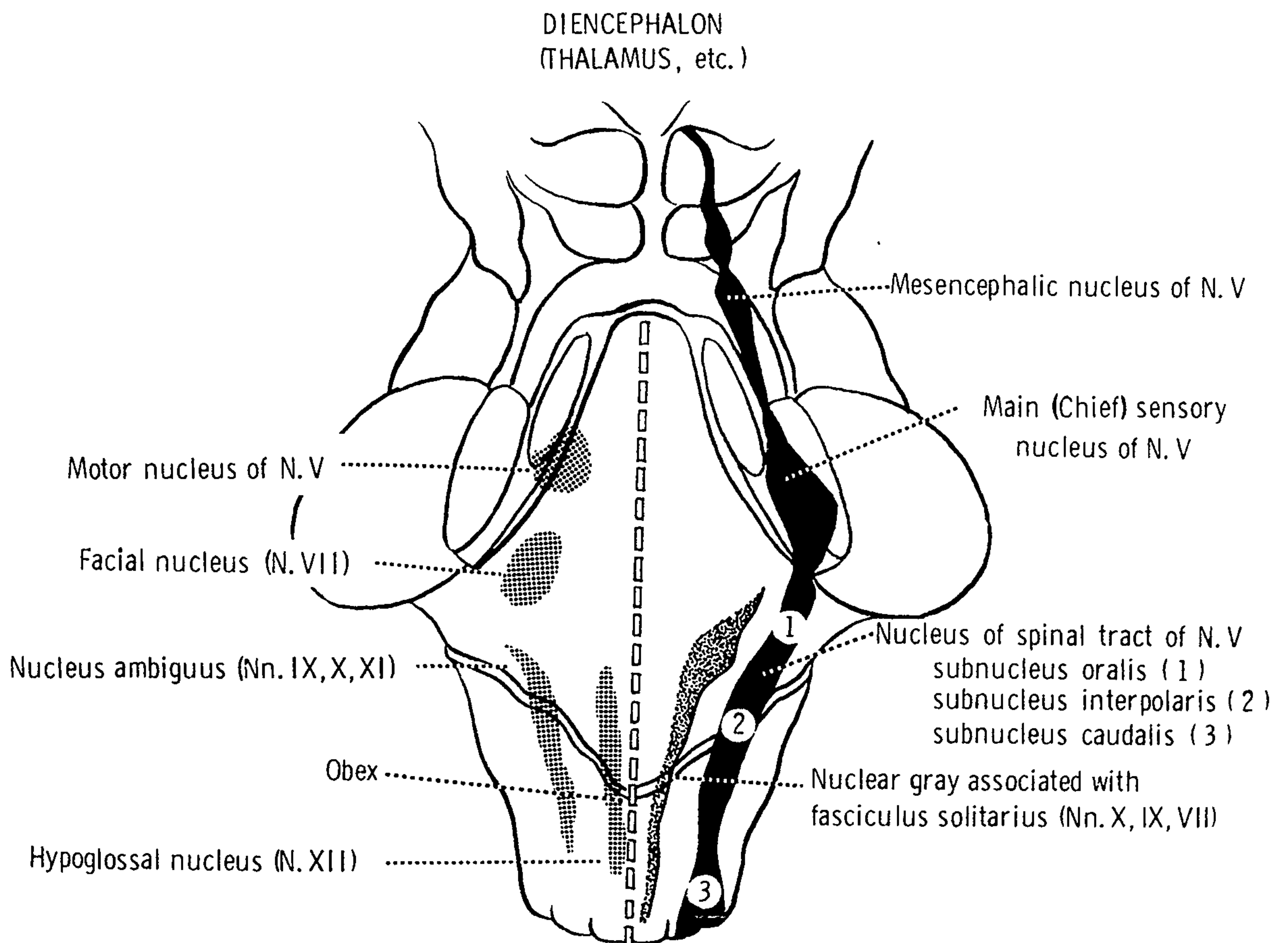


FIGURE: 2

Outline of dorsal aspect of brain-stem with major sensory (right side) and motor (left side) nuclei superimposed in appropriate medio-lateral locations. Pseudounipolar neurone cytons, located within the mesencephalic nucleus and conveying afferent impulses from muscle spindles, effect monosynaptic junctions with alpha motoneurons located within the trigeminal motor nucleus (Dubner, Sessle and Storey, 1978).

a single neurone afferent pathway from jaw elevator muscle spindles to the trigeminal mesencephalic and thence motor nuclei. At about the same time (Corbin and Harrison, 1940) and more recently (Cooper, David and Whitteridge, 1953), electrophysiological studies recorded slowly adapting action potentials from the trigeminal mesencephalic root during elevator muscle stretch. Lesions centred in the trigeminal mesencephalic root (Harrison and Corbin, 1942) and nucleus (Goodwin and Luschei, 1974) have been reported to abolish the jaw-closing reflex. In the former, rostrally placed lesions produced partial reflex depression whilst caudally-placed lesions completely abolished the response. In another study, reflex responses were not able to be evoked in patients with pathological lesions of the mesencephalic nucleus (Hufschmidt and Spuler, 1962). Also, electrical stimulation of the trigeminal mesencephalic nucleus has been shown to elicit a brief jaw closure similar to that seen for the jaw-closing reflex (Harrison and Corbin, 1942) and this has been more recently confirmed in cat (Kidokoro, Kubota, Shuto and Sumino, 1968a). In addition, monosynaptic EPSPs have been recorded in masseteric motoneurons in response to stimulation of the trigeminal mesencephalic nucleus (Nakamura, Goldberg and Clemente, 1967) and this confirms the monosynaptic excitatory linkage between the two nuclei. This series of studies have clearly demonstrated the trigeminal

mesencephalic nucleus as part of the jaw-closing reflex pathway. However, other studies (Bremer, 1923; Rioch and Lambert, 1934) did not reach this same conclusion and certain reasons may account for this. In Bremer's experiments, involving transection caudal to the inferior colliculus, collaterals from the mesencephalic root may have not, in fact, been interrupted or if they were damaged, they may have nevertheless, continued activity for some hours after (Harrison and Corbin, 1942). In addition, the level of transection could have been inappropriate to interrupt connections between the motor nucleus and the caudal region of the mesencephalic nucleus, an area associated with reflex jaw-closing (Harrison and Corbin, 1942). Rioch and Lambert (1934) were able to abolish the jaw-closing reflex by section of the sensory root near the brain-stem. However, it has been suggested that the sensory root is unlikely to have been completely severed without some damage to those mesencephalic root fibres lying between the sensory and motor roots (Harrison and Corbin, 1942). Possible damage to these fibres would remain undetected even during nerve trunk stimulation; furthermore, the ability of direct electrical stimuli to the motor root to evoke a response does not necessarily indicate that physiologic reflex activity could still occur.

In mammalian striated muscle, the myotatic reflex is subserved by an arc of two neurones (Jolly, 1911; Renshaw,

1940; Lloyd, 1943a, b and c). The afferent limb of this reflex in cat is formed by the large diameter group Ia fibres (Lloyd, 1943c), originating in the muscle spindles (Szentagothai, 1948; McIntyre, 1951; Hunt, 1952) which, for the jaw-closing reflex, enter the brain-stem via the trigeminal motor root (Szentagothai, 1948; McIntyre and Robinson, 1959) and effect monosynaptic junctions in the trigeminal motor nucleus (Szentagothai, 1948; Appenteng, O'Donovan, Somjen, et al., 1978). The monosynaptic nature of the reflex was suggested by Cajal in 1909 who traced dorsal root fibres through spinal gray to the ventral horn without interruption (Cajal, 1909). Neurophysiological proof of a single synapse came with Hugelin and Bonvallet's (1956) demonstration of a latency difference between antidromic and orthodromic activation of the masseteric nerve of 0.9msec which is consistent with a monosynaptic pathway.

The inability to abolish the masseteric stretch reflex following section of the trigeminal sensory root (McIntyre, 1951) provided electrophysiological confirmation of Szentagothai's histological findings that the trigeminal motor root contains afferent fibres from muscle spindles in cat. Although Rioch and Lambert (1934) were unable to demonstrate a jaw-closing reflex following section of the trigeminal sensory root, this probably related to accidental damage of the motor root during the experimental

procedure. Thus although the afferent pathway of the jaw-closing reflex in cat is likely to be via the motor root, the evidence for a similar route in man is tenuous. Persistence of the jaw-closing reflex following unilateral sensory trigeminal nerve rhizotomy was identified in only two of the four patients tested by McIntyre and Robinson (1959) and in five of the eighteen patients tested by Bratzlavsky (1972). However, it is generally considered that such surgical procedures to section the sensory root of the trigeminal nerve often damage the motor root. Therefore the possibility of damage to the primary Ia afferents has been assumed the reason for the abolition of the reflex response (Hufschmidt and Spuler, 1962). Recent work (Ferguson, 1978; Ferguson, Lenman, Jacobson and Turner, 1978) has criticised these earlier studies of McIntyre and Robinson (1959) and Bratzlavsky (1972) on the basis that no assessment was made of the degree of sensory loss and thus the extent of the surgical lesion to the trigeminal sensory root. In a study of 32 patients who had undergone a form of surgery for trigeminal neuralgia, Ferguson (1978) found a very high incidence of abnormality in the jaw-closing reflex response. This was inconsistent with the low clinical and electromyographic evidence of masseter denervation which would have been expected with damage to the motor root (Ferguson, 1978). In addition, it is recognised clinically that the motor root is likely to remain intact in a high percentage of

cases using the surgical technique employed in this study: that is, a combined extradural approach (Morello, 1971). Thus, Ferguson and his co-workers (1978) concluded that the proprioceptive fibres from human muscle spindle endings travel via the sensory division of the trigeminal nerve.

Histological (Szentagothai, 1949; Mizuno, Konishi and Sato, 1975; Mizuno, Konishi, Matsuda, et al., 1981) and electrophysiological (Landgren and Olsson, 1976) studies have clarified the somatotopic organisation of neurones located in the trigeminal motor nucleus. Mizuno and his co-workers (Mizuno et al., 1975; Mizuno, et al., 1981) have divided the nucleus into two regions: a dorsolateral division containing the temporalis, medial pterygoid, lateral pterygoid and masseter muscle motoneurones and a ventromedial division for the anterior digastric and mylohyoid motoneurones. Within this dorsolateral division, motoneurones innervating temporalis were located dorsally and dorsomedially, those innervating masseter, ventrolaterally, and those innervating the pterygoid musculature were ventromedially located. The size of the neurone cluster within the motor nucleus varied in different species which may relate to the different respective functional demands placed on different muscles. Digastric motoneurones were located in the ventromedial division in a caudal position. Within the mesencephalic

nucleus spindle afferents are not somatotopically organised according to the muscle of origin but are randomly interspersed (Cody, Lee and Taylor, 1972; Rakhawy, Shehata and Badawy, 1972).

Several electrophysiological studies have described the jaw-closing reflex to be unilateral. Lesions placed in the trigeminal mesencephalic nucleus or tract on one side partially or completely abolished the ipsilateral reflex response leaving the contralateral response intact (Corbin and Harrison 1940; Hufschmidt and Spuler, 1962). In addition, crushing the trigeminal motor root abolished the monosynaptic reflex response from the masseter and temporalis muscles on the side of the lesion (Griffin and Munro, 1971). During jaw opening, mesencephalic root potentials have been identified from ipsilateral fields only and not from the contralateral side (Corbin and Harrison, 1940; Jerge, 1963). Although McIntyre and Robinson (1959) suggested possible collateral spindle afferent projection to contralateral elevator alpha motoneurones, they considered such modulation to be facilitatory only and not capable of eliciting actual motoneurone discharge. However, it would appear that if alpha motoneurone excitability is near threshold then this facilitatory projection could be sufficient to do so. Goodwill (1968) also considered the neuronal pathways involved to be unilateral despite the bilateral response

routinely evoked following chin tap. This undoubtedly reflects stimulus transmission to receptors on both sides of the face as partial lateralisation occurred at extreme lateral positions (Goodwill, 1968). Other studies, however, have described projection of ipsilateral group Ia afferents to the trigeminal motor and mesencephalic nuclei of both sides without synaptic interruption (Smith, Marcarian and Niemer, 1967, 1968; Rakhawy et al., 1972; Kubota, Nagae, Katayama, Hosaka and Sato, 1981). In a recent animal investigation, the distribution of horseradish peroxidase (HRP) tracer following injection into the ipsilateral temporalis or masseter muscle was examined along with the cellular effects of unilateral tenotomy of these same muscles (Kubota et al., 1981). The latter procedure induced a disuse atrophy of spindles in the affected muscle and a bilateral asymmetric degeneration of cells in the trigeminal mesencephalic nuclei. In the former, HRP-labelled cells were demonstrated in the mesencephalic nuclei on both sides, albeit in low numbers on the contralateral side. Despite this clear evidence of bilateral representation, it was emphasised that HRP-labelled cells were only able to be identified on both sides in one-third of the specimens examined. To effect these contralateral projections, commissural interneurons are required and they have been described (Kidokoro, Kubota, Shuto and Sumino, 1968b; Mizuno et al., 1981). Such a bilateral projection therefore has the potential to produce

simultaneous activation of the masticatory muscles from unilateral receptors. As well, crossed inhibitory effects between the masseter muscles of each side have been identified (Kawamura, Kato and Takata, 1967; Kawamura, Funakoshi and Takata, 1960). However, this contrasts with the inability to detect group I crossed effects on masseteric motoneurons in acute spinal cats (Nakamura, Nagashima and Mori, 1973) but it was considered that this finding may relate to the less prominent effects of group I afferents in the acute spinal cat than in the chronic spinal preparation. Thus although the jaw-closing reflex is essentially a unilateral response, crossed inhibitory and direct excitatory projections may exist and if so, are capable of influencing trigeminal motoneuronal activity on the opposite side.

The jaw-closing reflex is therefore essentially a monosynaptic reflex subserved by an arc of two neurones, the afferent limb relaying probably through the trigeminal sensory root in man, the trigeminal mesencephalic nucleus and thence effecting monosynaptic junctions with the ipsilateral and possibly contralateral trigeminal motor nuclei.

2. METHODS OF EVOKING A MONOSYNAPTIC EXCITATORY ELEVATOR RESPONSE.

A monosynaptic reflex may be recorded in the elevator musculature under the following conditions:

- 2.1. During light downward chin tap
 - 2.1.1. at postural jaw position;
 - 2.1.2. with elevator muscle contraction.
- 2.2. During temporomandibular joint clicking.
- 2.3. With a mechanical tap to the facial skeleton.
- 2.4. Following electrical stimulation of masseteric or deep temporal nerves.
- 2.5. During tooth tapping - intercuspal and external mechanical.

2.1 During Light Downward Chin Tap.

2.1.1. At Postural Jaw Position.

The relaxed human subject lying in a supine position (Goodwill, 1968) or sitting upright with or without cranial support receives a perturbation to the chin. A non-standardised instrumentation, such as a hand-held reflex hammer is often employed to deliver the impulse

either directly to the chin or via an intervening object (Goodwill, 1968; Munro and Griffin, 1971; Goldberg, 1972c; Ongerboer de Visser and Goor, 1974).

Standardised systems for delivering mechanical stimuli to evoke reflex responses have been mentioned in the literature (Ott and Gassel, 1969; Bessette, Bishop and Mohl, 1971; Hannam, 1972; Bessette, Mohl and Bishop, 1974; Funakoshi and Amano, 1974; Godaux and Desmedt, 1975b; Lamarre and Lund, 1975; Bailey, McCall and Ash, 1977; Bratzlavsky, 1978; Cox, Al-Khateeb and Rothwell, 1982). These systems were designed to impart reproducible stimuli and thus minimise some of the variables encountered with the use of non-standardised systems (i.e. the hand-held reflex hammers used by Goodwill (1968), Munro and Griffin (1971) and Kugelberg (1952)) which principally involve wide variations in the magnitude, direction and rate of force application both within and between operators. Employing such standardised instrumentation, several workers (Hannam, 1972; Godaux and Desmedt, 1975b) have alluded to reproducibility of jaw-closing reflexes within a subject evoked under such conditions, however this has not been a unanimous view (Lewis, Pilcher and Yemm, 1978). In addition, although reproducibility may be attainable within an individual, such variables as jaw morphology and muscle fibre orientation would appear to preclude standardisation between individuals (Goodwill, 1968; Widmalm and Hedegård, 1976a and b).

