HUMAN MOVEMENTS AND MANDIBULAR STABILITY

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ABSTRACT

Intensive studies of the positioning and movements of the human jaw in both healthy and diseased subjects have been undertaken because of the importance of the mouth in daily human activities, such as verbal and non-verbal communication, breathing, chewing and swallowing.

The observation that our teeth do not crash together in a potentially harmful way during locomotion and other whole body activities is common, although the reason for this is not clear. The aim of the present study was to investigate the mechanisms controlling the rest position of the human jaw and the influence of whole body movements such as running and hopping on these mechanisms. While there have been numerous studies relating jaw elevator muscle activity with jaw movement and position in seated subjects, there are no reports of this in fully ambulatory humans. I developed specific equipment, built around miniature accelerometers and magnetic sensors, to enable a rapid and accurate measurement of small excursions of the mandible in response to take-off and landing during multi-dimensional movements. Accurate detection and recording of short-latency reflex activation in muscles attached to the jaw was required during unconstrained movements of the subject. I developed a recording system that was robust yet non-invasive for this purpose.

In the present study short-latency excitation was found in the masseter after an abrupt landing (heel land) from a hop. No reflex activation was seen in either a soft landing (toe land) or a hard landing with the teeth fully occluded in which there was minimal displacement of the mandible with respect to the maxilla. This provides strong evidence that the excitation is a stretch reflex and not of vestibular origin. This is the first report of short-latency stretch reflex in the human masseter resulting from a natural movement.

Landing on the heel or on the toe in different forms of locomotion on a treadmill was followed by rapid deceleration of the downward movement of the head and slightly less rapid deceleration of the downward movement of the mandible, i.e., the mandible moved downwards relative to the maxilla, then upwards again to near its normal posture, within 200 ms. No tooth contact occurred in any forms of gait or at any inclination of the treadmill. The movement of the mandible relative to the maxilla was found to depend on the nature and velocity of the locomotion and the effects on head deceleration. The least deceleration, and hence the minimal mandibular displacement, occurred during toe-landing, such as occurs during "uphill" running. The maximum displacement of the mandible relative to the head was less than 1 mm, even at the fastest running speed. The mechanisms that limit the vertical movements of the jaw within such a narrow range are not known, but are likely to include passive soft-tissue visco-elasticity and stretch reflexes in the jaw-closing muscles. The techniques developed in the present study will allow the investigation of the role of stretch reflexes under these conditions in a future study.

DECLARATION

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and to the best of my knowledge and belief, contains no material previously published or written by another person except where due reference has been made in the text.

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CHAPTER 1. INTRODUCTION

Different components of the human masticatory system have been studied in detail, including the jaw kinetics and biomechanics, sensory inputs, muscular components, neural connections including a range of mono- and poly-synaptic reflexes. Some control mechanisms are similar to limb systems, while others are uniquely adapted to rapid postural and rhythmical control of the jaw muscles (Kidikoro et al., 1968; Matthews, 1976; Dubner et al., 1978; Lennartsson, 1979; Cruccu et al., 1989b; Lund, 1990).

To date, however, there are few reports on the stability of posture of the human mandible during whole body movement or of the mechanisms by which this is controlled. This contrasts sharply with the wealth of information available on limb and whole body postural control in a wide range of vertebrate species under a wide range of external stimuli and gravitational conditions (See Alexander, 1982, 1988; McMahon, 1984; Duysens et al., 1991). Some questions remain unanswered, in particular, why is there no tooth contact when we walk, run and jump or play sport?

In the awake adult at rest, the postural position of the mandible has the upper and lower incisor teeth two to five millimetres apart (Atwood, 1968). Variations occur when the head posture changes, and when the jaw drops during sleep (Nakamura, 1980).

There has been discussion about the nature of the physiological mechanisms acting to maintain a stable resting posture. Proposals have been advanced favouring both an active, reflex-driven mechanism (Møller, 1976) and a purely passive system reliant on the elastic and viscous properties of muscle (Lynn and Yemm, 1971; Yemm, 1975; Korioth and Versluis, 1997; Peck et al., 2002). More recently, it has been shown that, while in its rest position, the mandible is subject to the action of a centrally driven pulsatile excitation of agonist and antagonistic muscle which may or may not contribute to maintenance of its position (Jaberzadeh et al., 2003). For a current review on mandibular postural constraints and their significance see Woda et al., (2001).

Lund et al. (1984) experimented with cats walking on a treadmill and recorded skull acceleration and electrical activity from jaw opening and jaw elevator muscles. They showed that twice in each step cycle there is an upward movement of the head, which due to the inertia of the jaw caused the mouth to open. Activity in all the jaw closing muscle pairs was synchronized to peak negative accelerations, suggesting that maximal muscle activity occurs reflexively in response to a downward movement: this dampens the downward jaw movement and maintains postural stability of the jaw during locomotion.

To date there have been no comparable studies of human jaw movements and muscle activity in freely moving humans, due to the technical difficulties in measuring the mandibular position relative to the maxillary position under these conditions. This shortcoming is addressed in the **First Aim** of this study, which was to develop a system for measuring maxillary and mandibular acceleration and relative position in a freely moving human. This is described in Chapter 3 of this thesis.

The **Second Aim** of this study was to quantify movements of the mandible with respect to the maxilla during locomotion of different types, including hopping, walking and running. This is described in Chapters 4 and 5 of this thesis.

The **Third Aim** of this study was to investigate whether stretch reflexes are elicited in jaw-closing muscles during locomotion, in order to assess their potential role in the stabilization of mandibular movements in humans undergoing a range of natural movements. Chapter 5 describes the application of the technique to analyse the effects of hopping on mandibular postural stability, and shows that short-latency reflex activation of masseter muscle may indeed help to slow downward movement of the jaw after abrupt landing and return it to the original position.

CHAPTER 2. A REVIEW OF THE LITERATURE

2.1. THE HUMAN MASTICATORY SYSTEM

The muscles of mastication consist of six pairs of muscles, all attached to the mandible, which are primarily responsible for elevating, protruding, retruding, and moving the mandible laterally. The major muscles that actively contract and move the mandible against gravity are the jaw-closing (jaw-elevator) muscles: masseter, temporalis and medial pterygoid. The jaw-opening muscles comprise digastric, lateral pterygoid and the suprahyoid group. In addition to moving the mandible, the masticatory muscles create reactive forces between the teeth and the temporomandibular joint.

These muscles develop from the first (mandibular) pharyngeal arch, from which some of the bony facial structures also develop. Consequentially they are innervated by the nerve of the first arch, the fifth (V) cranial (trigeminal) nerve (Brand and Isselhard, 1994).

Muscles

The anatomy of the masticatory muscles is quite complex, as the muscles have multiple points of insertion and are often multi-layered (Hannam and McMillan, 1994). Analogous to muscle action in limbs, the jaw-closing muscles act as anatomical flexors and the jaw-opening muscles as anatomical extensors. The directions of contraction of the jaw closing muscles are not, however, parallel and differ between the masseter muscles, which pull the mandible forwards and upwards, and the temporalis muscles, which tend to pull the mandible backwards and upwards. The mandible is considered a class three lever, with the temporomandibular joint (TMJ) acting as the fulcrum, and with the net closing force perpendicular to the lower teeth (Luschei and Goldberg, 1981; Hannam and McMillan, 1994; Langenbach and Hannam, 1999).

The fine structure of jaw-closing muscles indicate that they have architectural features that suit them for force production (Rowlerson, 1990; Korfage and van Eijden, 1999, 2000) while the jaw-opening muscles are better designed to produce rapid and precise displacement during regular breathing, speech and mastication (Luschei and Goldberg, 1981; Basmajian and DeLuca, 1985; van Eidjen et al., 1997; Korfage et al., 2001).

Masticatory muscles have no tendinous attachment to bones, and unlike skeletal muscles, the nervous supply to masticatory muscles lies deep within the bony and muscular processes. The inaccessibility of human jaw muscle motor nerves, with the resultant difficulty in isolating them, means that there are few studies in intact humans of muscle activation by electrical or mechanical stimulation (Lobbezoo et al., 2000).

Muscle fibres are traditionally classified into three groups depending on their physiological behaviour. Type I fibres are slow contracting, fatigue resistant, and generate small forces; type IIA fibres are fast contracting, fatigue resistant, and generate larger forces; and type IIB fibres are fast contracting, fatigue quickly, and generate the largest forces (Korfage and van Eijden, 1999; van Eijden and Turkawski, 2001).

Masticatory muscle fibres are homogeneous within each motor unit, however there is considerable structural and histochemical variation between units within jaw muscle groups: between jaw-opener and jaw-closers, between species, and even a sexual dimorphism within a species (Kubota and Masegi, 1977; Lennartsson, 1979; Rowlerson et al., 1988; Rowlerson, 1990; van Eijden et al., 1997).

Functional studies of low-threshold motor units in human masseter found that twitch contraction time was comparatively fast at approximately 38 ms (range from 25 to 50 ms) time to peak force (Nordstrom and Miles, 1990) which is generally faster than motor units in limb muscles which vary from 75 to 100 ms (Basmajian and DeLuca, 1985; Taylor, 1990).

Proprioceptors

Proprioception plays a fundamental role in reflex control of movement, both in the organization of spatial frames of reference for movement production and in the position and velocity-dependent regulation of muscle activity (Feldman and Latash, 1982; Feldman and Levin, 1995). The most studied proprioceptors in the striated muscle of the human masticatory system are the muscle spindles (Karlsson, 1976), whereas the presence of Golgi tendon organs is controversial (Taylor, 1990). The nearby cutaneous mechanoreceptors have received even less attention.

Muscle receptors

Muscle Spindles

The recognition of spindle-shaped structures within muscle fibres dates back to the classic works of Sherrington (1894) and Ruffini (1898). The observation that applied stretch caused the activation of (alpha) motoneurons and muscle contraction was first made by Merton (1953). The functional significance of this observation was, however, only fully realized in the 1980s, when Matthews (1981) and Boyd (1985) differentiated types of intrafusal fibres along with their patterns of innervation. Bundles of specialised intrafusal muscle fibres are contained in spindle shaped capsules and these lie parallel to extrafusal fibres of the skeletal muscle. When muscle spindles are stretched the intrafusal fibres produce a burst of action potentials in their afferent Ia and group II nerves. The intrafusal fibres of the spindle can be shortened by γ motor activation, which alters its sensitivity to stretch. When both α motoneurons and γ motoneurons are simultaneously driven from the motor nucleus, the resulting co-activation of intrafusal and extrafusal fibres allows an accurate reflex control of muscle length, resisting stretch deformation (Matthews and Stein, 1969; Matthews, 1981).

It has been demonstrated in both humans and cats that sensory afferents from masticatory muscle spindles ascend via the trigeminal nerve, with cell bodies in the trigeminal mesencephalic nucleus (MeV), and project monosynaptically to the trigeminal motor nucleus (Bratlavsky, 1976). Luschei and Goldberg (1981) reviewed the existing knowledge of the nature of muscle spindle topography and related it to the masticatory functions, with the assumption that the major part of the regulation is produced by muscle spindle afferents under the control of fusimotor innervation. Rowlerson et al. (1988) demonstrated that two distinct groupings of primary and secondary spindle afferents exist in human masseter muscle.