Hannam (1972) and Lamarre and Lund (1975) both developed systems to evoke reproducible reflex responses by delivering downwards mechanical stimuli to the teeth. However, such systems were not used to elicit jaw-closing reflexes at postural jaw position as stimuli were imparted during elevator muscle contraction. Other researchers (Bessette et al., 1971; Bessette et al., 1974; Godaux and Desmedt, 1975b; Bailey et al., 1977; Bratzlavsky, 1978; Cox et al., 1982) have employed a solenoid-driven plunger to elicit jaw-closing reflex responses with menton tapping at postural jaw position. Although attempts were made to calibrate some of these systems under laboratory conditions, their ability to impart reproducible stimuli during actual delivery to the subject's chin has neither been monitored nor assessed. In addition, many aspects of apparatus design have not been fully explained; for example, Bessette et al., (1971) employed a solenoid-driven plunger, the tip of which was said to be maintained 0.5cm from the subject's chin. The means whereby this was achieved is not apparent, yet this is critical as it directly influences the magnitude of the impulse delivered. If evoked reflex responses are to be used as baseline and test data in the evaluation of physiological parameters as possible diagnostic and prognostic aids in the management of muscle-joint pain problems, it is important to fully describe the features of the system employed as it relates to reproducibility in order to allow valid

comparisons to be made with other data.

Some inconsistencies exist in the literature regarding the ease with which a jaw-closing reflex may be evoked in different individuals (Bessette et al., 1971; Goldberg, 1971; Ongerboer de Visser and Goor, 1974; Widmalm and Hedegård, 1976a and b; Ferguson, 1978; Lewis et al., 1978). Several workers have reported the reflex to be readily evoked from the masseter muscle (Goldberg, 1971; Ongerboer de Visser and Goor, 1974; Ferguson, 1978; Ferguson et al., 1978). Ferguson et al. (1978) were able to evoke a response on each occasion for all thirty-two subjects tested. In a similar study of fifty-one 'normal' individuals (Ongerboer de Visser and Goor, 1974) all those under the age of seventy years demonstrated a jaw-closing reflex bilaterally whilst in five of the nine subjects over seventy years a reflex was not evoked. They concluded that absence of a jaw-closing reflex is not necessarily indicative of pathology in subjects of advanced age. However, Lewis et al., (1978) were unable to demonstrate a response in the relaxed jaw closing muscles in all seven subjects tested except at the highest levels of applied tap and then only occasionally. Other researchers have reported varying abilities to evoke the response in

different individuals (Bessette et al., 1971; Widmalm and Hedegård, 1976a and b; Widmalm, 1982). In one study (Bessette et al., 1971), there was no detectable response at postural jaw position in 40% of a 'normal' sample and in 35% of a temporomandibular joint dysfunction sample. These results may reflect more accurately the frequency of evoking a measurable response in a group of subjects. Widmalm and Hedegård (1976a and b) experienced difficulty in taking accurate measurements at every recording and this related to the response not being elicited or the measuring points being too vague.

Several factors may account for these varying abilities to evoke a reflex response and these include:

a recording variations: equipment employed; magnitude, rate and direction of applied tap (the presence of preceding painful stimulation has been shown to inhibit the masseteric reflex elicited by chin tap (Godaux and Desmedt, 1975b) and thus an excessively hard tap may be inhibitory); environmental influences: external sounds, lighting and temperature which may influence the central excitatory state.

b subject variables: small sample sizes biasing the results; sampling from restricted community groupings, such as dental students; age and health of subjects; variations in motoneuronal activity at postural jaw

position. As the jaw-closing reflex is commonly evoked at this position, this latter factor is of importance and will be considered further.

The term 'postural jaw position' has been called a state of dynamic postural equilibrium, that is infinitely variable between individuals and from one moment to the next in each individual (Wyke, 1974). At any given moment in time the tension present in a muscle depends on the static elastic properties of the myofibrillar connective tissue components and also the size, number and frequency of firing of active motor units (Møller, 1966; Kawamura et al., 1967; Yemm and Berry, 1969; Lund, Nishiyama and Møller, 1970; Yemm and Nordstrom, 1974). The intrinsic characteristics of the passive determinants remain essentially unchanged in the absence of pathology at least in the short term, and several workers (Yemm and Berry, 1969; Shpuntoff and Shpuntoff, 1956) considered postural jaw position to depend on these static forces alone. However, active determinants appear more important than formerly believed in influencing short-term postural variations (Wyke, 1974; Møller, 1976).

The large, phasic, fast-fatiguable motor units of the supramandibular muscles are primarily involved in the generation of fast and powerful contraction. Small tonic, fatigue-resistant motor units maintain a continuous

low level of activity and this contributes to postural regulation in concert with the passive controls of gravity and the static elastic tension of the supra and inframandibular musculature. The number and frequency of firing of alpha motoneurons at postural position depends on the balance of facilitatory and inhibitory influences from segmental, intersegmental and suprasegmental systems. The main segmental systems are the myotatic and articular postural reflex systems. In addition, longitudinally disposed inter-segmental projection systems may modulate trigeminal alpha and fusimotoneurons. Thus projections from vestibular, cerebellar and reticular regions impose facilitatory or inhibitory influences on the postural motor unit activity of the supramandibular musculature (Møller, 1966; Lund et al., 1970; Wyke, 1974). The reticular formation has a profound effect as a wide range of projections may influence activity in this system which include indirect cortical projections via basal ganglia; limbic system inputs via the amygdaloid nucleus; pain receptor inputs from oro-facial tissues; influences from specific centres located in the reticular formation, for example, the respiratory centre; hormones; drugs and so on (Matthews, 1972; Wyke, 1974). Anything potentiating the facilitatory influences of the reticular system on elevator motoneurone excitability will have a tendency to cause approximation of the mandible with the maxillae, for example, the inspiratory phase of respiration; increase

in emotional tension; oral pain; hypercarbia; adrenaline. In contrast, any influence reducing excitatory projections from the reticular formation will tend to cause an increase in vertical dimension (Wyke, 1974). In addition, corticobulbar projection systems are known to cause tonic reflex facilitation of the mandibular motoneurons (Evarts, 1965; Kostjuk and Vasilenko, 1968). Thus a wide range of centrally and peripherally derived projections influence postural jaw position by modulating motoneurone excitability and the ease with which monosynaptic facilitation may occur.

The contribution to postural motoneurone activity from segmental myotatic reflexes derives from the level and frequency of tonic spindle afferent discharge at postural jaw position which, in turn is dependent on:

a passive stretch from gravity which varies with head position and the total weight of the lower jaw, and

b prevailing static fusimotor activity (Matthews, 1971). In the trigeminal system, spontaneous activity from low threshold, slowly adapting TMJ mechanoreceptors at postural jaw position (Thilander, 1961; Klineberg, 1971; Wyke, Greenfield and Klineberg, 1972) would appear to establish an excitatory projection onto the dynamic fusimotoneurons of the trigeminal motor nucleus (Kawamura and Majima, 1964; Freeman and Wyke, 1967) as has been demonstrated in limb muscle (Appelberg, Hulliger, Johansson and Sojka, 1979). However, studies of the muscles

acting at the ankle joint and those of the forearm have shown that spindle endings in relaxed human limb muscle, at least, are not subjected to significant background fusimotor drive (Burke, Hagbarth, Lofstedt and Wallin, 1976; Burke, McKeon, Skuse and Westerman, 1980; Burke, Skuse and Stuart, 1979). Section of afferent endings to these muscle spindles did not alter background spindle afferent discharge or the responsiveness to tendon percussion, tendon vibration or muscle stretch (Burke et al., 1976; Burke, Hagbarth and Skuse, 1978). In addition, at a comfortable resting position of the hand, less than 10% of the spindle endings recorded were found to be spontaneously active (Burke et al., 1976; Burke et al., 1979; Vallbo, 1974). Thus the tendon jerk seen in spinal systems does not appear to require background fusimotor activity for its elicitation; in addition, fluctuations in its amplitude and variations in the ease of eliciting the reflex in different muscles and in different subjects appears not due to changes in background fusimotor drive but rather to differences in central reflex excitability independent of the fusimotor system (Burke, 1981). There appears to be no evidence that mental state, motor preparedness or anticipation of the need to contract a muscle result in preparatory activation of the fusimotor system in advance thus potentiating an evoked reflex response. The changes in gain of proprioceptive reflexes that occur in these situations appear to result from central processes independent

of the fusimotor system (Burke, 1981). Thus if a muscle is not contracting, fusimotor sensitisation of its spindle endings does not appear to be significant, however, this does not preclude some subthreshold fusimotor discharge. These studies do not yet appear to have been attempted for the trigeminal neuro-muscular complex and thus extrapolation from the spinal to the cranial reflex systems must be made with caution. For example, it appears that, with the jaw at postural position there is indeed activity in trigeminal alpha motoneurons (Goldberg, 1976a) which implies that, consistent with a concept of alpha-gamma coactivation, fusimotoneurone activity could be more prominent for cranial elevator muscles at 'rest' than for resting limb muscles. It may be therefore that spindle endings in jaw elevator muscles are subjected to a more significant background fusimotor drive than that evident in limb muscles. Thus the variability encountered in the literature concerning the ease of eliciting the jaw-closing reflex and the highly variable amplitude of this response between individuals may relate to variations in fusimotor drive as well as variations in the central excitatory state independent of the fusimotor system.

2.1.2. With Elevator Muscle Contraction.

During a voluntary contraction and with increased voluntary effort, fusimotoneurons are recruited in an

orderly manner at individually specific thresholds in a similar fashion to that for alpha motoneurons and the net effect of this is to increase spindle afferent discharge. The thresholds for fusimotor activation are reproducible and differ markedly for different spindle endings in the same muscle (Burke, Hagbarth and Skuse, 1978), thus during elevator contraction different endings are subjected to different degrees of fusimotor activity and threshold differences are due, at least in part, to alterations in fusimotor input to each spindle (Burke, 1981).

Skeletomotor and fusimotor outflows to muscle are co-activated during voluntary contraction and co-silenced during relaxation via a flexible alpha-gamma linkage (Burke, 1981). Modulation of this balance in favour of either motoneurone depends on the relative projection from supra-segmental descending systems and from ascending afferent pathways. Thus enhanced facilitation of fusimotoneurons and/or enhanced inhibition of alpha-motoneurons will shift the balance in favour of the fusimotoneurone pool. Either way, spindle endings will be easier to activate (Burke, 1981). During isometric contractions or slow purposeful movements, especially involving learning, the fusimotor system establishes a "carrier frequency" of spindle afferent discharge which facilitates encoding of irregularities and departures from the intended movement (Vallbo, 1973; Burke,

Hagbarth and Löfstedt, 1978a and b). Now, mechanical perturbations delivered to the menton region at intercuspal position clench appear to be transmitted through bone and soft tissue to alter spindle ending discharge by vibration (Matthews, 1972). Overt spindle stretch does not appear necessary since jaw opening during menton tapping was not observed in one study attempting to move thin, essentially non-deformable strips placed between the teeth at clench (Goldberg, 1972c). Rather, vibration appears to evoke monosynaptic reflex responses by becoming encoded as irregularities in ongoing spindle afferent discharges and projecting centrally to a trigeminal motoneurone pool that is itself the target of marked descending facilitatory projections from higher centres. Whether or not a reflex is evoked with menton tap at clench depends therefore on the final relative level of alpha-gamma balance and whether motoneurone excitability is altered sufficiently to evoke a response.

The ongoing level of background emg activity may modify the manifestations of the various reflexes (Ott and Gassel, 1969; Matthews, 1976). For example, a monosynaptic reflex evoked during clench has been reported to exhibit a shorter latency (Goldberg, 1972c; Widmalm, 1976b; Widmalm and Hedegård, 1976a and b; Yamada & Ash, 1982) and a larger amplitude (Hagbarth and Finer, 1963; Hannam, 1972; Lamarre and Lund, 1975; Vural, 1981) than a similar reflex evoked at

postural jaw position. Widmalm (1976b) reported a significantly shorter latency (1% level significance) in the relaxed masseter (5.8msec) as compared with that elicited during clench (6.4msec). However, Bessette and his coworkers (1971, 1974) did not identify a reduction in jaw-closing reflex latency at intercuspal position clench, but this appears to have been a visual observation rather than a statistically validated one. Nevertheless, a decrease in latency and an increase in amplitude would be anticipated on theoretical grounds; firstly, the associated enhanced descending projection onto trigeminal alpha and fusimotoneurons will potentiate the motoneurone response to incoming afferent discharge and will increase spindle primary ending sensitivity to vibratory stimuli. As a result, it is likely that less temporal summation would be required before threshold for motoneurone activation is exceeded and this would produce a shorter latency; in addition, the same stimulus intensity will generate an enhanced afferent return potentially capable of activating higher threshold motor units sooner which, although they may not be firing initially, are approaching threshold (Munro and Griffin, 1971; Lennartsson, 1980; Goldberg, 1972c). Secondly, contracting muscle may exhibit an altered rate of vibration transmission in contrast to that of relaxed muscle through the effects of damping and resonance. This may affect the activation time of muscle spindles (Goldberg, 1972c) contributing to the altered latency values.

Similar segmental reflex potentiations have been reported to occur following sudden changes in external load in contracting limb muscle. These effects have not primarily been attributed to increased fusimotor activity but rather to central mechanisms independent of the fusimotor system (Burke, Hagbarth and Löfstedt, 1978a and b) acting to alter reflex transmission within the spinal cord or to potentiate an already discharging motoneurone pool. However, as previously discussed, extrapolation from limb muscle studies to the jaw musculature must be done with caution. Thus, the relative contributions made by central mechanisms independent of the fusimotor system and by the fusimotor system itself in the modulation of evoked reflexes during voluntary contraction may not necessarily be identical for both motor systems.

Several studies, however, have reported an inability to elicit a monosynaptic jaw-closing reflex at intercuspal position clench (Hufschmidt and Spuler, 1962; Goldberg, 1972c). Although the tracings published by Hufschmidt and Spuler (1962) do not clearly demonstrate a monosynaptic reflex superimposed on the high background emg level, the response may nevertheless be present, being just submerged by the ongoing activity. Other workers (Bessette et al., 1971; Widmalm and Hedegård, 1976a and b; Murray and Klineberg, 1981) have been readily able to elicit superimposed responses during light (Widmalm and Hedegård, 1976a

and b; Widmalm, 1976b) and even maximum clench (Bessette et al., 1971); in fact, the response has been reported to be easier to elicit than at postural jaw position (Bessette et al., 1971) and, as mentioned previously, the amplitude was greater. In a study of the ankle jerk reflex (Ott and Gassel, 1969) the facilitatory effect on this response with light levels of voluntary activity in the triceps surae became an inhibition with increased voluntary effort. These observations have not been described in jaw musculature which probably reflects the inherent differences between spinal and cranial reflex systems. Vural (1981) has reported a potentiation of the jaw-closing reflex amplitude at intercuspal position over those evoked at four other jaw positions in the following order of decreasing amplitude: protrusion clench; contralateral side clench; ipsilateral side clench and postural jaw position. This is consistent with Goldberg's (1972c) findings of reflex enhancement in the masseter contralateral to the biting side. In another similar study, however, subjects biting on a bung placed between the ipsilateral premolars (Matthews, 1976) demonstrated reflex facilitation on the biting side; but this procedure is not the same as clenching on the teeth in lateral excursion which may be the reason for the altered pattern of efferent excitation observed. Nevertheless, despite these inconsistencies it is still apparent that simply changing the side on which the subject bites produces a dramatic reversal in the pattern of the masseteric mono-

synaptic stretch reflex. The diminished voluntary activity present in the ipsilateral muscle during clenching directly on the teeth parallels the change in stretch reflex response amplitude on that side. Several reasons may account for these positional modulations of motoneurone excitability: firstly, biting at different jaw positions alters muscle and spindle length and this may modify fusimotor and then alpha motoneurone susceptibility to the menton tap stimuli (Goldberg, 1972c). Secondly, alterations in capsular tension accompanying changes in jaw position will provide an afferent projection from joint receptors capable of exerting complex modifying influences on trigeminal motoneurone excitability (Kawamura, 1967; Clark and Wyke, 1974; Wyke, 1974; Klineberg, 1971) and this could modulate jaw reflex manifestation. Thirdly, an enhanced afferent projection from periodontal membrane mechanoreceptors on the biting side may exert ipsilateral inhibitory influences on elevator motoneurons.

Yamada and Ash (1982) have been able to evoke reflex responses with monosynaptic latency from the masseter muscle during active jaw opening. The latency of this reflex was found to be similar to that evoked at postural jaw position and thus longer than that at clench.

If only alpha motoneurons were activated during a voluntary elevator muscle contraction then a monosynaptic reflex elicited during clench would exhibit a reduced ampli-

tude due to the shift in alpha-gamma balance favouring alpha motoneurons (Matthews, 1976). However, a correlation between the magnitude of the reflex response and the degree of voluntary activity in the elevator muscles has been established (Hannam, 1972; Lewis et al., 1981). Hannam identified reflex facilitation during sequentially increasing voluntary elevator muscle contraction and this was attributed to one of the following:

- a. Jendrassik-type reinforcement by the contraction of synergistic muscles, for example, medial pterygoid, temporalis. The degree of elevator motoneurone facilitation with increased voluntary biting effort was greater than that seen during forceful limb contraction (Hannam, 1972). Therefore this Jendrassik-type facilitation during clench probably derives from synergistic elevator muscle groups exerting a greater potentiating effect than from the more distant limb musculature. Or,
- b. autogenic facilitation may occur caused by voluntary contraction of the muscle itself. This may potentiate gamma motoneurone activity and increase the sensitivity of the muscle spindle to applied stretch, in addition, alpha motoneurone excitability will be brought closer to threshold. A perturbation of similar magnitude would then be expected to elicit a larger response. Or,
- c. a combination of both factors together may be involved.

Extrapolation from studies of the ankle jerk reflex (Ott and Gassel, 1969) have emphasised the role of synergistic muscle contraction, especially on the contralateral side, in reflex enhancement (Jendrassik-type re-inforcement). However, ipsilateral muscle contraction was seen to produce an early reflex inhibition in the same muscle, and this was attributed to the presence of refractory motor units, autogenic inhibition from Golgi tendon organs and/or recurrent collateral inhibition (Ott and Gassel, 1969). However, Hannam criticised the results of this study on the basis that with increased muscle activity, the amount of spindle stretch produced by the applied stimulus may well have been less since heel displacement was not monitored and thus the apparent reflex inhibition may have in fact related to a reduced spindle length change. In his study, Hannam (1972) concluded that although he had demonstrated progressive facilitation of the jaw-closing reflex with increased voluntary effort, the exact aetiology of the reflex potentiation was still unknown, that is, whether the enhancement was due to autogenic factors, synergistic factors or both. An additional factor may further complicate the issue. Hannam's studies were not performed at intercuspal position clench but rather employing a device that imparted reproducible stimuli as the jaw was voluntarily closed. However, in order to produce the same amount of jaw opening during stimulus delivery, and thus a standard degree of spindle stretch at greater levels of elevator contraction, higher forces were imparted.

Since spindle stretch is not essential to evoke a monosynaptic response (Lamarre and Lund, 1975) then the increase in stimulus strength itself may have contributed to the larger amplitude (Lewis et al., 1978) in addition to any Jendrassik potentiation or autogenic facilitation that may have been associated with elevator muscle contraction.

It is apparent therefore that a monosynaptic reflex may be elicited in the elevator muscle electromyogram following chin tap during sustained isometric elevator contraction. The perturbations generate vibration which becomes encoded as irregularities in ongoing spindle afferent discharge and which then project centrally to activate motor units in a synchronous fashion.

2.2 During Temporomandibular Joint Clicking (Widmalm and Hedegård, 1976a and b).

A close time association between short latency electromyographic reflex responses in the temporalis and masseter muscles and recorded arthrosounds has been reported. The response so recorded may be unilateral or bilateral with a latency shorter (5.5msec) than for a menton tap evoked jaw-closing reflex (6.3msec; Widmalm and Hedegård, 1976a and b).

The uncoordinated jaw movement characteristic of joint clicking could cause vibration transmission through the zygomatic arch and/or stretch of the lateral ligament (Widmalm, 1976b). Oscillations generated in the zygomatic bone and causing longitudinal vibrations in the masseter will activate primary spindle endings if of sufficient magnitude (cf. the zygomatic jar reflex - Fujii and Mitani, 1973). Stretch transmitted via the lateral ligament may be adequate to activate the primary spindle endings - a peak-to-peak amplitude of 10 μ m being adequate (Matthews, 1972).

2.3 With a Mechanical Tap to the Facial Skeleton

A tap to part of the facial skeleton, for example, the zygomatic bone, elicits a so-called "jar reflex" in the resting elevator muscle electromyogram (Harrison and Corbin, 1942). The phenomenon was first described by Sherrington (1895) who identified a brief twitch response in some limb muscles of the decerebrate cat when a tap was applied to a nearby bony prominence. Elevator muscle activates at a latency of about 7msec following delivery of a mechanical tap to the skull of cat (Harrison and Corbin, 1942; Rioch and Lambert, 1934) and to a head clamp cemented into the frontal sinus (Matthews, 1975). This response may be facilitated by simultaneously evoking the stretch reflex in the elevator muscles (Matthews, 1975).

2.4 Following Electrical Stimulation of Masseteric or Deep Temporal Nerves.

The H-reflex or H-wave may be evoked in masseter or temporalis afferents by electrical stimulation of the masseteric or deep temporal nerves (Fujii and Mitani, 1973). Orthodromic activation of group Ia afferents causes a mono-synaptic reflex in masseter and temporalis emg recordable as the H-reflex. This response has a shorter latency (6.4msec; Ogawa, 1972), than the zygomatic jar reflex (7.0msec; Matthews, 1975). The H-reflex appears to be recordable only in masseter during a voluntary isometric contraction and not at postural jaw position (Bratzlavsky, 1978). This suggests that facilitation of the reflex arc from descending cortical projections may be necessary to allow an H-reflex response to be evoked.

2.5 During Tooth Tapping - Intercuspal and External Mechanical.

Mechanical stimuli to upper teeth have been shown to evoke an excitatory reflex in the elevator muscles (Goldberg, 1971; Sessle and Schmitt, 1972; Orchardson and Sime, 1981) which has been variously reported to derive from direct

stimulation of periodontal membrane mechanoreceptors (Goldberg, 1971) or vibration transmission to muscle spindles (Hannam et al., 1969a and b, 1970) or both (cf. Periodontal Membrane Mechanoreceptors). Axially directed tooth tap (Orchardson and Sime, 1981) may cause some skull movement relative to mandible and this could stretch spindle afferents directly.

Similar transient elevator muscle activations in association with inhibitory phases (Matthews, 1976) have been reported during tooth tapping at intercuspal position clench. The aetiology of these excitatory phases may relate to muscle stretch following slight rebound of the mandible after tooth contact or vibration transmission through bone to muscle spindles (Hannam et al., 1969a and b, 1970) or both. With an increased tooth tapping effort the response is likely to be potentiated from two sources: firstly, an enhanced stimulus to the muscle spindles will increase primary ending afferent discharge and contribute greater facilitatory projection to trigeminal motoneurones. Secondly, increased voluntary effort may enhance the response through Jendrassik reinforcement from synergistic muscles and/or autogenic facilitation from the same muscle (Hannam, 1972).

3. PERIPHERAL REGULATORY INFLUENCES - THE PHYSIOLOGY OF CHIN TAP

Many receptors are undoubtedly activated during delivery of a mechanical stimulus to the chin at postural jaw position or during clench (Dubner, Sessle and Storey, 1978; Figure:3). Their relative contribution to motoneurone excitability is subject to modification at the final common pathway from suprasegmental, intersegmental and other segmental projections, which are themselves highly variable between individuals. Because of these widespread modifying influences, reflex response production is modulated accordingly. These peripheral influences derive from muscle spindles and temporomandibular joint, cutaneous, periodontal, periosteal and mucosal mechanoreceptors (Figure 3; Klineberg, 1971; Goodwin and Luschei, 1974; Widmalm, 1976b; Stein and Edwards, 1978; Linden, 1978). The marked reduction in the amplitude of an evoked monosynaptic reflex at postural jaw position (Bessette et al., 1974) following local anaesthesia of various sensory branches of the trigeminal nerve attests to the existence of an extensive afferent projection. Nevertheless, the presence of a small response during anaesthesia at postural position indicated that Ia afferent projection was still functional. Therefore the reduction in the amplitude of the monosynaptic reflex was attributed to a disfacilitation of alpha-motoneurone excitability from the markedly impaired sensory input. Now, monosynaptic reflexes evoked during elevator muscle

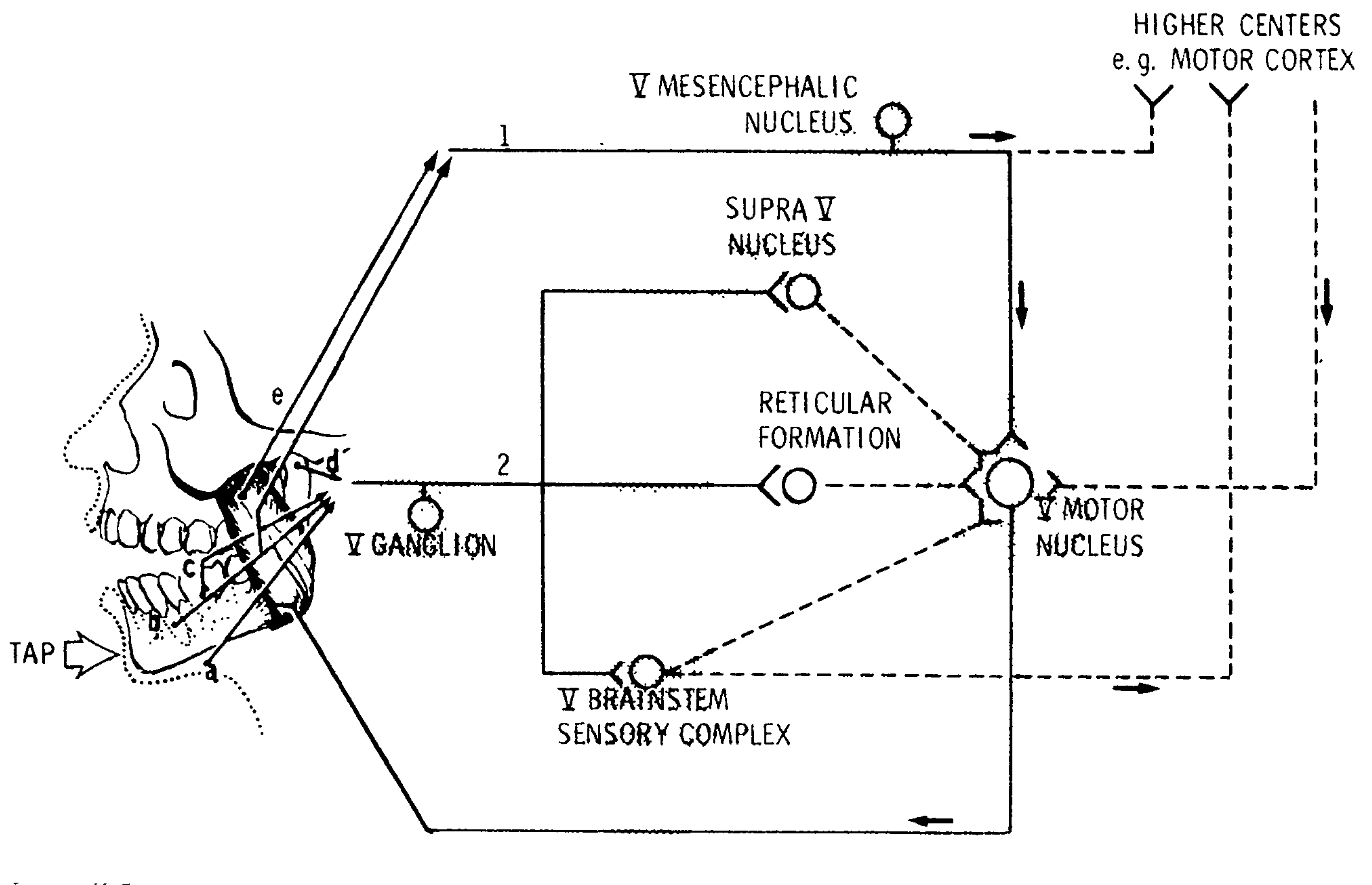


FIGURE: 3

Illustration of possible diverse sources of afferent projection following mechanical tap to the menton region of a human subject. Afferent data from cutaneous (a), periodontal (b), gingival (c) and temporomandibular joint (d) receptors, and golgi tendon organs may project via a variety of pathways to the motor nucleus (pathway 2) which itself may be modulated by projections from higher centres. Muscle spindles and possibly periodontal receptors appear to be the only receptors that may effect monosynaptic junctions with the trigeminal motor nucleus (from Dubner, Sessle and Storey, 1978).

contraction and whilst anaesthesia was still present, regained reflex amplitude (Bessette et al., 1974). Thus descending facilitatory projections from higher centres appear to alter trigeminal motoneurone excitability sufficiently to compensate for the diminished afferent projection associated with the anaesthesia.

Thus, the direct or indirect projection of afferent data from these widespread peripheral fields to trigeminal alpha motoneurons (Yu, Schmitt and Sessle, 1973; Bratzlavsky, 1976; Goldberg, 1976b and c; Greenwood and Sessle, 1976; Gurza, Lowe and Sessle, 1976; Sessle and Greenwood, 1976) provides a modulating influence on and contributes to monosynaptic elevator reflexes (Thexton, 1974a).

Sources of afferent projection which may be involved in the production of a jaw-closing reflex during menton tap include:

- 3.1 intraoral afferents,
- 3.2 muscle spindles,
- 3.3 periodontal membrane mechanoreceptors,
- 3.4 Golgi tendon organs,
- 3.5 temporomandibular joint mechanoreceptors,
- 3.6 cervical articular and vestibular receptors,
- 3.7 acoustic stimuli,
- 3.8 cutaneous receptors.

3.1 Intraoral Afferents

Auditory stimuli and stimuli applied to limb and oral-facial sites may produce inhibitory effects in the elevator muscles (Gurza et al., 1976; Yu et al., 1973; Meier-Ewert, Gleitsmann, Reiter, 1974; Morimoto, Sakan, Inoue, Takebe, Kawamura, 1981). However, electromyographic studies in animals (Goldberg, 1972a; Funakoshi and Amano, 1974; Thexton, 1974b; Gurza et al., 1976) and in man (Goldberg, 1971; Sessle and Schmitt, 1972; Achari and Thexton, 1974) have demonstrated weak facilitatory influences of short and long latency in masseter and temporalis alpha and fusimotoneurons with stimulation of various intraoral receptors (cat infra-orbital nerve; cat glossopharyngeal nerve; cat superior laryngeal nerve; cat lingual nerve and monkey gingiva (Goldberg, 1972a); cat tooth pulp; cat forepaw and human tooth (Goldberg, 1971; Sessle and Schmitt, 1972); human tongue and palate, human tooth (Achari and Thexton, 1974)). Mechanical stimulation of structures in the oral cavity has been shown to evoke reflex jaw-closing in experimental animals (Sherrington, 1917; Harrison and Corbin, 1940; Thexton, 1968, 1973, 1974b; Goldberg, 1972a; Matthews, 1975). However, mechanical stimuli to the palate will produce a variable response in the elevator muscles depending on the nature of the stimulus delivered. Thus slow application of pressure to anterior hard palate in cat has been reported to produce inhibition in elevator muscle

alpha and fusimotoneurone activity evidenced as a sustained jaw opening (Achari and Thexton, 1974; Morimoto et al., 1981). This inhibitory effect has been implicated in the reflex control of jaw movement through the modulation of alpha and fusimotoneurone activity to assist subcortical and brain-stem motor centres in the control of motoneuronal activity (Morimoto et al., 1981). In contrast to slow pressure application, a rubbing stimulus between tongue and palate evokes an excitatory reflex in the masseter with a latency of between 15 and 30msec (Achari and Thexton, 1974). Topical anaesthetic ointment applied to the region of mucosa stimulated, abolished the excitatory response for the period of the anaesthesia, and this finding suggested that superficial receptors were involved in this response (Achari and Thexton, 1974). That vibration is probably not significant in the aetiology of this reflex is indicated by the production of a similar response but with a significantly shorter latency (of between 9 and 12msec) following stimulus application intended to generate vibration, that is, a rubbing stimulus applied between incisor teeth. Nevertheless, vibration transmission has been implicated in the aetiology of a similar reflex response elicited following tooth tap, that is the periodontal-masseteric reflex (Hannam et al., 1969a and b, 1970). However, Goldberg (1971) attributed this response to periodontal membrane mechanoreceptors (see section on periodontal receptors for further discussion).