Muscle spindles are found in high density in the deep portions of the masseter and temporalis muscles, in close association with fibres of small fatigue-resistant motor units, but are absent or poorly represented in the jaw-opener muscles lateral pterygoid (Ostry et al., 1997) and anterior digastric (Sessle and Greenwood, 1976; Kubota and Masegi, 1977; Lennartsson, 1979).

Muscle spindles in masseter are believed to be important in fine-tuning the activity of the jaw-closing muscles during activities such as chewing food of uneven consistency, and thereby maintaining appropriate levels of force in the muscle (Bratlavsky, 1976; Hellsing, 1987; Appenteng, 1990; Rowlerson, 1990; Taylor, 1990; Ottenhoff et al., 1992a,b; Poliakov and Miles, 1994).

Spindles also play a particularly important role in halting the activity of the jaw-closing muscles when they are unloaded, as, for example, when one cracks through hard food (Miles and Wilkinson, 1982b; Miles and Madigan, 1983; Miles and Poliakov, 1997).

Miles et al. (1995) reported that in human masseter, typically only about two thirds of the motoneurons show a stretch reflex response from Ia afferent connections but the reason for this is unexplained. Studies have concluded that muscle spindles provide minimal activation of the jaw-closing muscles at rest and thus do little to maintain a stable mandibular resting posture (Yemm, 1977;

Eriksson et al., 1984; Scutter and Türker, 1999, 2001), however there is one report of a precise linkage of masseter activation and mandible stability in seated humans (Goldberg and Derfler, 1977).

There is evidence for spindles playing a stabilising role in jaw elevator muscles during dynamic and whole body movement in cats (Lund et al., 1984) and monkeys (Larson et al., 1981): this has also been suggested for humans (Lund and Olsson, 1983). Direct evidence for this was one aim of the present study.

Golgi tendon organs

Golgi tendon organs are mechanoreceptors found in musculotendinous junctions within limb muscles. Reports from studies in cat temporalis muscle (Kawamura, 1972; Lund et al., 1978) and soleus muscle (Houk and Henneman, 1967) have described their actions, and their significance in posture and locomotion has been reviewed by Jami (1992), Dietz (1998) and Dietz and Duysens (2000).

Given that there is no tendinous attachment of masticatory muscles to bone in humans, the evidence for and location of Golgi tendon organs in human masseter is not conclusive(Taylor, 1990). Their role in mastication in humans is unknown (Matthews, 1976). There is, however, some suggestion that their Ib afferent output, together with spindle afferents, may be important as negative feedback in a force control system and as a compensation mechanism for variations in muscle properties (Karlsson, 1976; Lund et al., 1978). If Golgi tendon organs are not present in masseter, their functional role is most likely accomplished by periodontal receptors (see section 2.1.2.3).

2.1.2.2 Joint receptors

There are three types of receptors in human joints. The most common are free endings found with connective tissue, followed by un-encapsulated Golgi endings also found in connective tissue, and also Ruffini endings in the joint capsule (Kawamura and Abe, 1974; Storey, 1976; Vallbo et al., 1979; Gandevia et al., 1992; Rothwell, 1994).

Despite the difficulties of investigating receptors in the temporomandibular joints (TMJ), these have been studied in rabbits by Kawamura and Abe (1974), who concluded that their output was important in jaw positioning tasks. In contrast, studies on cat (Lund, 1991) and rabbit (Lund and Matthews, 1981) temporomandibular joints undergoing passive movements, found evidence that joint afferents with cell bodies located in the Gasserian ganglion had a significant role in angular determination but no clear evidence for their involvement in active jaw positioning. This conclusion was supported by the human studies of Broekkhuijsen and van Willigen (1983), and Morimoto (1990).

There is a consensus that TMJ receptors are similar to other joint receptors in humans in their capacity to provide proprioceptive information. Clark and Burgess (1995) and McCall et al. (1974) showed that joint receptor output is generally very low, with a variable sensitivity at the extremes of joint movement. Morimoto (1990) also showed that the loss of joint afferent output due to disease or local anaesthetic did not alter discrimination of jaw separation. There is some anecdotal evidence that anaesthetizing the receptors causes a change in jaw posture by altering the proprioceptive feedback from the joint but this is most likely in combination with decreased output from overlying cutaneous receptors (Storey, 1976).

There is thus little evidence of joint receptor involvement in controlling jaw position but their overall importance is still under debate. They are not considered in this study.

2.1.2.3. Periodontal Receptors

Applying force to the teeth at different rates and intensities can evoke sensations of touch, pressure and pain, which is attributed to receptors in the tissue supporting the teeth. The various tissue types supporting the teeth are the gingiva, cementum, periodontal ligaments and the alveolus (Linden, 1990). Mechanoreceptors are either capsulated Krause-like or Meissner-like terminals or compact and loose un-encapsulated whorls, and are essentially of the same structure in the papillary, subpapillary gingival tissue and the periodontal ligament (Hannam, 1976). Functionally, mechanoreceptors are subdivided into those that rapidly adapt with a high activation threshold and those that slowly adapt with lower thresholds (Anderson et al., 1970).

Although periodontal receptors have been shown to mediate both inhibitory and excitatory reflexes in human jaw-closing muscles (Hannam and Matthews, 1969; Johannson and Olsson, 1976; Lund et al., 1983a,b; Trulsson et al., 1992; Brodin et al., 1993; Yang and Türker, 1999), they are not likely to provide any role in the postural control of the mandible, as the teeth are not in contact at rest or during any of the locomotor tasks undertaken in this study. They are thus generally not stimulated, and cannot play an important role in postural control of the jaw under these conditions (Trulsson and Johannson, 1996, 2002).

2.1.2.4. Mechano-receptors of the skin and oral cavity

Human skin and mucosa contains 3 types of receptors: nociceptors, thermoreceptors and mechanoreceptors. Mechanoreceptors provide important information on applied force and are found in areas where movement and gripping tasks are undertaken, such as in the feet and hands and in the oral cavity. They consist of Ruffini endings in the dermis, the subcutaneous Pacinian corpuscles (which are absent in the lips and oral cavity) and Meissner corpuscles, and by Merkel disks deeper down in the dermal-epidermal interface (Burgess and Perl, 1973; Johannson et al., 1988). They provide important sensory feedback in gripping tasks and modulate reflex changes in gripping force (Johannson and Westberg, 1984).

The facial skin, buccal mucosa and the peri-oral skin all have extremely dense populations of mechanoreceptors, which are closely spaced and have well-defined receptive fields. Single unit recordings from large diameter afferents during vertical jaw opening and closing, indicate responses that adapt slowly to the deformations and stresses of the skin, thus providing kinaesthetic information rather than information about the absolute position of the mandible (Trulsson and Johannson, 2002). This contrasts with the fast adapting output from the many small afferents originating in the mechanoreceptors in the tongue, which rapidly respond to deformation due to direct contact with other intraoral structures and objects (Trulsson and Essick, 1997; Connor and Abbs, 1998). There is no consensus on how much this proprioceptive input from facial skin or oral cavity contributes to the stability or maintenance of jaw posture in humans, but it has been demonstrated that increased afferent output from receptors in the facial area (Cruccu et al., 1989a) and lips (Cruccu et al., 2001) strongly inhibited both masseter Hoffman (H-) reflexes and tonic stretch reflexes (see section 2.2.4 below).

2.2. STRETCH REFLEX MECHANISMS

History of the Stretch Reflex

Early reports of the stretch reflex arose from a study of decerebrate cats (Liddell and Sherrington, 1924). They showed that when a muscle is lengthened, a contraction occurs in the muscle that opposes the applied stretching force. This response is proportional to both the speed of the applied stretch (the dynamic component) and to the displacement (the static component).

This response is the result of stretching muscle spindles within skeletal muscle which activates the primary muscle-spindle endings, which in turn leads to the excitation of the homonymous motoneurons, and hence muscle contraction which opposes the stretch.

Stretch reflexes have been investigated in many different skeletal muscles and are generally considered to contribute to postural stability (reviewed in Rothwell, 1994).

Reflexes in Masticatory Muscles: Methods of Investigation

Reflexes observed in the masticatory muscles in humans under controlled laboratory conditions provide important information about the connections existing between the afferent and efferent nerves involved in muscle control, but very little direct information about the mechanisms that control the masticatory muscles in normal function (Matthews, 1976). A range of techniques applying mechanical or electrical stimulation to muscle or nerves is available to demonstrate segmental reflex pathways within the masticatory system. The classification of the elicited reflex may be defined either by the receptors that were initially stimulated or by the action observed in the activated muscle. The repeatability and accuracy of quantifying observed motoneuron and reflex responses by different methods has been systematically reviewed by Türker (1988, 2002), Türker and Miles (1989) and Brinkworth and Türker (2003).

2.2.3. Jaw Jerk Reflex

The demonstration of stretch reflexes in the masticatory muscles of decerebrate cats by Sherrington (1917) was the earliest systematic study of jaw positional control. In humans, a tendon hammer tap on the chin causes a sudden downward movement of the mandible, elicits a short latency reflex contraction in the masseter and temporalis muscles. The reflex afferents are Ia fibres from muscle spindles of these muscles, although whether the afferent fibres travel in the trigeminal motor root (Cruccu et al., 1989b) or the trigeminal sensory root (Ongerboer de Visser, 1983) is controversial. This jerk reflex, analogous to a limb tendon jerk reflex, is the simplest jaw reflex, and is considered to be monosynaptic, owing to a short latency of 7 to 8 ms, which is due to the anatomical proximity of the jaw to the brainstem and hence the short conduction distance (Lamarre and Lund, 1975; Godaux et al., 1975a; Lund et al., 1983a; Murray and Klineberg, 1984).

The amplitude of the EMG response increases if the elevator muscles are partially contracted prior to the tap and reduced when digastric muscle is contracted prior to the tap (presumed to be due to presynaptic inhibition by the antagonistic jaw opening muscle). The amplitude of this reflex is also proportional to the strength of the stimulus, occlusal position of the mandible (hence length of jaw closer muscles) and the overall excitability of the motoneuron pool (Matthews et al., 1975; Lund et al., 1979; Lund et al., 1983a; Miles et al., 1995).

Bishop et al. (1984) found that a 15^0 extension of the neck and a voluntary contraction of the platysma consistently increased the size of the stretch reflex in jaw-closing muscles proportionally to the intensity of the stimulus. Likewise, voluntary clenching also increases the reflex activation in direct proportion to force of clench (Lennartsson, 1980).

Hoffman (H-) reflex in human masseter

Low intensity electrical stimulation of the motor nerves supplying partially contracted human masseter muscle elicits an Hoffman (H-) reflex in the muscle with latencies of 5.5 to 5.9 ms, while at higher stimulation levels the motor neurons are directly stimulated (M response) with a latency of 1.3 ms (Godaux and Desmedt, 1975a; Macaluso et al., 1990; Macaluso and De Laat, 1995).