Although these reflexly induced excitatory responses in man appear only to occur with a background of voluntary activity (Hannam et al., 1969a and b, 1970; Goldberg, 1971; Sessle and Schmitt, 1973; Achari and Thexton, 1974), this requirement appears unnecessary in experimental animals (Thexton, 1973; Goldberg, 1972a). Yet the ability of a palatal rubbing stimulus to evoke an excitatory response in human subjects during voluntary muscle contraction indicates that afferent projection is occurring but is nevertheless insufficient to bring 'resting' alpha motoneurons to threshold (Achari and Thexton, 1974). This latter observation, that certain types of afferent projection activate motoneurons only under specific conditions, has also been reported by Thexton (1968) who observed that a train of stimuli, each subthreshold for the jaw-opening reflex, could evoke jaw closing if they were delivered shortly after a single larger stimulus, which itself produces jaw opening (Thexton, 1968). A dual excitatory reflex response has been identified in temporalis and masseter motoneurons following lingual nerve stimulation: an early phase has a latency of about 5msec and a late phase has a latency of about 18msec (Goldberg, 1972a). A more recent study also demonstrated facilitations following weak repetitive lingual nerve stimulation, however, at high levels of stimulation jaw elevator muscle activity was inhibited (Morimoto, Manderli and Scharer, 1975). Although stimuli applied to tooth pulp (Bratzlavsky,

de Boever and van der Eecken, 1976) were unable to facilitate the jaw-closing reflex, several studies have confirmed short latency excitatory responses in the masseter electromyogram following mechanical tooth stimulation (Funakoshi and Amano, 1974; Goldberg, 1971; Sessle and Schmitt, 1972). These non-spindle afferent excitatory reflexes may involve monosynaptic linkages (Goldberg, 1971, 1976b; Sessle and Schmitt, 1972), however, the longer reflex latencies associated with intraoral afferent stimulation compared with that of the jaw-closing reflex suggests a disynaptic linkage from intraoral afferents (Kidokoro et al., 1968a; Sumino, 1971). The palatal receptors involved in short-latency excitatory responses following rapid application or removal of pressure from oral mucosa are probably rapidly adapting (Thexton, 1973). The reduction in elevator muscle activity with maintained pressure highlights the role of slowly adapting mechanoreceptors in contributing inhibitory projections to trigeminal afferents under these conditions (Morimoto et al., 1974).

In addition to these facilitatory influences, innocuous and noxious stimuli applied to extraoral or intraoral sites in man are able to produce inhibitory phases in the masseter muscle (Yu et al., 1973). Recent intracellular studies involving stimulation of low threshold afferents in inferior alveolar, superior alveolar, infra-orbital and lingual nerves, have identified complex sequences of excitatory and inhibitory phases in elevator motoneurons (Goldberg

and Nakamura, 1968; Kidokoro et al., 1968a; Goldberg, 1971; 1972a, 1972b; Sessle and Schmitt, 1972). These modulations in trigeminal motoneuronal excitability may be monitored by evoking a masseteric reflex at varying intervals of time following the afferent stimulus. Employing this technique a polyphasic series of membrane potential changes have been described in masseteric motoneurons following intraoral afferent stimulation. An early inhibitory phase, occurring 2.0 to 3.0msec after a single shock stimulus to an intraoral afferent nerve, has been shown to peak at 8 to 10msec (Goldberg and Nakamura, 1968; Kidokoro et al., 1968a and b). This phase may derive from inhibitory post-synaptic potentials arriving at the motoneurone pool via a disynaptic path involving internuncial neurones which probably reside in the nucleus supratrigeminalis (Lorente de Nó, 1922; Goldberg and Nakamura, 1968; Kidokoro et al., 1968a and b). This nucleus is believed to mediate trigeminal reflex activity and, in particular, inhibition of the jaw-closing muscles. It is of interest that hypoglossal nerve stimulation may also produce inhibition and this may be illustrated as a prolonged suppression of the ipsilateral and contralateral masseteric reflex (Nakamura, Goldberg, Mizuno and Clemente, 1970). This effect appears to be mediated via a polysynaptic pathway to the trigeminal motor nucleus from hypoglossal afferents. These phases of hyperpolarisation following intraoral afferent stimulation may be abolished by strychnine administration to unmask an early excitatory phase 2.5msec after stimulus delivery (Kidokoro

et al., 1968a and b; Goldberg, 1972b; Takata and Kawamura, 1970). This facilitatory wave of depolarisation appears to involve a disynaptic pathway (Kidokoro et al., 1968b; Sumino, 1971; Sessle, 1977b) with interneurons in the trigeminal nucleus oralis and interpolaris (Sessle, 1977b), however, the presence of a monosynaptic pathway cannot be excluded (Goldberg, 1971; Sessle and Greenwood, 1976). A second depolarisation occurring at a latency of 18msec with a peak at 20msec is considered to be an active excitatory phase and not merely a post-inhibitory phase rebound phenomenon (Goldberg and Nakamura, 1968). This conclusion was based on the ability of midline section, which abolished the initial hyperpolarisation, to potentiate the excitatory reflex (Kidokoro et al., 1968a). This would not be expected if the excitatory phase was evoked as a rebound event. After this later facilitatory phase, a second wave hyperpolarisation with a peak of 40msec interrupts recovery with then a gradual return to pre-stimulus levels.

Research into human oral reflexes (Goldberg, 1976b) employing the jaw-closing reflex as an indirect measure of motoneurone excitability following intraoral afferent stimulation have supported the results from these intracellular studies. Periods of hyperpolarisation occur corresponding with those identified from intracellular research, the time of occurrence depending on the type of stimulus (Yu et al., 1973). Thus innocuous mechanical or electrical stimuli applied to various intraoral and extraoral sites,

such as controlled mechanical perturbations to upper lip and upper incisor, have evoked periods of early inhibition in masseter activity (Sessle and Schmitt, 1972; Yu et al., 1973) exhibiting latencies of 15 to 20msec and durations of 8 to 18msec. However, noxious stimulation of lip or intraoral sites causes late polysynaptic inhibitory influences on trigeminal motoneurons with latencies of 40 to 50msec or more. High threshold afferents are thought to make a significant contribution to these late phases (Kidokoro et al., 1968a; Godaux and Desmedt, 1975) via pre-synaptic inhibitory mechanisms (Goldberg, 1972a; Goldberg and Nakamura, 1977) involving pathways relaying in the trigeminal nucleus interpolaris and the reticular formation (Sumino, 1971). However, electrical tooth stimulation, which presumably activate A-delta pain fibres, can evoke short latency phases of depression similar to those seen following stimulation of non-nociceptor, low threshold, labial and periodontal mechanoreceptors (Bratzlavsky et al., 1976).

As well as the type of stimulus, the strength of the stimulus and the level of maintained muscle activity appear to modulate parameters of the evoked response. Thus the incidence and the duration of the period of inhibition following noxious or innocuous stimuli is markedly decreased with increased voluntary motoneurone activity. Increase in stimulus strength to noxious levels will generate later

periods of inhibition and prolongation of inhibitory phases in both animals and man (Bratzlavsky, 1972; Yu et al., 1973; Meier-Ewert et al., 1974; Godaux and Desmedt, 1975b; Matthews, 1975; Gurza et al., 1976). In addition to suppression, a short latency (7 to 11 msec) excitation in the masseter electromyogram may be observed following low-intensity mechanical and electrical stimulation of intraoral and adjacent sites (lip, tongue, tooth and palatal mucosa) innervated by the trigeminal nerve (Gurza, Lowe and Sessle, 1976). Stimuli delivered to more remote sites, forepaw and tail, failed to evoke short-latency excitations (Gurza et al., 1976) even with high intensity stimuli; auditory stimuli were also without effect. However, a late facilitatory effect clearly separates the two inhibitory phases and, corresponding with that identified in intracellular studies (Kidokoro et al., 1967a), is demonstrable in the elevator electromyogram of man and animal (Bratzlavsky, 1972; Yu et al., 1973; Meier-Ewert et al., 1974; Godaux and Desmedt, 1975b; Matthews, 1975; Gurza et al., 1976). Thus, higher intensity stimuli have been associated only with periods of inhibition and possibly a late period of excitation (Gurza et al., 1976). Nevertheless, spindle afferents from synergistic jaw muscles can produce an early facilitatory effect in elevator afferents following low intensity stimuli (Hamada et al., 1974).

Alpha and fusimotoneurons have been identified in the trigeminal motor system (Sessle, 1977b; Morimoto et al.,

1981). Excitatory and inhibitory modulations of fusimotoneurone activity with similar latencies and durations as seen in alpha motoneurons have been described (Gurza et al., 1976). These simultaneous effects suggest the possibility of a peripherally induced coactivation of elevator alpha and fusimotoneurons. This peripheral control of fusimotoneurone activity may act to reinforce and perfect a segmentally induced reflex response by modulating the excitability of the fusimotor loop. As an overriding influence on the entire system, central descending projections modulate the activity of both types of motoneurone (Sessle, 1977a).

The rationale of a presynaptic inhibitory mechanism in motor control could relate to the need for protection of ongoing movement patterns from excessive reflex influences inherently related to the movement sequence (Goldberg, 1976b). Chewing sequences activate large numbers of receptors and as their afferent projections will exert powerful influences on centrally-controlled trigeminal motoneurons, they could possibly disrupt, unnecessarily, ongoing movement patterns. The existence of a presynaptic inhibitory mechanism would control the reflex effects of peripheral receptor stimulation and allow centrally controlled jaw movement sequences to proceed independent of peripheral feedback (Goldberg, 1976b). For example, muscle spindle stretch occurring during jaw-opening will exert

monosynaptic facilitatory projections onto elevator motoneurons which could possibly inhibit a phase of continued jaw-opening that may be part of the centrally programmed sequence patterning. Thus the existence of a mechanism of hyperpolarisation, of peripheral or central origin or both (Kidokoro et al., 1968a; Sauerland, Nakamura and Clemente, 1967), would discourage elevator motoneurone activation inappropriate to an ongoing movement sequence (Goldberg and Tal, 1978; Bratzlavsky, 1981). Both pre- and post-synaptic mechanisms appear to be involved in these inhibitory modulations (Goldberg and Nakamura, 1977; Goldberg and Tal, 1978).

In conclusion, the elevator motoneurone pool receives projection of sensory information from afferents in the second and third divisions of the trigeminal nerve, the glossopharyngeal, vagus, superior laryngeal and limb nerves (Kidokoro et al., 1968; Greenwood and Sessle, 1976; Sessle, 1977b). Afferent information along trigeminal nerve branches is capable of generating a complex interaction of inhibitory and facilitatory effects on elevator motoneurons which will modulate the characteristics of reflexes evoked utilizing these same pathways.

3.2 The Muscle Spindle (Boyd, 1980; Dubner et al., 1978; Karlsson, 1976; Matthews, 1972; Figure: 4).

The muscle spindle is a sensory receptor primarily concerned with length measurement (Burke, 1980). It consists of a bundle of specialised intrafusal muscle fibres which, although developing negligible tension (less than 5mg) in comparison with that developed by the extrafusal fibres of the main muscle mass (several kg), nevertheless exert powerful modulatory influences on alpha motoneurones (Matthews, 1972).

Most of our understanding of spindle structure has derived from light and electron microscopy (Karlsson, 1976) of muscles other than those associated with the face or jaw. However, muscle spindles have been identified in the jaw elevator muscles in man (Freimann, 1954) and they do not appear to be functionally or structurally different from spindles located elsewhere (Matthews, 1976; Cody et al., 1972).

The muscle spindle may be several millimetres in length but is rarely more than 100 μ m wide. Being fusiform in shape, hence the name, it is somewhat broader in its central or equatorial region and tapers slightly towards the polar regions. A highly vascular capsule encloses the equatorial and part of the polar regions and houses a jelly-like material

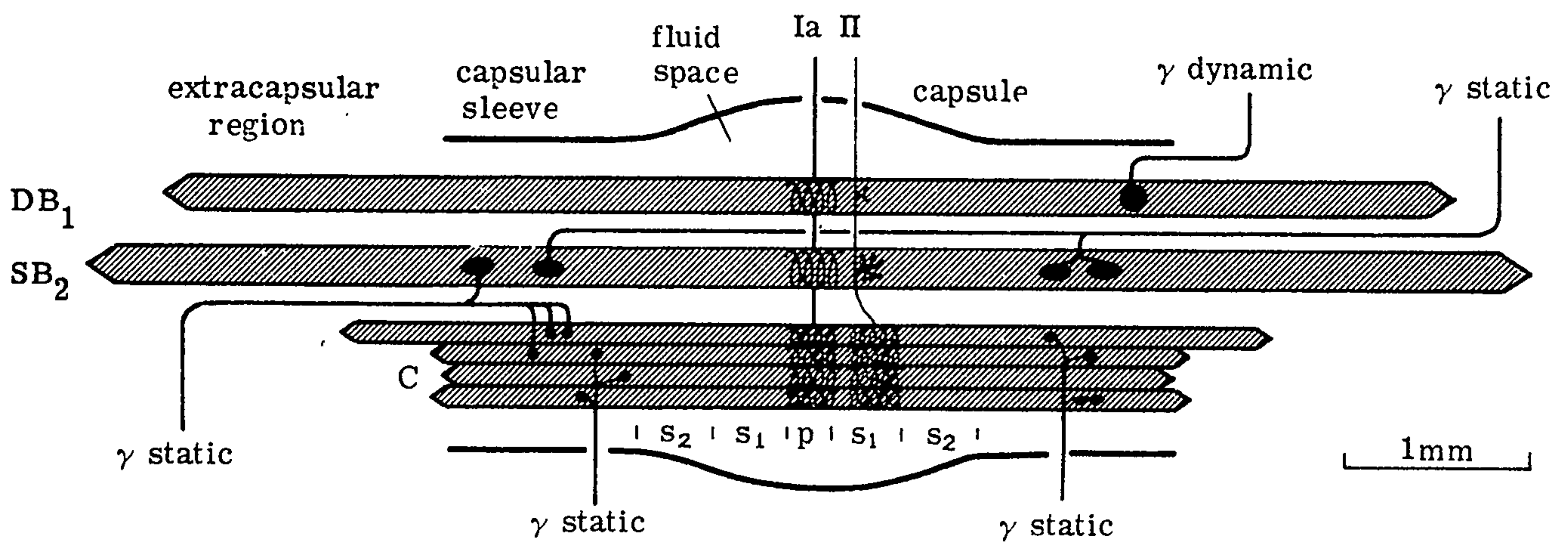


FIGURE: 4

Diagram illustrating intrafusal structure of a muscle spindle (from Boyd, 1980). There are three types of intrafusal fibre: dynamic bag₁ (DB₁), static bag₂ (SB₂) and chain (C) fibres. The group Ia afferent fibre arises from the primary sensory ending in the equatorial region (p region); the group II afferent arises from the secondary sensory ending in the s₁ region. The motor supply to the spindle is from dynamic and static efferent nerve fibres.

which lubricates internal spindle structure thus assisting the uninhibited sliding of intrafusal fibres. Each spindle contains up to ten specialised striated muscle fibres lying in parallel with the main fibres of the muscle (Kubota and Masegi, 1977).

The cat muscle has been extensively studied and provides an appreciation of spindle structure essentially the same as that seen in humans. Two types of intrafusal fibre may be distinguished on morphological and functional grounds:

- a) the nuclear bag intrafusal fibre, of which one or two are usually present in human muscle spindles (Kubota and Masegi, 1977), and
- b) the nuclear chain intrafusal fibre, of which there are two to eight in human spindle (Kubota and Masegi, 1977) and which are half the length and diameter of the nuclear bag intrafusal fibres (Matthews, 1971).

On the basis of histochemical, ultrastructural, and mechanical properties, two types of nuclear bag fibre have been identified in cat spindle (Boyd, 1981):

- a) the dynamic bag₁ fibre (DB₁), and
- b) the static bag₂ fibre (SB₂).

Two types of afferent ending reside on intrafusal fibres, and their presence has been confirmed in elevator muscle spindles (Taylor, 1976b):

- a) the primary ending, and
- b) the secondary ending.

Each spindle contains one primary ending only which encircles each intrafusal fibre in its equatorial region and is supplied by a single, large diameter (12 to 20 μm), fast-conducting group Ia afferent. The dynamic responsiveness of the primary ending may reflect an enhanced stretchability associated with the reduction of myofilamentous material evident in this region (Hunt and Ottoson, 1975).

The secondary ending, of which there is usually only one, is supplied by a single group II afferent (4 to 12 μm diameter) and innervates the polar regions of the nuclear chain fibres almost exclusively with only a variable low density spray to the nuclear bag fibres.