Externally applied vibration causes a marked inhibition of both the Achilles tendon reflex and the soleus muscle H-reflex in humans (Marsden et al., 1976). However, similarly applied vibration cause a marked excitatory effect (approximately 30% increase) on human masseter stretch reflexes (Godaux and Desmedt, 1975b; Cruccu et al., 1989a; Macaluso et al., 1990), which is presumed to be due to the lack of spindles (and thus the absence of presynaptic inhibition) in the antagonistic (digastric) jaw opening muscle. Similarly H-reflex potentiation in human temporalis muscle is also reported with muscle vibration (Cruccu et al., 1989b; Macaluso et al., 1998; Cruccu et al., 2001).

Short- and long-latency stretch reflexes in masseter

Marsden et al. (1976) reported a long-latency reflex elicited when a slow stretch is applied to human jaw muscles. This loading reflex was shown to have latencies of 35 to 80 ms. Reports of the presence of this reflex in jaw elevator muscles were sporadic and contradictory with some suggestion that they were variations of jaw jerk reflexes (Luschei and Goldberg, 1981). However Poliakov and Miles (1994) reliably demonstrated that, for the same displacement of human masseter muscle, a smooth slow stretch elicited a long-latency (35 to 70 ms) stretch reflex and a more abrupt stretch produced the classical short-latency (10 to 12 ms) stretch reflex.

The structures and pathways in the central nervous system involved in the long-latency stretch reflex in masseter are not known but in contrast to the finger muscles for example, the motor cortex is not involved (Pearce et al., 2003).

2.2.6. Jaw Unloading Reflex

The rapid removal of resistance against actively contracted jaw-closing muscles causes a simultaneous unloading and shortening of their muscle spindles. This results in a decreased Ia afferent output and a consequent reflex reduction in masseter muscle activity after 6.5 to 11 ms. This was reported first in humans (Hannam et al., 1968) and then in cats (Taylor, 1976).

Later studies of the unloading reflex of humans clearly show that digastric muscle activity is potentiated if there is prior anticipation of the unloading event. This results in increased resistance to jaw closing because of the greater muscle stiffness (Miles and Wilkinson, 1982; Miles and Madigan, 1983; Abbink et al., 1998)

Jaw Opening Reflexes

The absence of muscle spindles in human digastric muscle, and the absence of reciprocal inhibition originating from muscle spindles within jaw-closing muscle, were once considered enough reason to ignore reflex-like events in the jaw openers (Lamarre et al., 1975). Ostry et al. (1997) however, gives some evidence of reflex activity after rapid unloading of human jaw-opener muscles, as indicated by a longer latency inhibitory response (24 to 34 ms). This had been previously attributed to the delayed inhibitory phase of the stretched jaw-closing muscles, and thus synergistic to the unloading reflex of jaw-closer muscles and to other proprioceptive inputs (Yemm, 1972; Lamarre et al., 1975).

2.2.8. Vestibulo-trigeminal reflexes

The semicircular canals and otoliths in the inner ear signal head acceleration and velocity via the vestibular neurons to the vestibular nuclei in the medulla. Reflexes derived from the vestibular system include the vestibulo-ocular reflex, which keeps the eyes fixated while the head moves, and the vestibulo-spinal reflex, which enables the skeletomotor system to compensate for head movement (Goldberg, 2000).

When the upright stance of humans is disrupted by rotation or landing during locomotion, proprioceptive afferents excite motoneurons to stiffen various antigravity joint systems as a stabilization strategy. Some authors have argued that the source of the excitation is long-latency stretch reflexes from the leg muscles (Devanne and Maton, 1998, Dietz, 1998, Dietz and Duysens, 2000), while others consider short-latency vestibulo-spinal reflexes to be the source (Allum et al., 1989; Kubo et al., 1997; Aoki et al., 2001).

Bishop et al. (1984) and Hickenbottom et al. (1985) demonstrated that vestibular stimulation from whole-body rotation produced a transient excitatory input to the trigeminal motoneuron pool with a decreased threshold for evoking a jaw jerk reflex in human masseter.

Vestibular stimulation (Tolu and Pugliatti, 1993) and forelimb afferent stimulation (Tolu et al., 1994) individually produce reflex excitation in guinea pig masseter muscle with 14 to 29 ms latency. Interestingly, if both stimuli are applied simultaneously, a marked inhibitory response is seen in the same muscle. In human experiments, stimulating the vestibular system by static tilting reduced the excitability of trigeminal motoneurons supplying masseter muscle by 25% (Deriu et al., 2000).

Thus there is evidence of functional vestibulo-trigeminal connections in man; however their functional significance in assisting passive or active control of jaw posture, particular during locomotion, in which the vestibular system is constantly stimulated in multiple axes, remains to be determined. This is addressed for hopping in the present study (see Chapter 5).

2.3. THE HUMAN MANDIBLE

The adult human mandible is a single bone with an approximate mass of 110 g (± 19 g) (Zhang et al., 2002) suspended along with skin and peri-oral tissue by bilateral jaw-elevator muscles that rotate the mandible around the temporo-mandibular joint. The combined mass of the functional unit is 440 g (± 100 g) in an adult (Koolstra and van Eijden, 1995).

Mandibular Posture

The rest position (or postural position) of the mandible is an important point of reference in humans as it relates to a harmonious positional relationship of teeth, bones, joints and muscles to be maintained in normal persons (Bracco et al., 1998) or after prosthodontic, orthodontic or remedial oral and dental work (Burnett, 2000).

The rest position may be either obtained by verbal instruction to allow the mandible to remain in a natural position, or by monitoring muscle activity and using measurements of external soft-tissue landmarks, manual intra-oral (inter-incisal) distance, kinesiograph recording (i.e., using magnets attached to incisor teeth and a fixed detector) and radiographic techniques (Michelotti et al., 1997; Tingey et al., 2001).

Sleep studies involving continuous recordings of inter-cuspal occlusion show that the jaw opens progressively from 2.5 mm to more than 5 mm as sleep deepens, and this occurs independently of sleeping position (Miyamoto et al., 1998).

2.3.2. Mechanisms determining Mandibular Posture

In a purposely relaxed, upright person with lips (but not teeth) held together, there is little or no surface electromyographic (sEMG) activity arising from masticatory muscles (Basmajian and DeLuca, 1975; Vitti and Basmajian,1977; Sgobbi de Faria and Berzin, 1998). However, any induced occlusion will increase jaw-closer EMG (Burnett, 2000), and transient changes are reported with variations in head and body posture (Møller, 1976; Michelotti et al., 1997; Rugh et al., 1989; Bracco et al., 1998).

The presence of weak background EMG activity in jaw-closing muscles has often been observed in the resting mandibular posture. However, reviews by

Watkinson (1987) and more recently, by Woda et al. (2001) concur that the mandibular rest position, in which EMG activity is least occurs at an inter-occlusal distance of 4.5 mm to 7 mm, compared with the conventional clinical rest position, which has an average of 2 to 6 mm inter-occlusal distance. This suggests that there is some active contraction required to maintain a clinical rest position.

There is no consensus on the mechanisms that support the mandible at rest. These could include passive elastic forces (Lynn and Yemm, 1971; Yemm, 1976), a "position servo" based on stretch receptors in the jaw-closing muscles (Møller, 1976; Broekkhuijsen and van Willegen, 1983), a combination of these, or some other mechanism entirely. This issue has not been resolved by simple observation of either surface EMG or intramuscular records. Surface EMG is probably too insensitive to identify tonic activity in a small number of active motor units, particularly if they are deep in the muscle, and the insertion of intramuscular electrodes may in itself activate motor units.

It could also be considered that an overall increased tone, caused by co-contracting jaw opening and closing muscles could retard vertical movement of the mandible. This viscous stabilization of the mandible might well enable the elevator muscles to absorb any vertical shocks, thereby minimizing movement and maintaining the resting position.

The passive and active components of the masticatory system that contribute to muscle contractile forces and the corresponding mandible movements have more recently been modelled by Koolstra and van Eijden (1997a, b). Their studies suggest that all of the jaw-opening and jaw-closing muscles contribute to the resting jaw-posture, whether by active contraction or by passive elasticity and in conjunction with the non-active biomechanical properties of the mandible and the temporo-mandibular joints.

2.3.2.1. Passive Control

Lynn et al. (1971) demonstrated a passive mandibular positioning control system in humans. Their results described a system based on elastic forces dampening movement and holding the mandible in a position that is the equilibrium point of opposing elastic elements in muscle and peri-oral tissues. The `evidence supporting this idea comes from three observations. The first is that the elastic properties of inactive jaw-closing muscles can lift the jaw as the jaw-opening muscles are gradually relaxed. The second is that jaw opening can only occur by activation of jaw-opening muscles while the much stronger jaw-closers are almost completely inactivated. Third, in studies of jaw-opening and closing muscles that had been disabled by lesions or anaesthesia, a considerable force (6 to 20 N) is still required to move the mandible in either direction from the resting position (Yemm and Nordstrom, 1974; Yemm, 1975; Sooch et al., 1999).

For passive control to be effective in maintaining resting position the supporting muscles must be sufficiently stiff or resilient to disperse external force by dampening or absorbing the energy of the stimulus. This has been demonstrated in limb and jaw muscles by tonically stretching an opposing muscle and measuring the elastic force and power spectrum. A strong passive elastic force is generated that is proportional to the amount of stretching (Koolstra et al., 1997a).

Yemm (1976) reasoned that in the normal resting jaw posture there is insufficient sensitivity in the spindle stretch receptors to detect small displacements, but in experimentally controlled stretches, reflexes are detected in response to rapid displacements of the mandible at the incisor teeth of as little as 10μm at both resting posture and an extended gape of 30 mm (Poliakov and Miles, 1994; Miles and Poliakov, 1997).

Yemm (1976) also claimed that there was minimal surface EMG in resting masseter and digastric muscles, a phenomenon that was also found in temporal and suprahyoid by Sgobbi de Faria and Berzin (1998), but other authors have found significant EMG levels under similar conditions (Basmajian and DeLuca, 1985; Michelotti et al., 1997).

Many studies on limb muscles have shown that the muscles and their attachment tendons have a high capacity to store and release energy during flexor/extensor phases in rhythmic movement (Alexander, 1988; Blickhan, 1989; Blickhan and Full, 1993). However, in the masticatory system, with its short muscles and no tendinous attachment to bone, there is no evidence for this.

Recently, Peck et al. (2002) argued that the passive position of the jaw is due to the viscosity of muscle rather than its elastic properties. The viscosity effect is held to dampen the movements of the jaw within frequency bands depending on muscle activation levels. Passive elements may be sufficient in a relaxed stationary or sitting person to maintain a stable jaw position at rest; however, the dynamics of a moving mass undergoing single or cyclical vertical displacement (as during locomotion) may still require an active feedback or a stiffer supporting musculature to arrest motion and maintain occlusion (Christensen and McKay, 2000).

2.3.2.2. Active Control

Active control can be recognized in a dynamic system when there is a coherent relationship between cause and effect acting on that system. A stimulus applied to the jaw and causing any deviation from resting position must be able to be sensed, and to elicit a response in the form of increased muscle stiffness or tone in order to resist movement. In the jaw this might relate to a downward force on the mandible of sufficient amplitude and velocity to stretch the masseter and excite muscle spindle afferents, and produce a monosynaptic stretch reflex which increases muscle tone and stiffness in the masseter sufficient to resist the length perturbation. Goodwin et al. (1978) showed a complete loss of jaw elevator muscle tone in monkeys when the stretch reflex pathway was destroyed or blocked.

Møller (1976) proposed a reflex driven, active servo-system using a muscle spindle based feedback system to control jaw position. He proposed that spindles are sensitive to small stretch displacements and that their afferent output would excite alpha motoneurons supplying the jaw-closing muscles. He demonstrated that even at rest a continual low level EMG activity in the anterior temporalis is apparent.

Using mechanical stretches applied to human masseter muscle Cooker et al. (1980) found a significant increase in force required to stretch muscle with small (200 μm) displacements once short-latency (8 ms) reflex activation occurred. Similarly Poliakov et al. (1993) found that slow imposed stretches of small amplitude in the masseter muscles of seated humans produced considerable reflex muscle force, thereby resisting further stretching.

It is suggested that afferent output from different groups of jaw-closer muscle spindles begins after very short displacements, while other muscle spindle populations are optimised for output at a greater gape, continuing up to a muscle elongation of up to 30 mm. This is particularly true of the range of spindles located in the posterior temporalis (Taylor, 1990). The large dynamic range of spindle sensitivity supports the idea that even when the jaw is wide open (as during heavy breathing or chewing large food items) there is the ability to maintain jaw closing tension and position reflexively (Taylor, 1990).

Lund et al. (1983a) commented "It is probable that load-induced variations in spindle input may be of great importance in helping to maintain a stable mandibular position relative to the skull during locomotion." This mechanism would actively support the mandibular position against gravity using continuous low levels of reflex muscular activity. This is consistent with the observation that jaw-elevator muscles continually show small amounts of asynchronous muscle activity in the order of 5 to 20 μV from surface EMG recordings under moderate perturbations of gravity and vertical movement (Michelotti et al., 1997).

Abbink et al. (1999) studied rhythmical movement in human flexor and extensor arm muscles and jaw-opening and jaw-closing muscles, and superimposed expected and unexpected loads. Anticipatory activation preceded load by 200 ms in arm and 100 ms in the jaw. Activation followed unexpected loads with latencies of 65 ms in the arm and 20 ms in the jaw. The conclusion was drawn that the force-velocity properties of the jaw muscles have a stabilizing effect on the jaw, and that this occurs before sensory responses occur. Previous studies have shown that anticipation of imposed loads may produce muscle activity with latency of 25 ms and a longer latency of 100 ms is utilized if an underestimate of load was made (Ottenhoff et al., 1992a, 1992b; Abbink et al., 1998).

The evidence presented by Ostry et al. (1997) of an active jaw unloading-reflex in digastric muscle responding to small downward forces may provide some evidence of overall control in a bi-directional movement. Vitti and Basmajian (1977) and Castro (1999), however, reported minimal electrical activity in the digastric muscle during both active head movements and at rest. Human jaw closing muscles are capable of generating greater than 400 N of contractile force (van Steenberghe et al, 1978; Christensen and McKay, 2000) and thus, only a small amount of pre-activation of jaw elevator muscles would provide a counter force to the transient increase of downward forces (3 N to 15 N) acting on the mandible during an abrupt landing (such as from hopping).

The question of whether these transient loads are absorbed or resisted by the stiffness or viscosity of minimally contracted jaw-elevator muscle and/or by stretch reflexes is examined in chapter 5.

2.3.2.3. Central Pulsatile Control

Junge et al. (1998) reported that, when subjects bit lightly onto spring-loaded position sensors near the vertical rest position, a tremor was observed in the jaw of about 7 Hz (just less than the frequency of physiological tremor 8-11 Hz). Their data indicate that this jaw tremor is unlikely to be the result of cardioballistic inputs as suggested earlier (Palla and Ash, 1979; van Steenberghe and de Vries, 1980), or of damped mechanical vibrations, but indicated that the tremor had a significant neurogenic component. It may, therefore, result from the activity of a central pacemaker or from stretch reflexes in the masticatory muscles (Elble et al., 1987). This “pulsatile control” mechanism, previously demonstrated in the finger muscles (Vallbo and Wessberg, 1993), has been compared functionally with the pattern of tremor in the mandible under similar static and dynamic conditions (Palla et al., 1979; Junge et al., 1998; Jaberzadeh et al., 2003). This is an important issue, because the control systems for the masticatory muscles differs in many ways from that of the fingers. In particular, the jaw-opening muscles contain few, if any, muscle spindles, and there is no reciprocal inhibitory reflex between the jaw-openers and closers which could participate in a pulsatile pattern of activation or in resting tremor (Luschei et al., 1981).

Langenbach et al. (1999) proposed that even under resting conditions the mandible is supported by passive muscle action with the teeth separated by about 12 mm, that is decreased by a small amount of tonic (and fluctuating) jaw-closer muscle activation which lifts the mandible to a reduced intercuspal distance of 2 to 3 mm.

Jaberzadeh et al. (2003) demonstrated low amplitude tremor (peak frequency of around 6 Hz) of the mandible during voluntary movements and at rest. They concluded that it is not the result of a reflex-based position servo maintaining a position, but is the consequence of centrally generated alternating bursts of jaw-opening and jaw-closing muscles.

These rhythmical activations are most likely the source of the small background surface EMG often reported from jaw-closing muscles at rest.

2.4. MEASUREMENTS AND MODELLING OF THE HUMAN MASTICATORY SYSTEM

A large number of methods have been used to track and measure jaw position in humans during manoeuvres such as chewing or speech. These have included a range of measurement technologies measuring one, two or three axes of rotation and translation giving up to six degrees of freedom (Griffin and Malor, 1975; van Rensburg, 1975; Hannam et al., 1980; Miles and Wilkinson, 1982; Ostry and Flanagan, 1989; Wilding and Lewin, 1991; Plesh et al., 1993; Hayashi et al., 1994; Naeije et al., 1995; Gallo et al., 2000).

Many of the systems that have been described are either bulky, heavy, complicated to attach, or require the head to be fixed, and all are expensive (e.g., Griffin et al., 1975; van Rensburg, 1975; Miles et al., 1982b; Hayashi et al., 1994).

While some of these systems measure jaw movements in three dimensions, the most important measurement in studies of jaw reflexes is the vertical position of the mandible relative to the maxilla. In most cases, the measurement is made using a movable actuator or transmitter that is glued to a mandibular tooth with a fixed sensor or reference point attached to the head. However, few of the systems so far used have sufficient spatial or temporal resolution to enable accurate measurements of small mandibular displacements that can be temporally related to the reflex activation of muscle and other important neurological events.

Systems like the widely used Optotrak® system rely on scanning video cameras and electroluminescent markers to provide temporal and spatial coordinates. However, the time limit of 10 ms is insufficient for detecting the rapid displacements of the mandible that were the subject of this study.

None of the foregoing techniques allow simple non-invasive assessment of mandibular movements, or offer sufficient resolution to detect fast and small movements in a freely-moving human undergoing normal locomotion tasks. These shortcomings are addressed in Chapter 3, where the novel approach developed for this study is described (Flavel et al., 2002).

The normal functions of the human masticatory system have been simulated using computer graphical and mathematical models in order to understand complex activities such as biting, mastication, speech, swallowing and facial signalling (Baron and Debussy, 1979; Hannam et al., 1980; Baragar and

Osborn 1984; Hannam and McMillan, 1994; Koolstra and van Eijden, 1995; Hannam et al., 1997; Koolstra et al., 1997a, 1997b; Korioth et al., 1997). While such models may be used as tools to predict forces and dimensions in order to allow the construction of remedial appliances in various fields in dentistry, they have limited use as predictors of actual neurologic and muscular processes that take place in real humans. The complexity of the human trigeminal nerves and masticatory system may be better simulated as more pathways are described, but a model can only work with data that is available.

The jaw movements were quantified during locomotion in Chapter 4. This information is needed for computer models of the masticatory system. Reflexes are described in chapter 5 which serve to limit mandibular movements when landing from a hop. The evidence suggests that these are stretch reflexes.

2.5. FORCES ACTING ON THE SKULL DURING LOCOMOTION

During locomotion in bipedal and quadrupedal animals, a rhythmic pattern of reaction forces is generated between the alternatively contacting feet and the ground (Vaughan et al., 1999; Seyfarth et al., 2002). Despite a highly complex neural control system, human gait is characterised by smooth, regular and repeating movements (Vaughan, 2003).

A simple spring-mass model has been used to describe the relationship of the forces and movements of the limbs, torso and head in a moving human. The reaction forces generated in the feet at each footfall are transmitted to the head through actively contracting muscles, soft tissue, ligaments and bones

(Blickhan, 1989; McMahon and Cheng, 1990; Blickhan and Full, 1993). As a result of being selectively filtered, somewhere between 50% and 80% of the transmitted force is absorbed before it reaches the head.

Cappozzo (1981, 1982) studied the forces and vertical displacements measured at the skull and showed that they increase linearly with walking and running speed. At rest, net vertical forces are equivalent to the earth's gravitational force (1 g = 9.88 $m.s^{-2}$) for both feet and head. Running at 10 $km.h^{-1}$ increases the forces at the foot by 200% to 300% (20 – 30 $m.s^{-2}$), and at the head by 50% to 100 % (15 to 20 $m.s^{-2}$). The acceleration transmitted from the tibia to the maxilla is reduced between 3.0-fold (Rao and Jones, 1975; Light et al., 1980; Cappozzo, 1981, 1982; Pozzo et al., 1990; Hirasaki et al., 1999) and 3.5 fold (Wosk and Voloshin, 1981).

Walking or running with different footwear produces a wide range of heel strike and force generation patterns (Light et al., 1980). For example, soft shoes reduce transmitted energy by 90% compared with barefoot walking. Likewise, walking on a surface such as carpet produces much lower reaction-forces than walking on tile or treadmill surfaces (Smothers et al., 2000).

There is a relatively small amount of data on the forces transmitted from the skull to the suspended mandible. However, Light et al. (1980) reported a 50% transmission in a fully occluded situation. While Hashimoto and Clark (2001) did attempt to measure vibration at different occlusal distances, and found a 10 to 50% transmission increase as occlusal opening increased from 10 mm to 54 mm, it should be noted that the externally generated forces had frequencies much higher (379 to 396 Hz) than the range of frequencies generated by heel-strike (5 to 70 Hz) (Rao and Jones, 1975) and those actually transmitted to the skull (5 to 25 Hz) (Rao and Jones, 1975; Cappozzo, 1982), and thus one could expect different spectral absorption by musculo-skeletal components.

The observation in animals and man that the mandible moves vertically up and down (closing and opening) relative to the maxilla during each step is anecdotal: this present study is the first report of measured vertical jaw velocities in freely moving humans: this is addressed in chapter 4 of this thesis.