Jaw muscle spindles exhibit histological (Karlsen, 1965) and physiological characteristics similar to those present in other skeletal muscles as typified by a comparable afferent behaviour and a similar static and dynamic innervation (Cody et al., 1972; Taylor and Davey, 1968). Thus it would appear that afferent information to the brain from jaw muscle spindles would be utilised in a fashion similar to that from spindles in non-facial muscles (Goodwill and Luschei, 1974).

The number and distribution of muscle spindles in animal (Kubota, Masegi and Osanai, 1974) and human (Kubota and Masegi, 1977) jaw muscles have been studied. In the latter, five groups of muscles were examined histologically and these were temporalis, masseter, medial pterygoid, lateral pterygoid and, digastric and mylohyoid. The total number of spindles present in the unilateral masticatory muscles was 521, 98.8% of which were localised in the elevator muscles with only 1.2% in the depressors. The temporalis muscle contained the greatest number of spindles which tended to be localised in the anterior vertical and posterior horizontal portions. The masseter muscle contained 114 spindles (22% of the total), most of which (80%) were localised in the superficial portion. This preferential localisation of spindles to the jaw elevator muscles was considered important in the control of jaw movement and the maintenance of jaw posture (Kubota and Masegi, 1977). Vibratory and stretch stimuli, as a result of chin tap procedures, therefore have the ability to evoke a considerable afferent response from spindles localised in elevator muscles.

The spindle is a highly sensitive, slowly adapting receptor responsive to stretch of the muscle in which it is located (Cooper et al., 1953). As spindles lie in parallel with the extrafusal fibres, then extrafusal contraction

without associated intrafusal fibre activation will unload the spindle and slacken the intrafusal fibres (Boyd and Ward, 1975). The primary ending lies on a region of the intrafusal fibre which, by virtue of its peculiar visco-elastic properties, monitors length and, in particular, velocity change (Matthews, 1972). The primary ending is, therefore, highly sensitive to the dynamic component of a stretch. The visco-elastic characteristics related to the secondary ending confer an instantaneous length sensitivity similar to that of the primary ending, however, the secondary ending exhibits a negligible response to the velocity of length change. Thus different stimuli would be expected to activate spindle receptors to different degrees depending on the relative proportions of length and velocity change. Linear stretch combines both stretch and velocity components and both primary and secondary endings will show an altered discharge. A brief tap has a small displacement component with a high velocity component, this latter will increase the rate of firing of the primary ending, whereas the secondary afferent discharge is only slightly changed.

The response of the primary ending to small stretches (less than $100\mu\text{m}$) has been studied in the decerebrate cat (Matthews and Stein, 1969; Matthews, 1972). Within this range the ending exhibits a very high sensitivity linearly related to stretch amplitude. This high sensitivity to

small stretch occurs at all degrees of muscle length as the primary ending can reset itself at the new length. The primary ending is thus an excellent detector of very small perturbations without the complication of saturation as occurs with many highly sensitive systems. The primary ending also appears to be a very good detector of vibration (Matthews, 1967; Matthews, 1972) at frequencies of several hundred Hz. Studies in limb muscle (McKeon and Burke, 1981) have identified muscle spindle responses to local changes in muscle length, in particular, the vibration generated by arterial blood flow.

The muscle spindle is involved in motor control in two ways (Burke, 1980): firstly, as a source of sensory return that may be employed in the programming of jaw movement; and secondly, as a source of afferent feedback in the moment-to-moment reflex modulation of jaw movement. Segmental reflexes may operate as velocity controlling mechanisms by compensating for unintentional irregularities in the speed of movement. Changes in spindle afferent discharge during a movement sequence are capable of modulating the discharge patterns of voluntarily activated motor units via the segmental reflex pathway, thus generating fast compensatory responses which smooth the ongoing movement. The fusimotor system provides a background discharge that encodes the unloading that occurs as part of sudden changes in the speed of movement (Burke, Hagbarth and Löfstedt, 1978a).

3.2.1 Fusimotor Control.

Three types of motor afferent may supply a muscle:

1. the alpha motoneurone,
2. the gamma motoneurone or fusimotoneurone, and
3. the beta motoneurone.

Alpha motoneurons are large fibres (less than $12\mu\text{m}$) with high conduction velocity (less than 50msec^{-1}) and supply the extrafusal muscle fibres causing gross muscle contraction. The fusimotoneurons are smaller fibres (2 to $8\mu\text{m}$) with lower conduction velocities (10 to 50msec^{-1}) and form an independent efferent supply to the intrafusal muscle fibres. Although producing negligible muscle tension per se, they exert powerful facilitatory influences on spindle afferent endings, thus indirectly influencing movement. In spinal systems there is now anatomical (Szentagothai, 1948; Karlsen, 1965; Rakhawy, Shehata, Badawy, 1971) and physiological evidence (Matsunami and Kubota, 1972; Goodwin and Luschei, 1975; Taylor, 1976b; Greenwood and Sessle, 1976; Sessle, 1977a) of the presence of gamma motoneurons in the trigeminal system.

Beta or skeleto-fusimotor neurones have been identified supplying some spindles in certain mammalian muscles (Adal and Barker, 1965), however there is no evidence of

their presence in the oro-facial musculature. Supplying both intrafusal and extrafusal fibres together, they have been proposed as a means whereby tight linkage between two groups of muscle fibre could be achieved, however such an arrangement would lack the flexibility and independence of the gamma system.

Gamma or fusimotoneurons may be subdivided into two types:

- a) static fusimotor fibres (γ_s). These terminate on the nuclear chain fibres as "trail" endings; they also terminate on the static nuclear bag fibres (SB_2).
- b) dynamic fusimotor fibres (γ_D). These terminate mainly on the dynamic nuclear bag fibres (SB_2) as "plate" endings (Fig. 1).

All intrafusal fibres possess several properties in common:

1. contraction of all three types of fibre is confined to the capsular sleeve or extracapsular region which therefore produces stretch in the central region;
2. as all three fibre types are unloaded during an extrafusal fibre contraction, concomitant intrafusal fibre activity is essential if spindle sensory terminals are to be capable of providing continuous afferent information to the central nervous system about muscle length during a muscle contraction; and

3. intrafusal fibres are capable of finely graded contraction independent of the need for action potential generation which is an essential part of extrafusal fibre contraction.

Activity in fusimotoneurones will activate one or more intrafusal fibre and cause stretch of the central and adjacent regions of the spindle on which primary and secondary endings are located. The ensuing increased spindle afferent discharge may evoke a variety of effects including enhanced alpha motoneurone activity. Each type of fusimotoneurone alters the characteristics of velocity and length responsiveness of the primary ending. Dynamic fusimotoneurones, which solely innervate DB₁ fibres, increase length sensitivity of the primary ending during movement. The associated altered responsiveness of the primary ending to large and small amplitude stretch (Brown and Matthews, 1966; Crowe and Matthews, 1964a and b) emphasises the importance of dynamic fusimotoneurone stimulation in the control of stretch reflex sensitivity. Stimulation of SB₂ fibres by static fusimotoneurones enhances the response of the primary ending to maintained length without altering the sensitivity of amplitude or velocity of length change. In addition, group II afferent discharge at constant length is potentiated without an appreciable change in the dynamic or static sensitivity of the secondary ending to stretch. Static fusimotoneurones also stimulate nuclear chain fibres by generating a one to

one driving of primary endings, however, with superimposed stretch there is an irregular discharge. The sensitivity of the secondary ending to maintained stretch is markedly increased under these conditions but with a somewhat decreased sensitivity during the dynamic phase of movement.

Brief stretch of spindle sensory endings generates a synchronous increase in group Ia and group II afferent projection to alpha motoneurons which may result in a reflex muscle contraction. Boyd (1980) comments that whilst the stretch reflex is obvious in resting muscle in the cat, its presence in human limb muscle seems to depend on muscle loading. He suggests a difference in resting static fusimotor outflow in the two species rather than a functional difference within the spindles themselves.

Activation of DB_1 fibres by dynamic fusimotoneurons during muscle contraction increases the gain of the stretch reflex by potentiating the output from the primary ending. When the muscle reaches its final position the gain of the stretch reflex may decline and disappear; the feedback that was necessary during the movement being no longer required (Boyd, 1980).

Activation of the SB_2 fibres by static fusimotoneurons does not appreciably change stretch reflex gain. However static fusimotoneurons may contribute to postural adjust-

ment by biasing the stretch reflex arc. Without such a mechanism to maintain the sensitivity of the intrafusal fibre, spindle discharge might become an insignificant contribution to reflex muscle tone (Boyd, 1980).

As well as primary endings, it is evident that secondary spindle endings are also important as sources of afferent discharge for the stretch reflex in limb muscle (Kirkwood and Sears, 1974) and this has been confirmed for jaw muscle (Appenteng et al., 1978). Activation of nuclear chain fibres by static fusimotoneurones increases stretch reflex gain by providing positive bias to the reflex via the group II afferent pathway. As the nuclear chain fibre system is the only intrafusal system that consistently increases the gain of the stretch reflex with the muscle at a constant length, then this system may contribute to alterations of afferent return occurring with variations in reflex amplitude at different times in the one subject and in different individuals.

Spindle afferents appear to project to all motoneurones in the trigeminal motor nucleus and thus both Type I and Type II fibres would receive a contribution during chin tap (Taylor, 1981). This extensive projection to all histochemical types of motoneurone ensures that the stretch reflex can provide a continual contribution to jaw movement control throughout a range of contraction strengths (Harrison and Taylor, 1980).

The temporalis and masseter muscles consist predominantly of the fast contracting, fast fatiguable Type II motor units (Taylor, Cody and Bosley, 1973). However, located predominantly in anterior temporalis and deep masseter of cat and rhesus monkey (Maxwell, Carlson, McNamara and Faulkner, 1979) are the high oxidative, fatigue-resistant Type I motor units (Taylor, 1976b). These regions in masseter and temporalis are also the sites where muscle spindles tend to be preferentially located (Lund, Richmond, Touloumis, Patry and Lamarre, 1978) and being vertically disposed they may be well suited for the detection of and responses to small jaw openings (Taylor, 1981).

A reciprocal relationship has been described between jaw-closing and jaw-opening muscles. Afferent projections from a particular jaw muscle were shown to exert facilitatory influences on motoneurons to that muscle but afferent impulses from antagonistic muscles or from the same muscle on the contralateral side were inhibitory (Kawamura et al., 1960; Kawamura et al., 1967). These reciprocal facilitatory and inhibitory projections to masticatory motoneurons were not able to be identified in the trigeminal mesencephalic nucleus and this suggested that they derived from primary neurone collaterals (Kawamura et al., 1960). These studies allude to the close interrelationship in the brain-stem among afferent impulses from antagonistic and symmetrical jaw muscles.

(For a discussion of Jendrassik reinforcement see section on Central Regulatory Influences).

Vibratory stimuli are capable of generating a gradual continuous recruitment of elevator motoneurones manifesting as a tonic vibration reflex (Desmedt and Godaux, 1975; Godaux and Desmedt, 1975c; Bratzlavsky, 1976; Hagbarth, Hellsing and Löfstedt, 1976; Hellsing, 1977). It is uncertain the contribution made to this response from monosynaptic and polysynaptic influences, however muscle spindles have been directly implicated via monosynaptic pathways in its aetiology (Godaux and Desmedt, 1975c), and it is also likely that other receptors contribute a projection, such as those from the temporomandibular joints, periodontal membranes and periosteal tissues. The delayed and gradual recruitment of elevator motoneurones during vibration suggests that projections from muscle afferents to elevator motoneurones are not necessarily direct and without interneurones (Jankowska, Jukes, Lund and Kundberg, 1967). Thexton (1972) also showed profound delayed excitatory influences on temporalis motoneurones following stimulation of low threshold afferents in the masseter nerve; the longer latency of the excitatory projections suggested involvement of interneurones.

Tonic vibratory stimuli applied to the chin in human subjects will potentiate the masseteric jaw-closing and H-reflexes evoked by, respectively, mechanical chin tap and

masseter nerve electrical stimulation (Godaux and Desmedt, 1975c; Bratzlavsky, 1976). This contrasts with the H- and tendon reflex inhibition evident in the triceps surae muscle group during similar vibratory stimuli. However, at the spinal cord level there is a reciprocal reflex organisation whereby vibration, by activating spindles in antagonistic muscles, could exert presynaptic inhibitory influences on agonists. The apparent absence of spindles in jaw depressor muscles (Szentagothai, 1949; Voss, 1956) reflects the unique functional organisation of jaw reflexes whereby masseter motoneurones are not subjected to any reciprocal inhibitory effect of proprioceptive origin from antagonistic motoneurones and this may at least partly explain the observed differences.

3.3 Periodontal Membrane Mechanoreceptors

Mechanoreceptors located in the periodontal membrane exhibit a wide range of sensitivities (Yamada, 1967), are directionally dependent (Ness, 1954) and are sensitive to the rate of force application (van Steenberghe and de Vries, 1978; van Steenberghe, van den Bergh, de Vries and Schoo, 1981). Several studies have demonstrated the potential for periodontal afferents to project to elevator motoneurones and evoke transient excitatory reflex responses of short and, even monosynaptic latency (Goldberg, 1971; Sessle and Schmitt, 1972; Funakoshi and Amano, 1974; Sessle and Greenwood, 1976; Sessle, 1977b). A similar excitatory phase has been

identified in the masseter electromyogram following mechanical tooth tap and although it appears to be present in normal function, its precise role in mastication is not clearly understood (Hannam et al., 1970; Goldberg et al., 1972). It corresponds to the early facilitatory phase preceding the inhibitory period identified intracellularly in cat motoneurons, although it is often suppressed in the cat unless the inhibitory phase is blocked by strychnine (Kidokoro et al., 1968a). Recently, in the decerebrate cat, a jaw-closing reflex attributed to periodontal receptors has been identified following delivery of a mechanical stimulus to a tooth during depression of the mandible (Matthews, 1975).

The existence of such excitatory influences following tooth stimulation might appear to conflict with Sherrington's (1917) observation of reflex jaw opening following blunt pressure stimulation of gingiva, tooth crown and hard palate. However, the short latency and duration of the facilitatory response would probably be incapable of overcoming mandibular inertia to initiate jaw movement (Widmalm, 1982).

The aetiology of the excitatory phase following mechanical tooth tap has been variously attributed to periodontal mechanoreceptors and muscle spindles. Hannam, Matthews, and Yemm (1970) discounted the role of periodontal receptors as major contributors by implicating vibration

transmission through bone and soft tissue to primary spindle endings. This was based on the observation that the latency of the reflex was identical to both the jaw-closing reflex and the excitatory phase following forehead tap, both of which have been directly related to muscle spindle activation (Matthews, 1972). However, this appeared to be a visual observation only without statistical analysis. In addition, even if latency values were identical this would not necessarily preclude periodontal mechanoreceptor involvement as rather direct pathways to motoneurons from these afferents (electrotonic junctions (Hinrichsen, 1970; Baker and Llinas, 1971; Hinrichsen, 1976), direct synaptic relays (Sessle and Schmitt, 1972)) appear potentially available. In the year following the study of Hannam and his coworkers, Goldberg (1971) implicated periodontal receptors in the aetiology of these reflexes based on several lines of evidence: firstly, a 21 to 65% reduction in the amplitude of the excitatory response was demonstrated following seemingly adequate local anaesthesia of the stimulated tooth (1.8ml labially and palatally plus topical anaesthesia of adjacent gingivae). In addition, electrical stimulation of unanaesthetised gingiva evoked a response similar to that seen with tooth tap which was also completely abolished by local anaesthesia. Thirdly, the latency of this excitatory phase was shown to be shorter than that of the menton tap jaw-closing reflex which would be expected based on the shorter afferent limb

pathway projecting from periodontal receptors (Orchardson and Sime, 1981). Finally, the ability of electrical stimulation of lingual nerve in cat and gingiva in monkey to evoke similar short latency excitatory reflex responses establishes an association between intra-oral, non-muscular, trigeminal afferents and jaw elevator muscle activity (Goldberg, 1972a). These four observations were considered to provide convincing evidence that periodontal mechanoreceptors, and not muscle spindles, were exclusively involved in the aetiology of this early excitatory phase, and it was therefore termed the 'periodontal-masseteric reflex' (PMR; Goldberg, 1971). However, this conclusion may not necessarily be valid for several reasons. Firstly, although local anaesthesia reduced the amplitude of the periodontal-masseteric reflex, its effect on the jaw-closing reflex was not studied; suppression of the periodontal-masseteric reflex could simply reflect generalised variations in motoneurone excitability related to the local anaesthesia (Orchardson and Sime, 1981). Secondly, as the periodontal-masseteric reflex was evoked during voluntary elevator activity, then its latency would be expected to be shorter than that of the jaw-closing reflex. This arises from the associated enhanced descending projection onto trigeminal alpha and fusimotoneurones during clench sensitising primary spindle endings to vibratory stimuli and potentiating the motoneurone response to incoming afferent discharge. As a result, less temporal summation would be required before threshold for motoneurone activation

thus producing a shorter latency. Thirdly, as there was only partial abolition of the periodontal-masseteric reflex following local anaesthesia then it is still conceivable that muscle spindles could at least contribute to the reflex. Fourthly, the presence of a response with gingival electrical stimulation simply confirms that gingival and/or periodontal receptors may be involved, not that they are exclusively. Finally, differences in timing of microswitch activation during stimulus delivery may contribute to the observed latency discrepancy. Employing a reflex hammer incorporating a microswitch, Goldberg (1971) evoked a periodontal-masseteric reflex by directly tapping an upper central incisor, and a jaw-closing reflex by tapping the chin. In each case, the timing of microswitch activation in relation to receptor activation is likely to be different. With chin tapping, the microswitch may trigger at some moment in time during soft tissue compression before activation of spindle receptors, and result in a relatively long jaw-closing reflex latency. However, during tooth tapping, microswitch triggering is likely to occur closer to the time of receptor activation, and this would result in a shorter latency.