This present study is also the first report of the presence of active or passive mechanisms that determine the relative position of the jaw during whole body movements and is presented in Chapter 4 of this thesis (Flavel et al., 2003).

2.6. SUMMARY

The masticatory system presents a unique model of active muscular control, and while the human jaw system is well documented in relation to structure, masticatory function and speech, the physiological mechanisms controlling the mandibular position during locomotion and other whole body movements are poorly understood. They are the subject of this study.

The lack of suitable techniques and equipment with sufficient resolution to detect small mandibular displacements required the development and construction of precise equipment and methodologies which are discussed and validated in Chapter 3.

Information on the dimensions of movement and the forces acting on the mandible in the masticatory system was obtained in normal subjects undergoing whole body movements. These included hopping, walking and running, all barefoot, at a range of speeds and inclinations, and with different foot landing styles. The trials were designed to give a range of stimuli for mandibular displacement, and are discussed in Chapters 4 and 5.

To gain a better understanding of the nature of the control and stabilization of the mandible during a vigorous whole body manoeuvre, surface EMG from masseter muscle was correlated with both accelerative forces and the position of the mandible during hopping on one leg, to find evidence of active control of mandibular posture by stretch reflexes. This is described in Chapter 5.

CHAPTER 3. A SIMPLE AND INEXPENSIVE SYSTEM FOR MONITORING JAW MOVEMENTS IN AMBULATORY HUMANS

3.1. INTRODUCTION

A number of methods have been used to measure vertical jaw position in humans during manoeuvres such as chewing or speech (Griffin and Malor, 1975; van Rensburg, 1975; Hannam et al., 1980; Miles et al., 1982; Ostry and Flanagan, 1989; Wilding and Lewin, 1991; Plesh et al., 1993; Hayashi et al., 1994; Naeije et al., 1995; Gallo et al., 2000). While some of these systems measure jaw movements in three dimensions, the important measurement in studies of jaw reflexes is the vertical position of the mandible relative to the maxilla. In most cases, the measurement is made using some form of transmitter that is glued to a mandibular tooth while a sensor is attached to the head. Many of the systems that have been described are relatively bulky, heavy, complicated to attach, or require the head to be fixed, and are expensive (e.g. Griffin and Malor, 1975; van Rensburg, 1975; Miles and Wilkinson, 1982; Hayashi et al., 1994).

Here I present a simple, inexpensive method to measure vertical movements of the mandible in relation to the maxilla, suitable in situations where the head is unrestrained and when rapid jaw movements are to be measured. This system is intended to measure over only the rotational component of vertical human jaw movements.

3.2. METHODS

Informed, signed consent was obtained from 8 volunteers, and the experiments were carried out with the approval of the Human Research Ethics Committee of Adelaide University.

Two methods were used in parallel to measure jaw position and movements. The first was based on records of the acceleration of the mandible relative to the maxilla. Single-axis accelerometers with an output of 400 mV per $m.s^2$ (model ADXL105Q, Analog Devices, Norwood MA USA) were chosen for their size (7 x 9 x 4 mm), low inertial mass (<1 g) and broad-band sensitivity (DC to 5 kHz). Velocity and position signals were derived from the accelerometer outputs. The electrical output signals from one of the two accelerometers were electronically subtracted in a precision differential amplifier to give the acceleration of the mandible relative to the maxilla. The resulting differential acceleration record was digitised at a 5 kHz sampling rate with a CED laboratory interface (1401plus, CED Ltd., Cambridge, UK), mathematically integrated once to give the velocity of the mandible relative to the maxilla, then integrated a second time to give relative jaw position. Integration was performed with software supplied with the laboratory interface (CED Signal version 1.85) but could equally be achieved with integrating amplifiers. The operation of the system was checked by asking subjects to shake and nod their head whilst clenching their teeth. In this situation there are large peaks in the acceleration of the maxilla and mandible but their relative acceleration is zero.

The major shortcoming of the accelerometer-based system is that it does not give stable records of static jaw position. To overcome this, a second transducer system was used, based on a Hall-effect device for measuring small distances. This consisted of a powerful rare-earth magnet 5 mm diameter by 2 mm thick whose field was detected by a Hall-effect magnetic sensor (part # 04-267, RS Components, Corby, UK). The effective working range of this device was 1 to 25 mm. The Hall-effect device gives a constant output when the separation between the magnet and the sensor is constant, and is calibrated by asking the subjects to grip spacers of known thickness between their teeth. Its output, however, is non-linear. The non-linearity can be compensated by re-scaling (e.g., by a curve-fitting program implemented in a spreadsheet), although this is inconvenient to achieve on-line.

One accelerometer and the magnet were glued to a bracket formed from a double thickness of 1.5 mm lead-free and resin-free solder wire that enabled it to be adapted to lip shape, dental overbite, etc. This bracket was then glued to the labial surface of an upper central incisor tooth with fast-curing, glass ionomer dental cement (GC Fuji IX GP, GC Corporation, Tokyo, Japan) as shown in Figure 3.1

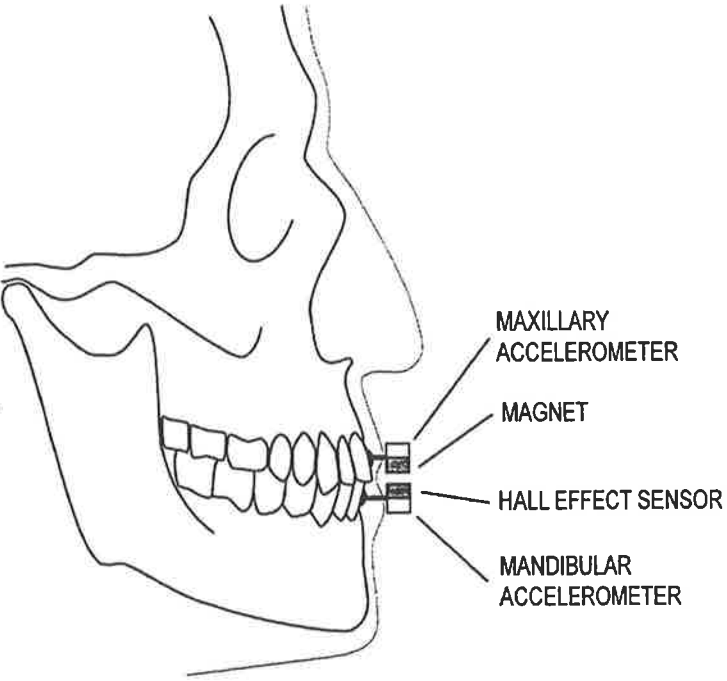

Figure 3.1 .... Mounting of transducers to teeth.
A flexible metal bracket carrying one transducer array is glued to an upper incisor tooth: another bracket carrying the second array is mounted directly below this on a lower incisor tooth. The canine teeth can also be used. The brackets are bent to enable them to pass between the lips to keep the transducers outside the mouth and optimally aligned to each other. Given appropriate waterproofing, it would also be possible to have the transducers inside the mouth, attached to the buccal surfaces of posterior teeth. Fine wires (not shown) carry the 5 V power to the transducers and the output signals to the data acquisition system.

This cement is normally applied to an acid-etched enamel surface, but the mechanical strength of the bond obtained without etching was appropriate for the present purpose. The bracket was easily removed from the tooth at the end of the experiment and small specks of residual cement were cleaned from the tooth with a hand-held dental scaler. The second accelerometer and the Hall-effect sensor were mounted on a similar bracket, which was glued to the labial surface of the lower incisor tooth on the same side. Care was taken to keep this bracket from contact with the upper bracket and teeth when the subject clenched.

The accelerometers were connected by fine, flexible ribbon cables to instrumentation amplifiers to match gains and allow offset adjustment of static acceleration (INA 125PA, Burr Brown, Tucson. USA). Other fine wires brought the ±5 VDC power for the accelerometer and the Hall-effect transducer. The lower and upper sensor assemblies weighed 3 g and 2.5 g respectively.

To check and calibrate the performance of the system, the devices were mounted on an apparatus used in other experiments to apply precise stretches to the jaw-closing muscles This "muscle-stretcher" system simulates the rotational component of movement of the human temporomandibular joint. That is, the lever arm on which the mandibular accelerometer is mounted is co-axial with the temporomandibular joint and has a lever arm that corresponds with the position of the incisor teeth (Fig. 1 in Miles et al., 1993). This device enabled the transducers to be moved known distances relative to each other at known angular accelerations under servo control.

In a series of preliminary experiments, the mandibular movement was measured in subjects who hopped on one leg, landing on one heel. The signals recorded during 100 hops were averaged, using the rapid deceleration of the maxilla on landing as a trigger.

3.3. RESULTS

Figure 3.2 shows the results of bench-testing the system on the servo-controlled displacement device. The position record obtained by integrating the accelerometer output corresponded closely with the output of the linear displacement transducer on the servomotor over accelerations ranging from 0.5 to 40 $m.s^{-2}$. Note, however, that the gain of the Hall-effect device is reduced about 10-fold when tested at a separation ("jaw opening") of 15 mm, compared with the gain when the separation was 5 mm.