A tap applied to the labial face of a maxillary central incisor has been recently reported to be unable to evoke a monosynaptic response in the elevator muscles during active jaw opening (Yamada and Ash, 1982). However, as a reflex

was induced in the digastric muscle then it was considered that periodontal mechanoreceptors would nevertheless have been activated. Therefore either this possible projection from periodontal receptors was insufficient to evoke a response during conscious jaw opening, or a pathway involving more than just electrotonic coupling between periodontal afferents and spindle afferent cytons is involved in the periodontal-masseteric reflex. This may involve vibration transmission to spindle afferents.

Similar facilitations in elevator muscles have been described during chewing and intercuspal tooth tapping in edentulous and dentulous subjects. These effects were attributed to elevator muscle spindle activation either from a slight rebound of the mandible stretching the elevator muscles and/or vibration transmission following tooth contact (Hannam et al., 1970; Munro and Griffin, 1971; Matthews, 1976). During voluntary tooth tapping the intricate wave form of the evoked response has been attributed to two reflex components: a periodontal-masseteric reflex and a jaw-closing reflex (Fujii, Inubushi, Mushimoto and Mitani, 1981). Following local anaesthesia of the tooth in question an increase in the latency of the excitatory response was observed in the masseter approaching that of the jaw-closing reflex. Thus blockade of periodontal afferent projection allowed the effect of spindle afferent discharge to be more clearly demonstrated. With progressively greater tapping forces and during

anaesthesia, latency decreased and amplitude increased, reflecting the greater excitability as part of the increased voluntary effort and the spread of the stimulus to other receptors. However, an increase in tapping force beyond a certain level effected a reduction in the amplitude of the monosynaptic response and this has been attributed to an occlusion of the reflex system (Fujii and Mitani, 1973; Fujii et al., 1981).

It would appear therefore that both periodontal membrane mechanoreceptors and muscle spindles are involved in the production of the so-called periodontal-masseteric reflex following tooth tap (van Steenberghe, 1979). The relative contribution from each, and also from other receptors, would depend on levels of central excitability present at the time and the characteristics of the peripheral stimulus evoking the reflex. From this discussion, it may be possible to implicate periodontal receptors in the aetiology of the excitatory phase following menton tap as such a perturbation may activate these and other receptors located nearby either through direct tooth movement or the transmission of pressure and vibration.

More recently, Lamarre and Lund (1975) demonstrated monosynaptic load compensation in human masseter muscles. They described a potentiation in amplitude of the monosynaptic reflex with downwards tooth loading following local anaesthesia of the teeth concerned. These observations

do not necessarily conflict with Goldberg's observations of reduction in reflex amplitude with anaesthesia. Firstly, during rapid loading of teeth, periodontal receptors may induce excitatory potentials in depressor motoneurons and inhibitory post-synaptic potentials in elevator motoneurons (Kidokoro et al., 1968) both tending to cause jaw opening (Sherrington, 1917). Therefore, removal of this inhibitory effect following local anaesthesia could potentiate the monosynaptic response in the elevator muscles to downwards loading (Lamarre and Lund, 1975). Secondly, in each paper, stimuli were delivered under different conditions. In the latter study of Lamarre and Lund, the periodontiums of teeth that were subsequently anaesthetised were being continuously loaded during stimulus application and, as a result, would be able to exert polysynaptic inhibitory projections onto trigeminal alpha motoneurons. With anaesthesia and the removal of these influences, evoked reflexes in the elevator muscles may be potentiated. However, in Goldberg's study, subjects clenched on cottonwood sticks between the ipsilateral first molar teeth which remained unanaesthetised. Any inhibitory projection from these periodontal receptors would presumably remain essentially unaltered during the experimental procedure, and thus, by exerting a constant modifying influence on motoneurone excitability, would not change the evoked reflex responses.

Orchardson and Sime (1981) have described an excitatory reflex in the relaxed masseter following axially-directed tooth tap. This tooth tap response (TTR) may be the periodontal-masseteric reflex of Goldberg (1971) but evoked under different conditions. The ability of axially directed taps to evoke a response in contrast to labially directed perturbations (Goldberg, 1971) may reflect the directional sensitivity of periodontal receptors (Ness, 1954). In addition, labially directed taps may be insufficient stimulus to excite muscle spindles without the priming of trigeminal motoneurone excitability from higher centres, as would occur during clench. Axially-directed taps may produce an additional afferent contribution from muscle spindle stretch occurring with skull movement. However as local anaesthesia, which would presumably abolish afferent projection from intra-pulpal, periodontal and local periosteal mechanoreceptors, was unable to influence the tooth tap reflex per se, then the response was considered to be a jar reflex resulting from vibration transmission through facial bones to the highly sensitive elevator spindle primary endings (Orchardson and Sime, 1981; Matthews, 1972). The observed similarity between the tooth tap response and the classic jar reflex evoked by mechanical tap to the zygoma supports this contention. In addition, the potentiation of both reflexes following the Jendrassik manoeuvre might appear to implicate muscle spindles in the aetiology of the tooth tap reflex, as such an enhanced response could be explained on the

basis of increased fusimotor projection to relaxed muscle (Burg, Szumski, Struppler and Velho, 1974). However, such reflex potentiation during Jendrassik reinforcement may operate via central mechanisms acting directly on skele-tomotoneurones independent of the fusimotor system (Burke, McKeon, Skuse and Westerman, 1980). Thus conclusions drawn from these latter results do not provide further evidence supporting a role of muscle spindles in the tooth tap response.

Although the tooth tap response exhibited a lower amplitude than the jaw-closing reflex, both had comparable latencies. This similarity in latency values support the role of the muscle spindle in the aetiology of both responses, with the larger amplitude of the jaw-closing reflex probably relating simply to an enhanced afferent projection from the combined effect of vibration and spindle stretch during the chin tapping procedure.

Depending on the level of background emg activity, continuous pressure applied labiolingually in anaesthetised rats has been observed to evoke facilitatory or inhibitory responses in the elevator and depressor muscles. With relaxed musculature, both jaw-closing and jaw-opening muscles were facilitated by mechanical tooth stimulation, however, inhibition occurred during maintained spontaneous activity (Funakoshi and Amano, 1974; Funakoshi, 1981). These responses were abolished after ipsilateral section of

the maxillary nerve and this result tended to exclude muscle spindles in the aetiology of the response. Continuous heavy force application to the incisal edge of the ipsilateral canine tooth in anaesthetised cats (Ardoin, Merg and Bowman, 1968) has been reported to produce a similar dual influence on masseter motoneurons and this was evidenced by an initial decrease and then an increase in tension. These results do not necessarily conflict with Sherrington's (1917) observations of a pure reflex jaw opening following blunt pressure stimulation of periodontal receptors as they can be explained on the basis of species differences and the degree of pressure applied in each study (Funakoshi and Amano, 1974).

As distinct from continuous pressure, a tap applied in the same direction to the maxillary incisor evoked dual excitatory phases of short (mode of 7msec, minimum of about 4msec) and longer (mode of 20msec) latency in rat, both of which were abolished following section of the maxillary nerve (Funakoshi and Amano, 1974). Brain-stem transections at various levels established separate pathways for each response, with the early transient phase probably utilising the trigeminal mesencephalic nucleus and the late tonic phase, the spinal tract nucleus (Funakoshi and Amano, 1974; Funakoshi, 1981). Both alpha and fusimotoneurons were implicated in the late tonic phase. These authors discounted muscle spindles in the aetiology of activating reflexes of the masseter muscle

following maxillary incisor tooth tap for several reasons: firstly, the response was abolished after section of the maxillary nerve; secondly, the latency of the evoked reflex was longer than for the classical jaw-closing reflex; and thirdly, two responses were evoked in the masseter muscle following application of an electrical stimulus to the trigeminal mesencephalic nucleus: the first response represented a monosynaptic reflex and the second related to a polysynaptic activation derived from periodontal mechanoreceptors. Nevertheless, it does not seem possible to discount muscle spindles in the aetiology of activating reflexes of the elevator musculature following mechanical tooth tap as the direction of the applied stimulus in this study may have been inappropriate for adequate muscle spindle activation. The existence of such a possibility has been suggested by Orchardson and Sime (1981) who were able to evoke facilitatory reflexes following axially directed tooth taps but not labially-directed perturbations.

As the trigeminal mesencephalic nucleus contains primary afferent cytons from muscle spindles (Corbin, 1940; Corbin and Harrison, 1940; Jerge, 1963; Smith et al., 1967, 1968; Szentagothai, 1948; Cody et al., 1972), periodontal membrane mechanoreceptors (Corbin and Harrison, 1940; Szentagothai, 1948; Jerge, 1963; Smith and Marcarian, 1968; Cody et al., 1972) and gingival receptors (Corbin and Harrison, 1940; Jerge, 1963), then the possibility exists

for excitatory electrotonic coupling to occur between muscle spindle and periodontal or gingival afferents (Hinrichsen, 1970; Baker and Llinas, 1971; Sessle and Schmitt, 1972). Thus periodontal and gingival primary afferents may induce action potentials in neighbouring spindle afferent cytons thus indirectly activating alpha motoneurons in the trigeminal motor nucleus (Goldberg, 1971). However, a direct monosynaptic, or disynaptic (Sumino, 1971), excitatory pathway between periodontal primary afferents and trigeminal motoneurons via the trigeminal mesencephalic or chief sensory nuclei is also possible. A neural basis for these pathways has been established in histological studies which when evaluated as a whole suggest the location of periodontal afferents in both sensory nuclei (Corbin, 1940; Kruger and Michel, 1962; Kawamura and Nishiyama, 1966), and the location of muscle spindle, periodontal and gingival receptor afferents in the mesencephalic nucleus (Jerge, 1963).

Thus in summary, it appears that both periodontal membrane mechanoreceptors and muscle spindles may contribute to short latency activating reflex responses in the masseter muscle. During menton tapping, as well as direct stretch of and vibration transmission to muscle spindles, pressure on mucous membrane or gingiva adjacent to teeth is likely to recruit periodontal receptors and, by exerting excitatory projections on elevator motoneurons, may contribute to the observed reflex response. However,

as would be expected, periodontal membrane mechanoreceptors do not appear to be essential for the jaw-closing reflex. A recent comparative study (Haraldson and Ingervall, 1979) examined the jaw-closing reflex in a control dentate group of subjects and a test group with osseointegrated oral implant bridges. Afferent return from periodontal receptors, that could be activated during chin tap in dentate subjects, would be absent in patients with osseointegrated bridges. However, both groups of subjects corresponded as regards the existence and characteristics of the jaw-closing reflex. Thus, although amplitude was not assessed, the existence of similar reflex response characteristics in both groups indicated that periodontal membrane mechanoreceptors are not crucial to the jaw-closing reflex, however from the above discussion it would seem that they are likely to contribute to the response.

3.4 Golgi Tendon Organs

Tension receptors do not appear to be a prominent feature in the masticatory musculature. Although Smith (1969) and Taylor and Davey (1968) both identified electrophysiologically the presence of receptors acting in a manner similar to that of Golgi tendon organs, more recent evidence has not supported this finding (Cody et al.,

1972). Beaudreau and Jerge (1968) were unable to provide electrophysiological evidence of units with the properties of muscle tension receptors (Beaudreau and Jerge, 1968) in the trigeminal ganglion. Conclusions drawn from studies in limb muscle of decerebrate cat suggest that tendon organ projection to homonymous motoneurons with muscle stretch does not appear to be significant (Proske, 1981). Thus the tendon organ contribution to the jaw-closing reflex would not appear to be very great.

3.5 Temporomandibular Joint Mechanoreceptors

The innervation of the temporomandibular joint capsule has been described by Thilander (1961). Branches from auriculotemporal, masseter and deep temporal nerves ramify in the capsule and extend to the periphery of the interarticular disc. The auriculotemporal nerve innervates the posterior, postero-medial and most of the lateral aspects of the joint capsule, with the posterior deep temporal nerve supplying the antero-lateral aspect and the masseteric nerve innervating the antero-medial tissues (Thilander, 1961). Several receptor types have been identified in the joint capsule. Type I mechanoreceptors are low threshold, spontaneously discharging, slowly adapting receptors that exert a continuous afferent projection important in the reflex control of the mandibular

musculature and the perceptual awareness of jaw position (Klineberg, 1971a). Type II mechanoreceptors are low threshold rapidly adapting receptors that discharge phasically at the onset of movement. Type III receptors are higher threshold and exhibit a sparse distribution in cat joint capsule and Type IV receptors are free nerve endings occurring throughout the capsule and they subserve nociception. Electrical stimuli applied to articular nerves produced facilitatory and inhibitory influences on elevator and depressor motoneurons and this illustrated the significant reflex contribution to the control of the mandibular musculature from TMJ articular mechanoreceptors (Klineberg, 1971a). Other studies have also confirmed the influence on masticatory motoneurons of joint capsule receptors (Kawamura, 1967; Kawamura and Abe, 1974; Clark and Wyke, 1974; Clark, 1976; Lund and Matthews, 1981). Specifically, jaw closure causes facilitatory projections on depressor motoneurons whilst jaw opening increases elevator motoneuron excitability (Clark and Wyke, 1974). Two functional groups of mechanoreceptor have been described in the posterior TMJ capsule of cat. One regional group of receptors exerted inhibitory effects on elevator motoneurons with jaw closure; another group were facilitatory during jaw opening (Clark and Wyke, 1974). The sensitivity of joint mechanoreceptors to alterations in capsular pressure and the known reflex projection of these afferents to masticatory motoneurons during functional jaw movement,

emphasise the complex segmental modulating influences that must project to motoneurones from these afferents during menton tap. It is possible that these effects are not symmetrical as variations in capsular tension between sides will occur depending on occlusal inter-relationships. Afferent projections from temporomandibular joint receptors onto trigeminal motoneurones may be different on each side and this discrepancy could be reflected in the ongoing level of excitability.

3.6 Cervical Articular and Vestibular Receptors

Mechanoreceptors located in the internal ear and the apophyseal joints of the cervical spine (Wyke, 1974) will exert modulatory influences on mandibular motoneurone pools (de Rueck and Knight, 1967). Kimura and Kawamura (1971) demonstrated modulations in ongoing emg activity in elevator and depressor muscles with rotation of the head, and flexion and extension of the neck, for example, head rotation enhanced contralateral temporalis muscle activity. Therefore, alterations in head posture will influence trigeminal motoneurone excitability (Møller, 1966; Lund et al., 1970). It is conceivable that the ease with which a jaw closing reflex might be evoked following menton tap and the amplitude of the evoked response would be modulated by influences from cervical and vestibular receptors as affected by changes in head posture.

3.7 Acoustic Stimuli (Meier-Ewert et al., 1974)

Strong acoustic stimuli may modulate the ongoing masseter emg pattern and generate inhibitory periods. Although a short latency excitatory phase has not been identified either during voluntary clench or at postural jaw position, the ability of a loud sound to inhibit the masseter emg could therefore alter the characteristics of an evoked jaw-closing reflex. This reflex is absent in completely deaf patients and thus depends for its manifestation on a properly functioning acoustic nerve.