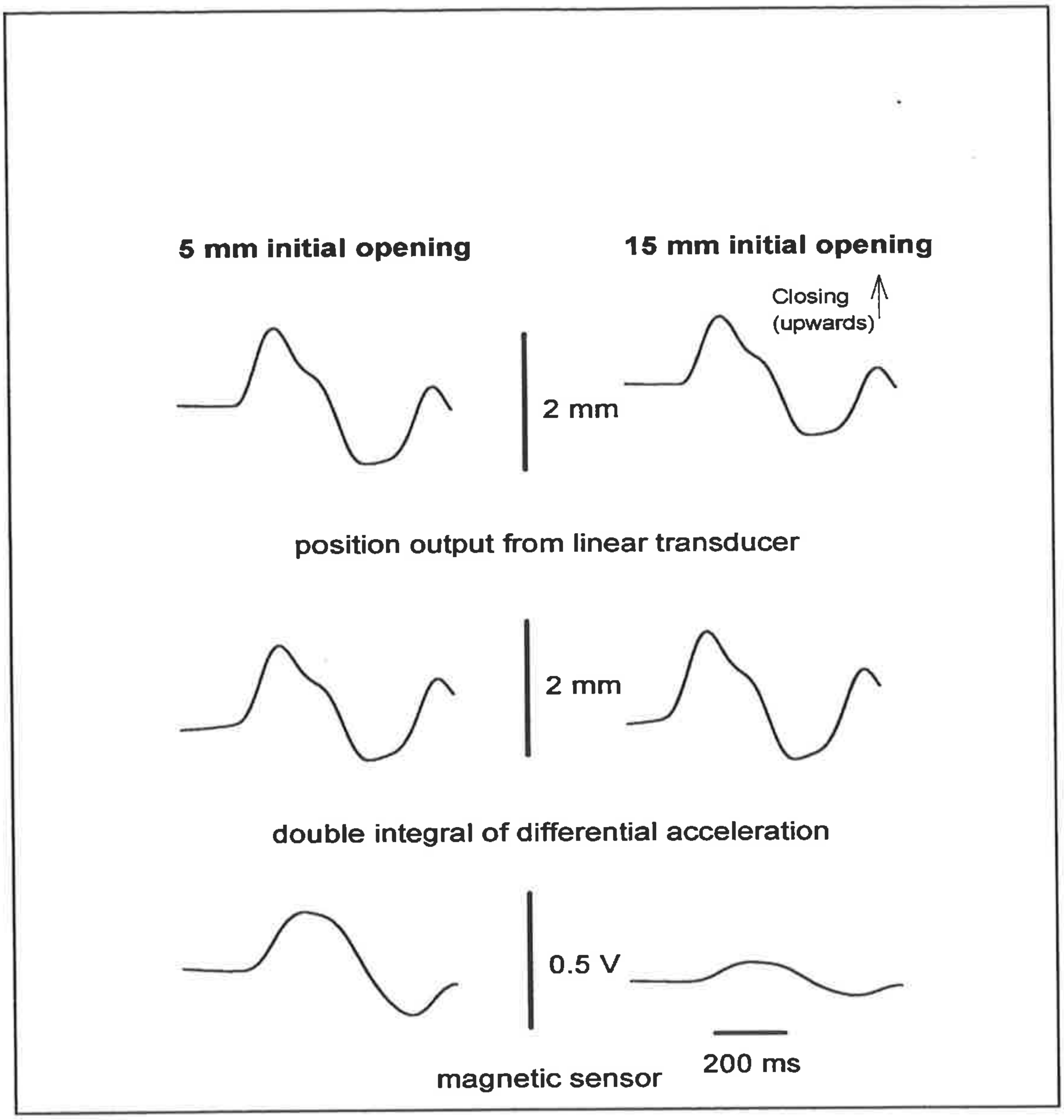

Figure 3.2 .... Comparison of the position record derived in a bench test from a precision linear output transducer (uppermost traces), double integration of the mandibular accelerometer (middle traces), and from the Hall-effect device (lowermost traces).

A servo-controlled displacement device moved the mandibular transducer in relation to the maxillary transducer at two initial separations (simulating two initial vertical separations of the incisor teeth). The movement consisted of a 0.5 mm upward ("closing") then downward ("opening") movement, before returning to the initial position. The vertical velocities were approximately 50 mm.s^{-1}. The left column shows the data obtained at the first "jaw opening" of 5 mm, and the right column the data obtained at 15 mm separation. The non-linear input-output properties of the Hall-effect device resulted in a signal whose gain is reduced about 10-fold at 15 mm compared with 5 mm, while the double-integrated output from the accelerometers is constant irrespective of starting position. All signals shown are the averages of 50 trials.

Vigorous head-shaking with the teeth clenched resulted in a zero difference signal in 8 subjects tested, indicating no relative acceleration (or movement) between upper and lower jaw. A minor misalignment of the upper and lower accelerometers would cause a difference in sensitivity, and thus a small non-zero signal in the difference signal. This was corrected by adjusting the gain of the other sensor.

The output of the Hall-effect device was calibrated for each trial and as necessary, corrected for non-linearity using a software-based curve-fitting program, off-line.

Figure 3.3 shows representative data obtained in an experiment in which the jaw position was monitored while a subject jumped down from a 100 mm step and landed on his heel. The accelerometer signals shown in the upper panel are the ensemble averages of 8 trials. The difference trace (relative acceleration) was obtained by averaging the mathematical difference between maxillary and mandibular accelerometer records in each trial. The result of integrating these three signals to give, respectively, the velocities of the maxilla and mandible, and the velocity of the mandible relative to the maxilla are shown in the middle panel. The lowermost panel shows the result of the second integration of the difference signal to give the vertical position of the mandible relative to the maxilla. Upon landing, the mandible moved first slightly closer to the maxilla as the result of a forward head tilt, and then downwards away from the maxilla. It then overshot upwards (presumably as the result of reflex action), but the teeth did not touch: touching of the teeth would appear as a sharp deceleration of the mandible in the uppermost trace, and as a flat peak in the mandibular position trace.

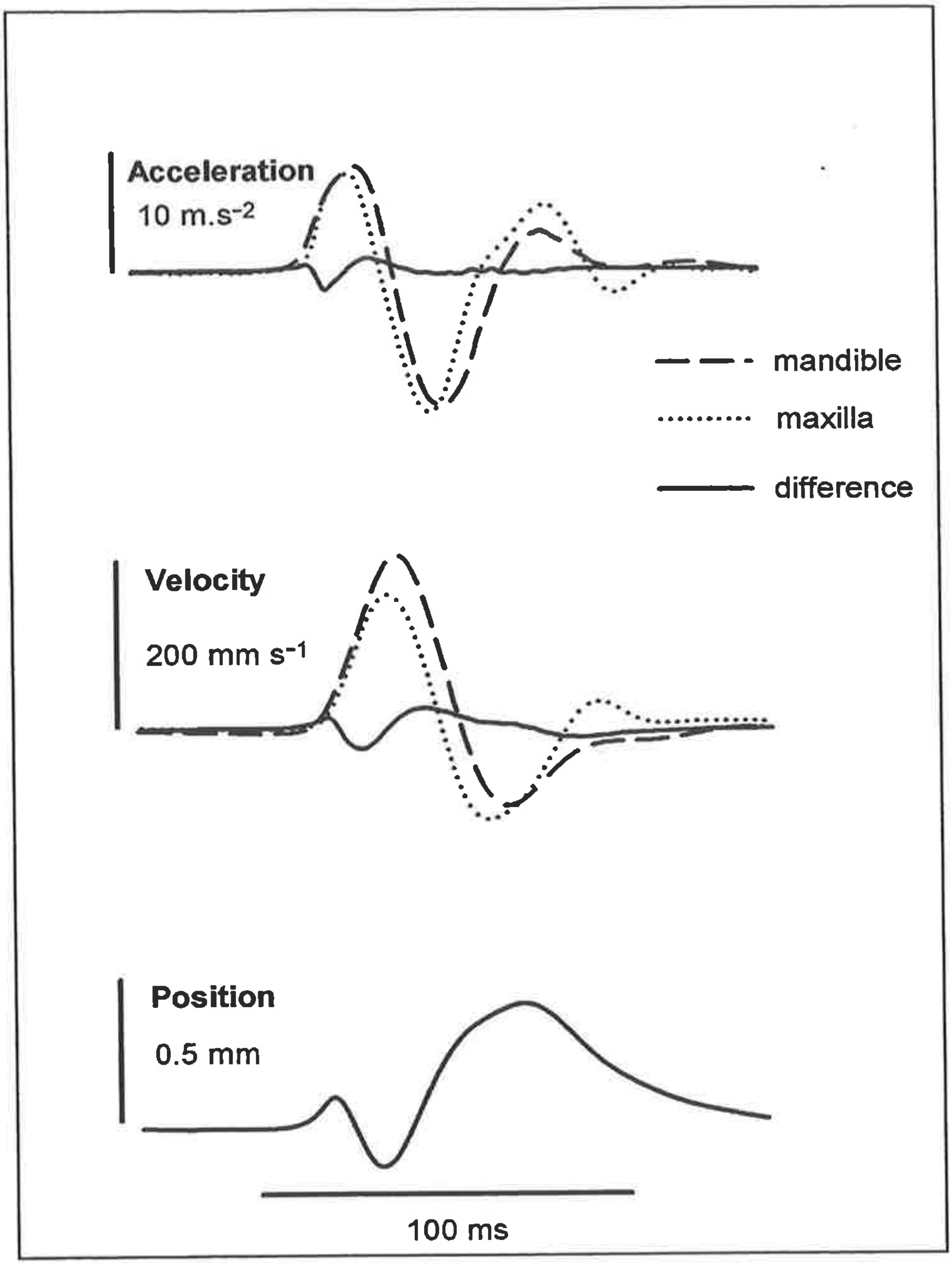

Figure 3.3 .... Jaw movements measured during landing on one heel following a jump from a height of 100 mm.

The resulting sudden deceleration upon landing caused the mandible to move downwards with respect to the maxilla. The uppermost panel shows the output from accelerometers mounted on the maxillary and mandibular teeth and the difference signal. The result of integrating these signals once to give maxillary and mandibular velocity is shown in the middle panel. The lowermost panel shows the result of a second integration of the differential acceleration signal to give vertical jaw position relative to the maxilla. Thus, heel landing caused the mandible to move about 0.3 mm downwards relative to the maxilla. All signals are averages of 8 trials, triggered by the rapid deceleration of the maxilla on landing.

The accelerometer system was relatively non-intrusive and was tolerated well by subjects who wore it during manoeuvres such as jumping, hopping and treadmill-running.

The response of the accelerometers is linear up to 5 kHz, which exceeds by several orders of magnitude the highest frequency at which the mandible moves under physiological conditions (van Eijden, 2000).

3.4. DISCUSSION

The teeth are rigidly fixed in the bone: hence, direct mechanical coupling of sensors to the lower and upper teeth allows the movements of the mandible relative to the maxilla to be estimated accurately.

The accelerometers and magnet systems each have advantages and disadvantages. The accelerometers give an acceleration signal that is valuable in, for example, reflex studies in which detecting the onset of jaw movements is critical (Hannam et al., 1968; Miles et al., 1982b; Miles et al., 1995). Jaw velocity can then be measured accurately by integrating the acceleration signal. Measurement of position of the jaw relative to the maxilla is more difficult. Double integration of acceleration gives a signal that is linearly related to position over a wide range of jaw openings; however, the drift inherent in the integration process prevents this method being used to measure a constant jaw position, or a very slow-moving jaw. The magnetic device gives a signal proportional to jaw position even when the jaw is not moving, but the relationship is highly non-linear and its resolution declines as the jaw opening increases. In practice, using both signals gives information about jaw position and movement over the range of vertical jaw positions and velocities.

This system is simple and non-invasive and has been shown in a series of treadmill-running experiments to be reliable and suitable for monitoring various parameters of natural jaw movements in the laboratory and in the field. Signals from the sensors are low noise and require minimal conditioning prior to storage on portable analog or digital recorders. The performance of the system is at least equal to commercially available optical tracking systems. One such system (Optotrak 3020, Northern Digital Inc., Canada) has an accuracy of 0.1 to 0.3 mm but is unavailable as a real-time signal. The systems based on magnet-sensing give real-time outputs but have coarser resolutions, e.g., 0.3 mm; (Gerstner and Fehrman, 1999; Gerstner and Kinra, 1999), and 0.5 to 4 mm (Hannam et al., 1980; Wilding et al., 1991).

The accelerometer approach could be used to monitor lateral as well as vertical jaw movements using dual axis accelerometers of the same size (e.g., ADXL205Q Analog Devices, Norwood MA USA). The Hall-effect method would require two magnets and two sensors but would require careful alignment to avoid problems arising from the interaction of the two magnetic fields.

This system could be also adapted for use in experimental animals. No modification would be necessary for use in anaesthetised animals. In free-ranging animals, appropriately waterproofed transducers could be glued directly to the buccal surface of posterior teeth after etching of the enamel to give the cement a stronger bond, and connected to a data logger.

This system provides a simple, low-cost solution to the problem of jaw-movement monitoring in biomechanical and physiological studies.

CHAPTER 4. POSTURAL STABILITY OF THE HUMAN MANDIBLE DURING LOCOMOTION

4.1. INTRODUCTION

The human masticatory system is used in the daily activities of mastication, swallowing and speech. The vertical position of the mandible relative to the maxillae remains remarkably constant when it is not participating in these motor tasks: this is its so-called rest position. However, the head and the mandible also move during all whole-body movements. For example, during walking and running the head oscillates vertically and may undergo rotational yaw (angular displacement about the vertical axis) and pitch (angular displacement about the horizontal axis). The velocity and frequency of head movements during such activities (Grossman et al., 1988; Grossman et al., 1989) and the stabilizing head movements to maintain constancy of gaze and posture have been described (Pozzo et al., 1989, 1990; Hirasaki et al., 1999). It has been suggested that the control of head movement is the result of multi-dimensional detection by the vestibular system and compensatory postural and muscular control (Pozzo et al., 1990). Others have suggested that the rhythmical pendular movements of the head are sufficient to maintain its posture (Winter et al., 1993; Eng and Winter, 1995).

Despite movements of the head during locomotion, common experience indicates that the mandible does not open and close in an unrestrained manner, nor do the teeth snap together with each step. It is not known how this is accomplished. While the nature of human mandibular movement during speech and mastication has been studied (Ostry et al., 1989; Plesh et al., 1993; Koolstra and van Eijden, 1997b; van Eijden, 2000) there is only one report of the jaw movements that occur during locomotion, and that was focussed primarily on the jaw movement compensations that occur during speech (Shiller et al., 2001). The magnitude of mandibular movements have not been quantified during locomotion, which is essential for determining how precisely mandibular position is maintained under these conditions, and whether this is likely to involve active neurogenic mechanisms (e.g., reflexes, feedforward control) or passive biomechanical properties of the system such as the viscoelasticity or stiffness. The paucity of information about movements of the jaw during normal daily activities probably reflects the lack of an appropriate, minimally intrusive method to measure the position of the mandible relative to the maxilla in freely-moving humans. In the present study, a novel, non-invasive technique developed in this laboratory (Flavel et al., 2002) has been used to measure the movements of the mandible relative to the maxilla during whole body movements in locomotion. Different speeds of level, uphill and downhill locomotion were explored for each subject to provide a wide range of ground reaction forces transferred to the head (Pozzo et al., 1989, 1990).

If the mandible is passively held in position by the supporting tissue we would expect to observe a proportional increase in relative jaw movement as external forces acting on the head and mandible increased. Alternatively, a non-linear relationship between jaw movement and the external vertical forces acting at the skull would suggest the operation of an active postural control system.

4.2. MATERIALS AND METHODS

Twelve normal adults (8 male, 4 female) aged 18 to 38 years with no identifiable neurological, vestibular or dental occlusal disorders were tested after giving informed written consent. This study was approved by the University of Adelaide Human Research Ethics Committee and conformed to the Declaration of Helsinki (1996).

Jaw Movement Measurement

Devices based on miniature accelerometers and Hall-effect sensors were reversibly glued to maxillary and mandibular incisor teeth with glass ionomer cement (for details, see Chapter 3). These devices measured the vertical acceleration of the head and the mandible as well as the interocclusal separation. Single-axis piezoelectric accelerometers with an output of 400 mV per m.s^2 (model ADXL105Q, Analog Devices, Norwood MA USA) were chosen for their size (7 x 9 x 4 mm), low inertial mass (<1 g) and broadband linearity (DC to 5 kHz).

The signal from the mandibular accelerometer was subtracted electronically from the signal from the maxillary accelerometer in a differential input amplifier to give the acceleration of the mandible relative to the maxilla. Once mounted, the accelerometers were checked for alignment. The subject clenched the teeth firmly and nodded his/her head vigorously up and down in the sagittal plane. In this situation, there was no relative movement between the two accelerometers; hence, when the accelerometers were correctly aligned, the difference signal was zero volts.

The major shortcoming of the accelerometer-based system is that it does not give stable records of static jaw position. To overcome this, a second transducer system was used, based on a Hall-effect device for measuring small distances. This consisted of a powerful rare-earth magnet 5 mm diameter and 2 mm thick whose field was detected by a Hall-effect magnetic sensor (part # 304-267, RS Components, Corby, UK). The effective working range of this device was 1 to 25 mm. The Hall-effect device gives a constant output when the separation between the magnet and the sensor is constant, and is calibrated by asking the subjects to grip spacers of known thickness between their teeth. Its non-linear output was compensated by re-scaling by a curve-fitting program implemented off-line in a spreadsheet.

Reaction Forces

Acceleration of the ankle (generated by foot contact with the treadmill surface) were recorded with an accelerometer (model ADXL 05CQ Analog Devices, Mannheim USA), which was mounted firmly within a moulded support covering the subject's right lateral malleolus, and attached by adhesive tape.

Protocol

Subjects practised barefoot walking and running on a motorised treadmill (Tetley Heartmaster Mk 2, Tetley Electronics, Sydney) over a range of speeds until they were comfortable with these manoeuvres. The treadmill could be adjusted to produce zero, positive and negative inclinations to allow "level", "uphill" and "downhill" running conditions.

To minimise changes in head posture and maintain a consistent walking and running style on the treadmill subjects were instructed to keep their head erect and gazing forward at a target placed at eye level at 2 m distance, with verbal reinforcement during the trial if head posture changed noticeably.

Acceleration signals were recorded while the subject walked or ran forward when the treadmill was activated at speeds of 0.7, 1.4, 2.1 and 2.8 $m.s^{-1}$ (2.5, 5. 7.5 and 10 $km.h^{-1}$) for between 2 and 4 minutes. This protocol of four different treadmill speeds was performed first with the treadmill flat. The protocol was repeated with the inclination of the treadmill changed to 5^0 negative (downhill slope) and 5^0 degrees positive inclination (uphill slope). The order of the uphill and downhill trials was randomised. The order of velocities was stepped from the slowest to the fastest speeds. There was at least 2 minutes rest between each trial.

Data recording and Analysis

The analog signals and a verbal commentary were recorded on a six-channel Pulse Code Modulated / Frequency Modulated data recorder (Model 402, AR Vetter Company, Rebersburg, PA, USA).

All data were analysed off-line. All of the acceleration records and the difference signal from the two tooth-mounted accelerometers were digitised at 5,000 $samples.s^{-1}$ with a laboratory interface and data analysis system (CED 1401 *plus* Cambridge Electronic Design, Cambridge, England). The averager was triggered by the rapid downward acceleration of the mandible relative to the maxilla following landing (see Fig. 1). The threshold was calculated as 50% of the average maximal acceleration and was adjusted so that smaller and slower fluctuations preceding a landing did not trigger the averager. At each gait and treadmill inclination, the acceleration signals recorded 300 ms before and after the trigger were averaged and stored. Each triggered frame was inspected visually and occasional (<1%) unsatisfactory trials which contained large jaw movements (for example related to speech or swallowing artefacts) were excluded from the average. At least 100 records were averaged under each set of conditions, and peak mandible accelerations and velocities in the direction of jaw opening were quantified against the resting baseline values. The resolution of all signals was at least 13 bits throughout the recording and analysis procedures.

Repeated measures ANOVA were used to assess the effects of Treadmill Speed (0.7, 1.4, 2.1, 2.8 $m.s^{-1}$) and Slope (flat, downhill, uphill) on the kinematic variables. Where appropriate, one-way ANOVA and Scheffe's post-hoc test were used to assess differences between levels of main effects. Significance level was $P < 0.05$ for all comparisons.

4.3 RESULTS

The general pattern of head and mandible movements during locomotion was similar in all subjects, subject to variations in gait pattern amongst subjects. An example of the raw data collected from a subject running bare-foot at 2.8 $m.s^{-1}$ on a level treadmill is shown in Fig. 4.1. This subject ran in such a way that his toe (T) struck the treadmill first, and was quickly followed by his heel (H). Note that the landing of the left foot on alternate steps is not detected with this accelerometer, although landing on either foot influenced the maxilla and mandible acceleration in a similar manner. Although the leg was moving downwards during the 150 ms period before landing, the head and mandible moved upwards. This probably reflects the tilting of the head either voluntarily to maintain gaze on the target, or as the result of the inertia of the head, which is supported by the spine at a point posterior to its centre of mass. The impact arising from toe-strike appeared to arrest the slow upward acceleration of the head then, about 10 ms after the sharp deceleration of the body due to heel-strike, the maxilla (skull) accelerated downwards (second trace). A similar pattern of deceleration was observed in the mandibular record (third trace). The difference acceleration (fourth trace) shows a smaller, rapid downward acceleration of the mandible relative to the maxilla immediately following each heel-strike. Finally, the lowermost trace confirms that the mandible moved sharply downwards then upwards again after each heel-strike. In this instance, the impact of landing caused the teeth to separate by about 0.75 mm. Note that at no stage did the teeth come together in this or in any other subject during any form of gait: this would be manifest as a rapid deceleration at the end of an upward movement in the relative acceleration record, and a flat upper end-point in the position record.

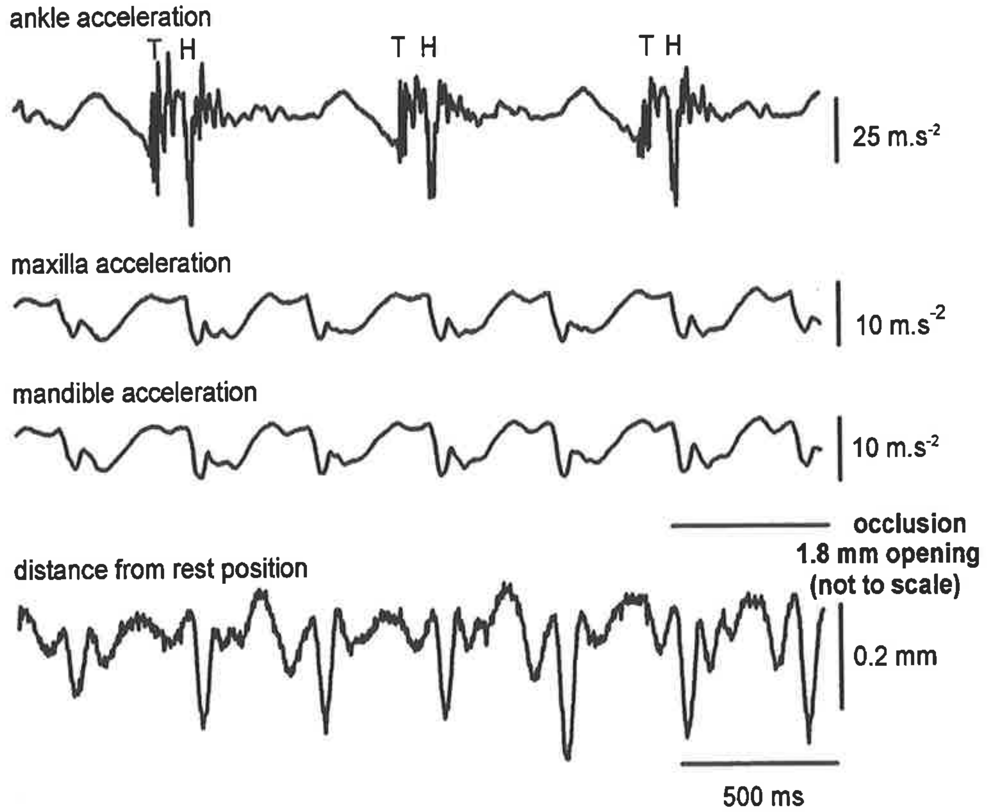

Figure 4.1 .... Raw kinesiological data from the leg, maxilla and mandible in a subject running barefoot at 2.8 $m.s^{-1}$ on a level motorised treadmill.