3.8 Cutaneous Receptors

FUNCTIONAL SIGNIFICANCE

Care must be exercised in extrapolating to functional reality the influence on masticatory motoneurons of artificial means of stimulation of various intra-oral sites. Nevertheless, following menton tap a wide variety of receptors would appear capable of activation. Muscle spindles, classically correlated with the jaw-closing reflex, are activated by stretch and most probably vibratory stimuli during stimulus delivery, however other receptors are also activated and include cutaneous, periosteal, mucosal, periodontal membrane, cervical and temporomandibular joint mechanoreceptors. These will exert

excitatory and/or inhibitory projections at the segmental level which may or may not be of consequence in the manifestation of a monosynaptic response depending on the ambient level of motoneuronal surround inhibition.

Many of these peripheral influences on elevator motoneurons are involved in "startle" responses and in the protection of the masticatory system. For example, noxious or potentially noxious stimuli provide an afferent feedback capable of modulating ongoing emg activity in the avoidance of possible damage (Sessle, 1981). In addition, during functional jaw movement afferent projection from peripheral receptors can halt or modulate the ongoing movement sequence so that an appropriate response in the jaw musculature can occur consistent with altered peripheral constraints.

4. CENTRAL REGULATORY INFLUENCES

4.1 Introductory Comments - Central Descending Influences

As well as peripheral segmental influences, jaw muscle activity is modulated by descending regulatory projections from cortical and subcortical systems including long loop reflexes. These latter, which may possibly involve transcortical pathways, could be aetiologic in the late excitatory and inhibitory modulations observed in the ongoing emg of jaw muscles following stimulus delivery (Lamarre and Lund, 1975).

The ability of descending projections from higher centres to affect trigeminal motoneurone activity is highlighted by the recordable increase in tonic elevator muscle activity when a person encounters a stressful situation (Yemm, 1971), and also, the potentiation of masseteric reflex excitability 25 to 45msec in advance of any increase in motoneurone activity associated with voluntary movement (Blair-Thomas and Luschei, 1975). It appears however, that direct monosynaptic corticomotoneuronal connections do not exist and that cortical stimulation mediates its effects through subcortical connections and/or interneurons which may be localised in the trigeminal sensory nuclei or adjacent reticular formation (Dubner et al., 1978).

With increased voluntary elevator muscle contraction (Goldberg, 1971; Hannam, 1972) and during simultaneous limb muscle activity (e.g. the Jendrassik manoeuvre; Hannam, 1972), the jaw-closing reflex has been reported to be enhanced. For example, Goldberg (1971) demonstrated an enhanced jaw-closing reflex amplitude on the side contralateral to the biting side. These reflex potentiations with increased voluntary elevator muscle effort have been attributed to autogenic facilitation of masseter motoneurone activity, synergistic facilitatory effects from the contraction of other jaw muscles, or both (see section on voluntary clench, p.40 ; Hannam, 1972). Despite earlier evidence to the contrary (Burg et al., 1974), the Jendrassik manoeuvre appears to mediate this increased reflex excitability through alterations in the central excitatory state independent of the fusimotor system (Burke, McKeon and Westerman, 1980; Burke, McKeon, Skuse and Westerman, 1980). However, the Jendrassik manoeuvre does not appear to have a consistent effect on reflex responses elicited in the relaxed masseter following the application of a rubbing stimulus between tongue and palate (Achari and Thexton, 1974). But with additional contact between the lips and the rod at the same time, there was a marked facilitation in response amplitude. This suggests that the pathway for this reflex is not influenced in any significant way by descending facilitatory projections activating limb motoneurons, whilst the recruitment of additional peripheral input from the orofacial area is capable of doing so.

These observations highlight the contribution from central descending projections in the modulation of motoneurone excitability. As previously discussed, peripheral influences are also significant, however the exact balance between central and peripheral modulatory projections is likely to vary with circumstance and in different individuals (Dubner et al., 1978).

4.2 Cortical Influences

The influence of the sensorimotor cortex on trigeminal motoneurone activity has been the subject of several studies. Stimulation of the facial region of the precentral gyrus in monkeys has been shown to produce predominantly short latency jaw opening movements characterised by strong anterior digastric muscle activation with an associated weaker elevator facilitation (Clark and Luschei, 1974). Occasionally, however, stimulation of certain loci within precentral gyrus evoked enhanced activity in elevator motoneurons thereby producing jaw closing (Clark and Luschei, 1974). These observations support neuronal studies of cortical activity in the precentral cortex of monkeys making voluntary and semi-automatic rhythmical jaw movements (Lund and Lamarre, 1974). During semiautomatic taste movements only a few neurones could be identified in this region responsible

for jaw closure. Thus jaw closure appeared to derive from a disinhibition of brain-stem mechanisms following the cessation of cortical jaw opening neurone discharge (Lund and Lamarre, 1974). Cortical control of closure was considered more important during voluntary clenching and the forceful closing movements of rhythmical mastication. These studies illustrate the action of the sensorimotor cortex in effecting predominantly inhibition of elevator motoneurons and facilitation of depressor motoneurons.

Many physiological processes have a sensory representation in orbital cerebral cortex and are therefore profoundly influenced by its excitation or ablation (Chase and McGinty, 1970). One of the patterns of activity occurring in conjunction with repetitive electrical stimulation of the orbital gyrus is movement of the jaw musculature (Chase and McGinty, 1970). The influence of such stimulation on elevator motoneurone excitability may be assessed by monitoring the masseteric reflex. The predominant effect observed was an inhibition of reflex amplitude (Nakamura et al., 1967; Sessle, 1977a) which was considered to relay via the ventromedial bulbar reticular formation as confirmed in transection experiments (Sauerland, Nakamura and Clemente, 1967). Orbital gyrus was shown to project via orbito-medullary fibres to the caudal portion of the reticular formation (ventromedial bulbar reticular formation) and thence to extend

inhibitory projections onto trigeminal alpha motoneurones (Sauerland, Nakamura and Clemente, 1967). This latter projection was subsequently shown to be a triphasic sequence of potential changes consisting of inhibition, excitation then inhibition (Nakamura, Takatori, Nozaki and Kikuchi, 1975). Orbital gyrus also exerts facilitatory influences on trigeminal motoneurones via the more rostrally located pontine reticular formation (Sauerland, Nakamura and Clemente, 1967). Although stimulation may induce both excitatory and inhibitory effects on alpha motoneurones, the effect on fusimotoneurones may be inhibitory only (Sessle, 1977a). Thus the excitatory and inhibitory effects of cortical stimulation appear to be mediated through subcortical centres such as the reticular formation and trigeminal brainstem sensory nuclei (Dubner et al., 1978; Sessle, 1981).

The state of the animal is also capable of influencing the manifestation of cortical inhibition of reflex activity (Sauerland, Knauss, Nakamura and Clemente, 1967). In the unanaesthetised freely moving cat the effectiveness of orbital cortical stimulation in the induction of either somatomotor suppression or excitation was impaired during sleep in comparison with that observed during wakefulness (Chase and McGinty, 1970). As described previously, the ponto-mesencephalic reticular formation appears to function as a relay mechanism whereby projection from the orbital cortex can exert facilitatory influences on

trigeminal motoneurons (Sauerland, Nakamura and Clemente, 1967). Now, depending on the state of sleep or wakefulness of the animal, there is an alteration in the modulating influence on masseteric reflex activity from this area of the reticular formation (Chase, Monson, Watanabe and Babb, 1976). Thus during quiet sleep and wakefulness, stimulation of the rostral reticular formation was observed to potentiate jaw-closing reflex amplitude (Sauerland, Nakamura and Clemente, 1967; Chase et al., 1976). During active sleep however, stimulation of the same area caused profound inhibition in reflex amplitude. Observations consistent with the above have been reported for limb reflexes where the human knee-jerk was found to be greatly diminished and frequently abolished during sleep (Lee and Kleitman, 1924; Tuttle, 1924). These results highlight the importance of the ponto-mesencephalic reticular formation in the modulation of somatic motor activity depending on the animal's state of consciousness i.e. wakefulness, quiet sleep or active sleep (Chase et al., 1976). Other researchers have correlated an increase in tonic depressive influence on the masseteric reflex with the progression from wakefulness to quiet sleep to active sleep (Chase, McGinty and Sternman, 1968; Enomoto, Fukuoka, Imai et al., 1968). The dropping of the mandible during sleep may therefore relate to inhibition of tonic elevator activity, whilst during para-sleep or active sleep, phasic facilitations and inhibitions occur reflecting the emg activity of rapid eye movement (REM) sleep. This

inhibition of reflex activity with progressive relaxation of the subject may provide a clue to the variability in the jaw-closing reflex observed in different individuals. Thus, depending on the subject's state of excitability and alertness, variations in descending projections from higher centres will modify trigeminal motoneurone excitability and the manifestations of the evoked response.

In subjects with overt clinical signs of temporomandibular joint dysfunction, Griffin and Munro (1971) described a delayed polysynaptic response in the masseter muscle resembling that normally seen in temporalis following mechanical chin tap. This was attributed to 'hyperactivity of the reticular formation' associated with alterations in capsular tension related to restrictive intercuspal tooth relationships (Griffin and Munro, 1971). However, other factors are also likely to be involved (see latency review, section 5).

4.3 Subcortical Influences

Although cortical influences afford control to jaw motility, e.g. during voluntary jaw movements, cyclical jaw movements can continue independent of this overriding influence (Dellow and Lund, 1971; Lund and Dellow, 1971). Subcortical structures, by their influence in the control of jaw movement, exert significant modulating effects on

trigeminal motoneurone activity. These subcortical areas include the basal ganglia, the hypothalamus, and the cerebellum. Jaw movements have been elicited independently from two distinct areas in the rabbit brain (Kawamura and Tsukamoto, 1960). Low frequency stimulation of the cortical jaw motor area and the lateral amygdaloid nucleus both evoke jaw muscle contraction. With high frequency cortical stimulation, rhythmic jaw movements occur predominantly in the opening direction, whilst stimulation of the lateral amygdaloid nucleus causes jaw closure (Kawamura and Tsukamoto, 1960; Sessle, 1977a). More recent studies in cat (Bobo and Bonvallet, 1975; Bonvallet and Bobo, 1975) have identified separate amygdaloid regions producing facilitatory, inhibitory and diphasic (i.e. facilitation followed by inhibition) modulations in masseteric reflex amplitude. Thus tonic stimulation of the basal amygdaloid nucleus resulted in a continuous facilitatory influence on the masseteric reflex; however, during the second phase of the diphasic response this facilitation became masked by powerful inhibitory projections from the trigeminal nucleus oralis, itself activated by a slightly delayed projection from the basal nucleus (Bonvallet and Bobo, 1975). Thus the basal amygdaloid nucleus appears to exert a dual control over the trigeminal motor nucleus mediating its inhibitory effect through the interpolaris region of the spinal trigeminal nucleus. These diphasic changes in masseteric reflex amplitude have been correlated with the diphasic negative responses that

may be elicited from the basal amygdaloid nucleus (Bobo and Bonvallet, 1975). Reflex facilitation during the early excitatory phase is associated with respiratory and cardiac deactivation - the initial 'alerting' or 'attentive' stage of the defence reaction. Transformation of facilitation into inhibition in the late 'defensive' stage correlates with progressive cortical, ocular, respiratory and cardiac activation. Thus stimulation of the amygdala produces a 'defence reaction' manifest as a dual facilitatory and inhibitory modulation of trigeminal motoneuronal activity (Bonvallet and Bobo, 1975). It has been suggested that the functional significance of the profound delayed inhibition of the masseteric reflex during the facilitatory phase is to avoid interference between facilitated central commands for jaw closure and peripherally induced discharges of masseteric motoneurons (Bonvallet and Bobo, 1975).

Hypothalamic lesions producing aphagia in chronic cat have been shown to inhibit the masseteric reflex in the first few hours after lesion placement (Wrywicka, Chase and Clemente, 1975). In addition, electrical stimulation of the defence attack area of the hypothalamus in anaesthetised animals exerted marked facilitatory influences on the monosynaptic jaw-closing reflex (Landgren and Olsson, 1976). It was suggested that powerful hypothalamic mechanisms exist capable of altering the balance of motor control towards increased elevator muscle activity

during stressful situations and this may contribute to the generation of parafunctional activities.

The existence of a direct projection to the trigeminal motor nucleus from the contralateral red nucleus has been the subject of debate. In monkey Marchi degeneration experiments, Carpenter and Pines (1957) identified crossed rubrobulbar fibres terminating in and around the trigeminal motor nucleus. However, Mizuno, Mochizuki, Akimoto and Matsushima (1973), in a more recent rabbit study, were unable to find evidence of a direct rubro-trigeminal afferent. However, a distribution of degenerated terminal rubral fibres has been described in the vicinity of the trigeminal motor nucleus (Mizuno et al., 1973) and particularly in the ventral portion of the region located between the trigeminal motor and chief sensory nuclei. Sessle (1977a) has identified the existence of many interneurons with widespread peripheral and central inputs in this same region which further illustrates the complex modifying influences that can be exerted on trigeminal reflex excitability.

A post-tetanic potentiation of monosynaptic reflexes possibly relating to central mechanisms and of pre-synaptic origin has been observed in limb muscle (Hagbarth, 1962). This phenomenon, however, does not appear to have been described in jaw muscle.

Spinal proprioceptive monosynaptic reflexes, in particular, the knee-jerk and Achilles reflexes, may be augmented during the inspiratory phase of respiration (King, Blair and Garrey, 1931). The phenomenon was not considered to be a reflex deriving from the respiratory tract or respiratory muscles, but rather was attributed to a diffuse projection of impulses from the respiratory centre augmenting reflex responses evoked at a particular phase of the respiratory cycle. Such a phenomenon may also operate in the masticatory system although no reference appears to have been made in the literature concerning this.

5. LATENCY OF THE JAW-CLOSING REFLEX

The jaw-closing reflex utilises a single synaptic pathway (Harrison and Corbin, 1942; Lloyd, 1943a, b and c; Szentagothai, 1948) and as such its latency is very short, reported values ranging between 6 and 12msec in the masseter and 7 and 9msec in the temporalis (Table: 1). Several studies (Goodwill, 1968; Ongerboer de Visser and Goor, 1974) have considered latency to be a useful measurement clinically as it appeared to facilitate the detection of pathology. However, as intra-individual differences in latency between sides were not considered probable (Goodwill, 1968; Goldberg, 1971; Munro and Griffin, 1971; Widmalm and Hedegård, 1976a and b) the use of a diagnostic test based on such comparisons did not appear to be of value (Goodwill, 1968). Nevertheless, in a study of fifty-one 'normal' subjects (Ongerboer de Visser and Goor, 1974), it was observed that 79% of the sample did not demonstrate significant differences between sides; 24% exhibited differences less than 0.4msec; and for the total group studied, the mean difference between sides was 0.07 ± 0.15 msec. Although these authors considered that latency comparisons between subjects may not be of practical merit due to the submergence of side differences from the wide range of values encountered, comparisons within a subject were considered a possibility. For example, a latency difference exceeding 0.5msec, a consistent unilateral

absence of the reflex or a bilateral absence in an individual under the age of 70 years was associated with pathology, notably with a diagnosis of trigeminal neuralgia (Ongerboer de Visser and Goor, 1974). In addition, symptomatology of multiple sclerosis has been correlated with an ipsilateral or bilateral absence or a delay in the response (Goodwill and O'Tauma, 1969). In another study, jaw-closing reflexes were evoked in patients with progressive muscular dystrophy following a quick tap to the mandibular anterior teeth during sustained elevator muscle contraction (Hamada, 1981). A prolongation of the mean reflex latency was observed in the masseter in comparison with the latency value recorded from healthy subjects (5.8msec in the 'normal' series compared with an average of 6.3msec in the patient series). Pathological damage interfering with the integrity of reflex arc conduction was considered a possible aetiologic factor. In another study of patients exhibiting weakness and wasting of jaw muscles with accompanying spasticity as occurs with such conditions as dystrophia myotonica and myasthenia gravis, the jaw-closing reflex was reported to be hyperactive (Earl, 1976). Patients with Parkinson's disease have also demonstrated increased spinal alpha motoneurone excitability which manifests as a reduced period of unresponsiveness to successive conditioning and test H-reflexes, in comparison with the similar effect in healthy subjects (McLeod and Walsh, 1972). Treatment with L-dopa subsequently reduced the hyperactivity of the alpha

motoneurone pool by increasing the duration of the period of unresponsiveness between successive stimuli.

The jaw-closing reflex in a large group (106 individuals) of 'normal' subjects (Munro and Griffin, 1971) has been compared with a group of patients (31 individuals) exhibiting definite clinical symptoms of muscle-joint pain and dysfunction (Griffin and Munro, 1971). In most cases, the responses recorded from the masseter and temporalis were not significantly different between the two groups. That is, the masseter muscle usually exhibited a short latency di- or triphasic excitation and this was followed in temporalis by a prolonged low amplitude response. In the masseter muscle of the dysfunction group, however, a late polysynaptic response similar to that seen in the temporalis was evoked on four occasions. This was attributed to hyperactivity in masseter motoneurons receiving enhanced excitatory projections from the suprabulbar reticular formation (Griffin and Munro, 1971; see section on Central Regulatory Influences: p. 105; and see p. 114 and 115 for further comment).

In patients with atypical facial pain, a significant increase in jaw-closing reflex latency has been observed in both masseter and temporalis muscles (Munro, 1972a). It is interesting, however, that carbamazepine administration, by delaying synaptic transmission at neuromuscular junctions (Theobald, Krupp and Levin, 1970), also produced

a similar increase in reflex latency. In another series of subjects who were grouped as 'potentially pathological', that is those exhibiting signs and/or symptoms possibly related to the temporomandibular joint, jaw-closing reflex latency values in masseter and temporalis were not found to be significantly different from the corresponding values of the normal group (Munro, 1972b). However, the duration of the second response observed in temporalis was significantly shorter at the five per cent level in the 'potentially pathological' group (Munro, 1972b).

A comparison of latency values in subjects with or without temporomandibular joint clicking did not demonstrate a significant difference between the two groups (Widmalm, 1976b).

The only study that appears to have commented on the influence of mechanical input characteristics on the parameters of the jaw-closing reflex is that by Goodwill (1968) who identified a reduction in latency with stronger stimuli.

The influence of subject age on response latency has been reported (Ongerboer de Visser and Goor, 1974). A mean latency value of 7.0msec in a 20 to 30 year age group was shown to increase to 8.4msec in a 60 to 70 year group, however, no statistical tests were performed on these figures.

In a study evaluating the jaw-closing reflex, Munro and Griffin (1971) identified two types of response. The 'Type I' response, recorded invariably from the masseter, consisted of one to three spike potentials. This classical manifestation of the reflex in combination with a short 'silent' interval and a series of low amplitude action potentials of characteristic duration, then constituted the 'Type II' response. This response pattern however, was almost invariably restricted to the temporalis muscle. Several possibilities were mentioned and discussed by Munro and Griffin (1971) concerning the aetiology of this late facilitatory phase as follows: a an after discharge of trigeminal motoneurons was not considered to be involved as this phenomenon had not been previously described for monosynaptic reflexes. b Variability in Group I fibre diameter may be involved but this phenomenon would probably be insufficient to account for the longer latency. c Cutaneous stimulation may evoke polysynaptic, low amplitude, long-latency responses (Lloyd, 1943a) very similar to the late phase of the 'Type II' response. However, this was discounted as the response was still present following chin anaesthesia. d Projection of afferent nerve fibres from the temporomandibular joints was not considered to be exclusively involved as jaw-closing reflex responses were still present in patients with condylectomies. e Differences in the central excitatory and central inhibitory states of temporalis and masseter motoneurons in association with their slightly

different functional roles in the control of jaw posture was considered the most plausible explanation of the late facilitatory phase.

It is also possible, however, that these longer latency responses could originate from other muscles in the vicinity of the surface electrodes. Electrodes positioned over temporalis in a manner similar to that suggested by Griffin and Munro (1969), i.e. posterior to the temporal line, superior to the zygoma and anterior to the hair line, may sample from other facial muscles in the area. It may be that the late response observed following menton tap is a recording of the blink reflex evoked in orbicularis oculi. Such a possibility is supported by Kugelberg's (1952) findings of low threshold, long latency volleys elicited in the oculi muscle with mechanical tap to any point over a wide area around the eye.

The latency of the jaw-closing reflex has been shown to be significantly shorter in masseter than in temporalis (Munro and Griffin, 1971; Lennartsson, 1980). The minimum latency values recorded by these authors were 3.5msec in masseter and 3.9msec in temporalis. They considered this latency difference of 0.4msec between the two muscles to be insufficient to allow for the presence of an additional synapse and concluded that consistent differences in the central excitatory and central inhibitory states related to each muscles' different functional roles may

account for these discrepant latency values. A similar explanation was proposed for the aetiology of the late components of the 'Type II' response in temporalis. A theoretical assessment of latency in masseter was calculated based on an afferent and efferent conduction pathway distance of 81mm, a mean conduction velocity of 116msec^{-1} , a synaptic (McIntyre and Robinson, 1959) and receptor delay of 0.5msec and an effector delay of 0.6msec. This totalled to a minimum latency value of 3.0msec. The corresponding value in temporalis was 2.9msec, the shorter latency probably reflects the slightly shorter pathway.

Synaptic delay is modulated by the level of surround inhibition from segmental, intersegmental and suprasegmental influences. Although the reflex is considered monosynaptic, variations in excitatory state and the possible recruitment of interneurones can modulate central delay time and thus overall reflex latency. In spinal cord ventral root recordings following stimulation of the dorsal root, conditioning stimuli reduced central reflex time from between 0.65 and 1.0msec to, but never lower than, 0.5msec (Renshaw, 1940). It was concluded that central reflex times of 0.5 to about 1.0msec represent activity in reflex arcs of two neurones, that is one synaptic relay (Renshaw, 1940). A similar time differential (1msec) was recorded at the masticatory muscles following shift of stimulating electrode from the trigeminal mesencephalic nucleus to the motor nucleus (Harrison and Corbin, 1942).

Conventional methods of latency assessment utilise a switch incorporated into the head of a reflex hammer, or a microphone taped to the skin overlying a portion of the skull which signals the moment of delivery of the menton tap (Ongerboer de Visser and Goor, 1974; Goodwill, 1968; Munro and Griffin, 1971). This methodology results in a mean latency value, as assessed from the literature, of seven to eight milliseconds (Table: 1). This period represents the summation of the following times: switch or microphone activation to the moment when perturbations arrive at spindle receptors; spindle primary ending activation time; afferent nerve conduction time to the motor nucleus of the trigeminal nerve; central synaptic delay; efferent conduction time and masseter fibre activation time (Bessette et al., 1971). Methods of latency assessment employing a microswitch or microphone may be unsatisfactory and liable to large error as the exact timing of receptor activation in relation to switch or microphone triggering is not known (Matthews, 1975 and 1976). Thus latencies based on the time of skin contact will tend to be too long, as they include the period associated with soft tissue displacement prior to receptor activation; values based on switch closure will tend to be too short if the resistance of the switch is greater than that required to initiate mandibular displacement which itself will immediately activate receptors (Matthews, 1975 and 1976; Lewis et al., 1978). Values based on microphone triggering will depend on the exact

temporal relationship between receptor activation and the recording of vibration by the microphone. Thus depending on these factors, variations in latency are to be expected between laboratories using different latency assessment systems. However, by monitoring the timing of stimulus delivery with a device such as a calibrated accelerometer fixed to the lower anterior teeth (Lewis et al., 1978), a more accurate assessment of the precise beginning of jaw displacement and thus spindle stretch may be made. If such corrections are described and made in other similar studies then more accurate comparisons of data are possible between and within laboratories.

During jaw opening against resistance, the jaw-closing reflex in the temporalis muscle appears difficult to evoke and, when present, exhibits a significant increase in reflex latency (Matthews, 1975; Lennartsson, 1980). This altered response may reflect a reduction in elevator fusimotoneurone activity and a potentiation of alpha motoneurone hyperpolarisation associated with digastric activation.

Monosynaptic activation of masseter alpha motoneurones has been described in experimental animals following electrical stimulation of the mesencephalic nucleus (Hugelin and Bonvallet, 1956; Kidokoro et al., 1968a). However, there is no evidence of an inhibition of this reflex that could be attributed to Golgi tendon organs in the elevators or spindles in the depressors, although

relaxation of elevator muscle tension in decerebrate animals following digastric muscle stretch has been reported (Kawamura et al., 1967).

In a comparative reflex study of patients with osseointegrated oral implant bridges and patients with natural teeth, Haraldson and Ingervall (1979) observed no difference in jaw-closing reflex latency for the masseter muscle among the two groups. Although latency was shorter for the anterior portion of the left temporal muscle in the implant patients in contrast to those patients with natural teeth, it was considered that this difference may be "an artefact caused by chance".

6. DURATION AND AMPLITUDE OF THE JAW-CLOSING REFLEX

The duration of the jaw-closing reflex has been measured from the moment of initiation of the response (i.e. the end-point of latency) to the peak of the last major deflection of the diphasic or triphasic summated action potential (Goodwill, 1968). Assessments of duration are not always straightforward and in 16% of a reported sample, irregularities present in the latter part of the monosynaptic response curve complicated duration measurement. In the remaining 84%, the mean duration was 6.2msec on the right side and 6.1msec on the left side with a standard deviation of 1.1msec and a range of 4 to 9msec. Duration values in subjects under 40 years were not significantly different from those values in subjects over 40 years. In three per cent of subjects, differences in duration between sides exceeded 2msec whilst in the remainder differences observed were within the experimental error of the reading of the traces.

As reported for latency, duration values also appear to exhibit considerable variability (Goodwill, 1968; Ongerboer de Visser and Goor, 1974). Nevertheless, the value has been suggested a useful diagnostic tool (Widmalm and Hedegård, 1976a and b). Although such utility has been ascribed to the parameter, other research does not support this, for example, duration did not correlate with

the presence of temporomandibular joint clicking (Widmalm, 1976b), nor did the insertion of osseointegrated oral implant bridges (Haraldson and Ingervall, 1979) produce significant changes in duration.

Amplitude values are usually assessed from the positive peak of the compound action potential to the negative peak along the ordinate axis, however other authors have only measured the negative phase of the compound spike to the baseline (Bessette et al., 1971). In a study of amplitude values (Goodwill, 1968), comparisons between sides were considered of limited value. Within a subject, the smaller mean amplitude value of one side was expressed as a percentage of the larger value. The mean percentage for all subjects was 68% with a standard deviation of 22% and a range between 10% and 100%. As with latency and duration, amplitude has been ascribed potential diagnostic value (Widmalm, Gill and Widmalm, 1979). The afferent limb of the stretch reflex provides continuous feedback of muscular performance thus facilitating ongoing regulation of the masticatory system. The integrity of this feedback system is very important in the process of learning (Burke, 1980), for example, the establishment of motor coordination required for chewing. The amplitude of the MSP, by providing information as to the sensitivity and functional ability of the muscle spindles, may be of potential diagnostic value in oral rehabilitation by establishing clues as to the ability of the patient to learn new or altered tasks, for example, the accommodation

of the motor system to inserted prosthetic appliances. However the amplitude of the MSP evoked under apparently fairly reproducible conditions appears to be highly irregular and thus to evaluate the clinical value of amplitude, the presence of trends in this variability was investigated. Although a hand-held reflex hammer was used, a tapping force as regular as possible was imparted to the chin (Widmalm, Gill and Widmalm, 1979). Since it was felt that reasonably reproducible taps were being delivered and yet a large inter- and, particularly, intra-individual amplitude variation was observed, fluctuating neuronal excitability was proposed as the aetiology. Nevertheless, despite this considerable variation, comparisons of amplitude data between different patient groups were considered reliable due to the presence of randomly distributed trend components (Widmalm, Gill and Widmalm, 1979).

7. REVIEW OF LITERATURE - SUMMARY

The jaw-closing or jaw jerk reflex may be recorded from the masseter muscle by a variety of types of electrode following the delivery of a sudden downward mechanical stimulus to the chin of a human subject. The response is usually insufficient to produce perceptible jaw displacement but may nevertheless assist mastication by establishing an afferent projection involved in the learning and modulation of ongoing movement sequences.

As the jaw-closing reflex is mediated by afferent and efferent pathways involved in motor control, then the excitability of the trigeminal motor nucleus, as determined by incoming projections, may influence the electromyographic manifestations of the response, that are, latency, duration and amplitude.

The pathway of the reflex has been frequently documented to be monosynaptic relaying via the trigeminal mesencephalic nucleus to the trigeminal motor nucleus. Although the afferent limb in cat appears to traverse the trigeminal motor root, it may occupy the sensory root in man. Spindle afferents from ipsilateral fields project essentially to ipsilateral motoneurons, however some contralateral projection has been observed. This could contribute to the bilateral manifestation of the reflex quite apart

from the bilateral physical effect of a menton tap on spindle receptors of both sides.

Monosynaptic reflexes may be evoked in the elevator musculature under a variety of conditions, a selection of which have been described. With regard to imparting mechanical stimuli to the menton region of human subjects, systems have been devised to deliver standardised and reproducible perturbations. Under these conditions, the monosynaptic response following chin tap may be studied and the effect of other variables on the response evaluated.

A wide range of peripheral receptors are capable of activation following menton tap. These include muscle spindles, intraoral receptors, periodontal membrane mechanoreceptors, temporomandibular joint mechanoreceptors, cervical articular receptors, vestibular receptors, cutaneous receptors and, possibly, Golgi tendon organs. The afferent projection of which will converge onto motoneurone pools and may produce activation.

In addition, descending regulatory projections involving a variety of cortical and subcortical structures may modulate the excitability of the motoneurone pool and the manifestations of evoked reflex responses.

A range of latency values have been reported with an overall mean value of 7.8msec being calculated from the literature reviewed. Relatively little research has been

done on the effect of pathological states on the jaw-closing reflex. Early work has established a correlation between anomalies in the manifestation of the evoked reflex and the diagnosis of trigeminal neuralgia, multiple sclerosis and progressive muscular dystrophy. Duration and amplitude did not, however, appear to reflect pathology. Latency also appeared to be the only parameter that could be correlated in some way with muscle-joint pain and/or dysfunction.

PART 2 - ORIGINAL RESEARCH

1. AIMS AND OBJECTIVES OF INVESTIGATION

1. AIMS AND OBJECTIVES OF INVESTIGATION

Recently, some doubt has been expressed (Hellsing and Klineberg, 1983) as to the clinical value of the masseteric silent period in assisting the detection of muscle-joint pain and dysfunction (Bessette et al., 1971). Nevertheless, characteristics of similar related reflexes may correlate with dysfunctional states. The trigeminal motoneurone pool represents a final common pathway that integrates a wide range of converging projections. Patterns of brain-stem motoneurone excitability, reflecting the coordination of jaw movement during mastication, are programmed based on data from peripheral receptors which encode the unique characteristics of prevailing intraoral constraints. Descending projections from limbic structures, reflecting anxiety levels, also modify motoneurone excitability. Thus the status of motoneurone pools, which mirror ongoing programmes of neuromuscular coordination, is subject to modifying projections from these diverse peripheral and central influences. Levels of motoneurone set and excitability resulting from the convergence of such influences are likely to modulate reflexes mediated by these pathways.

The electromyographic manifestation of the monosynaptic jaw-closing reflex exhibits three measurement parameters (latency, duration and amplitude) that may be modified by levels of motoneurone excitability and that mirror the

unique ascending and descending projections characterising dysfunctional states. However, in order to assess the clinical value of this jaw reflex, and jaw reflexes in general, a standardised system is needed to evoke the response so that the modulating influence from other variables can be controlled.

This investigation was initiated with the following aims and objectives:

1. To develop a system that automatically delivers mechanical impulses to the chin of a human subject.
2. To demonstrate the ability of this system to impart consecutive impulses of consistent magnitude and to assess the general level of this magnitude.
This was achieved by developing and employing an opto-electronic tracking system that monitored the rate and magnitude of jaw displacement during impulse delivery.
3. To demonstrate the ability of this system to impart menton taps at different force levels.
4. To record the incidence of a measurable jaw-closing reflex response in a group of young tertiary education students employing this instrumentation.
5. To determine whether jaw-closing reflex responses can be evoked with similar latency, duration and amplitude values in different subjects.
6. To observe the effects of variation in tap force on the parameters of the evoked jaw-closing reflex -

latency, duration and amplitude - and thus to assess the need for a standardised system.

7. To attempt to correlate characteristics of the evoked reflexes with the presence or absence of jaw muscle-joint pain or dysfunction.
8. To assess latency values that more closely reflect the true neurophysiological delay irrespective of physical soft tissue factors that must be overcome prior to the commencement of jaw movement. This will facilitate comparisons of latency data between studies.
9. To evaluate the effect of preventing jaw movement, and thus spindle stretch, during chin tap and thus contribute to knowledge of the aetiology of the reflex response.
10. To help clarify the contribution of movement artefact to the evoked reflex response.

A portion of this work has been accepted for publication (Murray and Klineberg, 1983a and b).