The uppermost trace shows the signal recorded from an accelerometer firmly strapped to the lateral malleolus of the right ankle: landing on the right foot appears as a large deflection. The second and third records show the outputs of accelerometers glued to a maxillary and a mandibular tooth, respectively. The lowermost record is the output of a Hall-effect device that gave an indication of the vertical separation between the upper and lower teeth. Jaw opening is downwards in the lower trace. T and H indicate acceleration peaks generated by the Toe and Heel striking the treadmill platform.

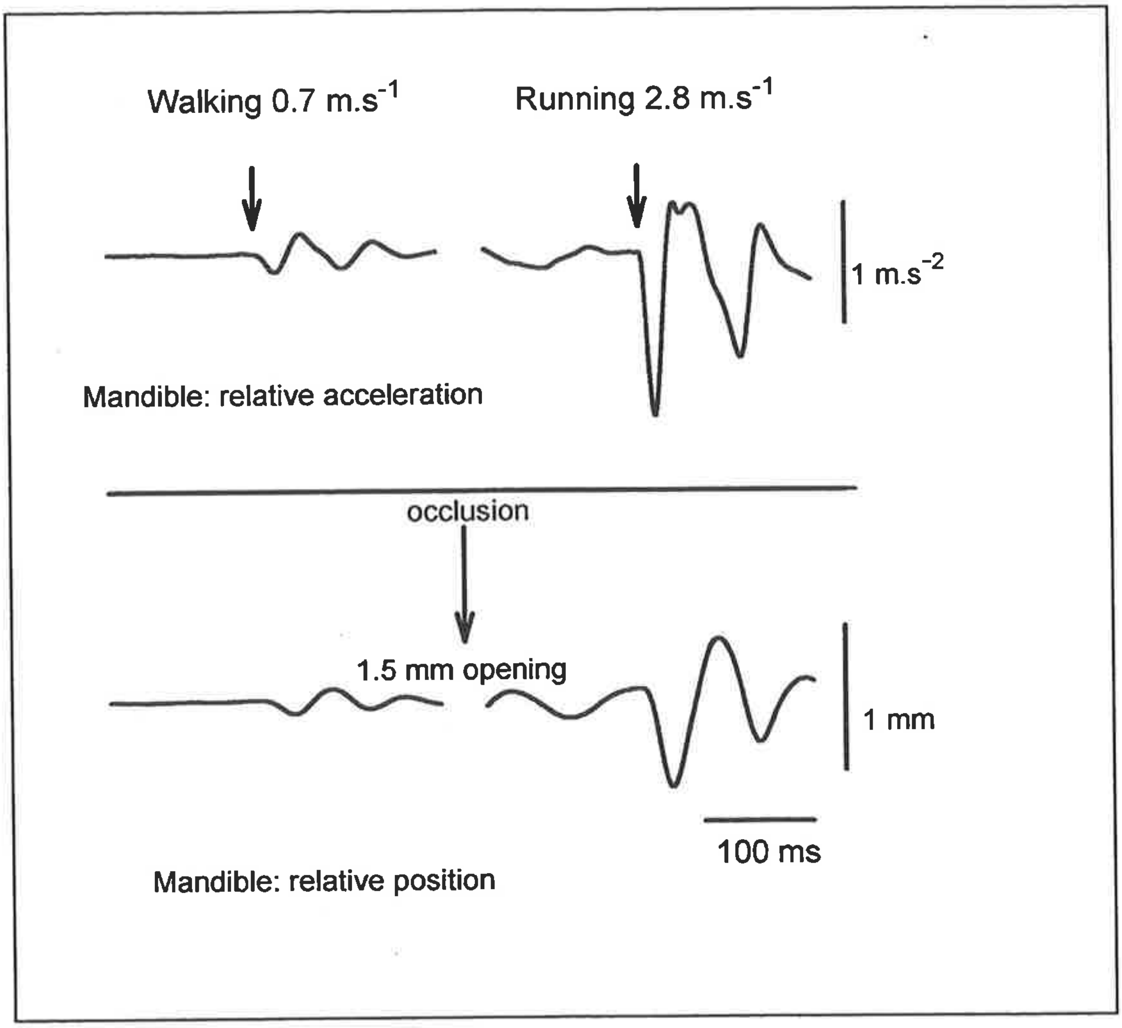

Figure 4.2 .... Movements of the mandible relative to the maxilla in a subject walking barefoot at 0.7 m.s^{-1} and running barefoot at 2.8 m.s^{-1} on a level motorised treadmill.

All records are ensemble averages of 100 trials. The upper records show the vertical acceleration of the mandible relative to the maxilla, and the lower records show the vertical displacement of the mandible from the maxilla (relative position), which follow landing in each step. The top arrows show approximately the time of heel-strike. Jaw opening is downwards. Note the approximately 5-fold difference in average acceleration and mandibular displacement in the two gaits.

An example of the result of ensemble averaging of the acceleration records from a different subject during walking (0.7 m.s^{-1}) and running (2.8 m.s^{-1}) on a level surface is shown on an expanded timescale in Fig. 4.2. For simplicity, only the relative acceleration and relative position of the mandible are shown. This subject landed heel-first in both walking and running. During walking, the preceding heel-landing triggered a similar downward acceleration/deceleration sequence in the mandible relative to the maxilla. This translated to a downward movement of about 0.2 mm. The stronger downwards acceleration induced by landing while running resulted in a downward jaw movement of about 0.75 mm. In both cases, the mandible moved quickly upwards again, overshooting the intermediate position, but without tooth contact.

The pooled kinesiological data from the ankle, maxilla and mandible relative to maxilla at various treadmill speeds and inclinations are shown in Fig 4.3. Note firstly that the deceleration resulting from landing was reduced by about half at the head compared with the ankle. The peak rate of deceleration of the mandible was still lower. The deceleration of all three structures increased with the treadmill speed, and was greater when the treadmill was inclined downwards and less when it was inclined upwards.

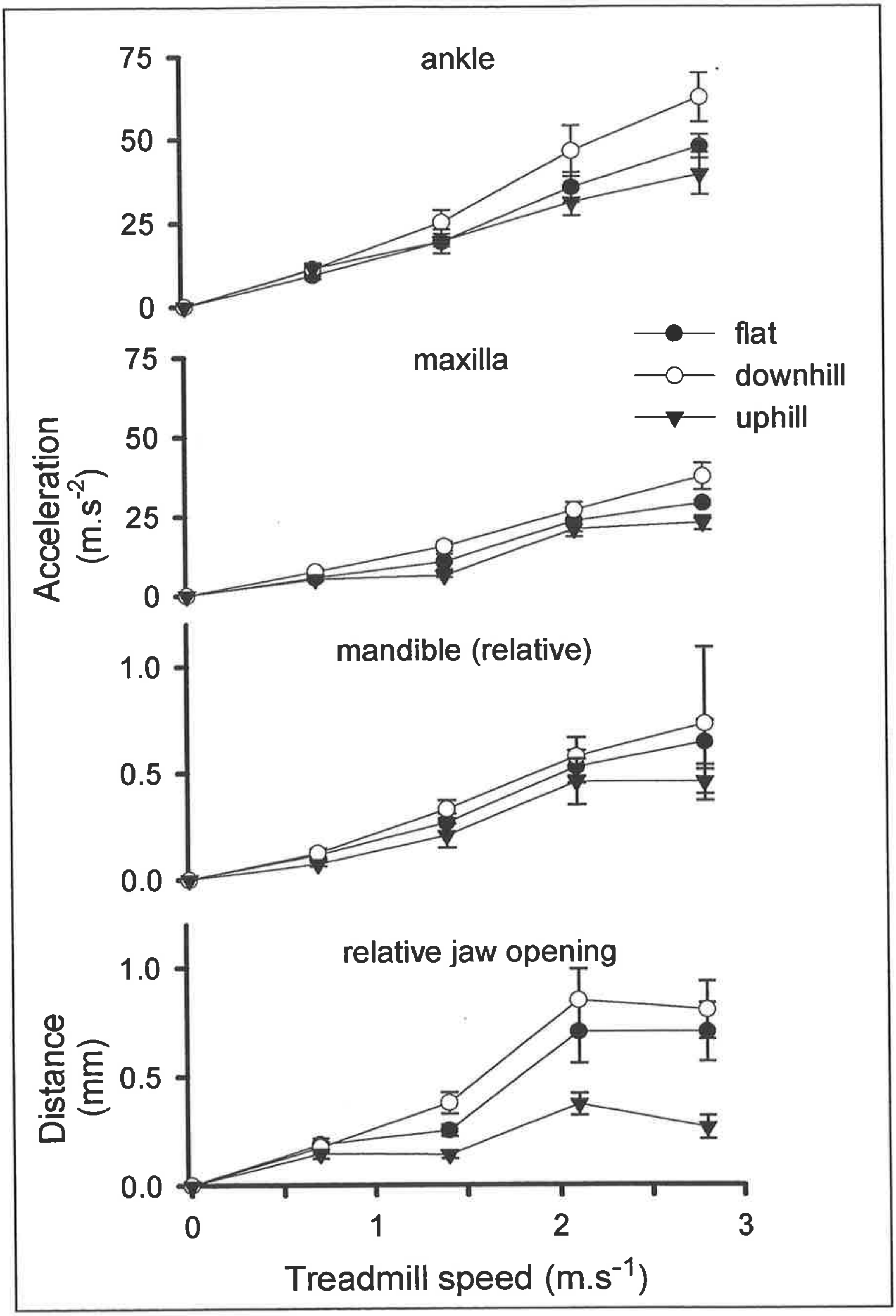

Figure 4.3 ....Group data showing mean (± SE) acceleration of the ankle, maxilla and relative mandibular acceleration, together with mandibular displacement at various speeds of locomotion on level and inclined surfaces. All data points are the average of 12 subjects.

The key measurements for the purposes of this study are the movements of the mandible relative to the maxilla. Fig. 4.3 shows that finite jaw opening and closing movements occurred even during walking. However, despite jaw-opening velocities of more than 20 $m.s^{-1}$ (data not shown), the actual up-and down movements of the mandible occurring even when subjects were running downhill averaged only about 0.8 mm. For both mandible relative acceleration and jaw opening, values at the two lower treadmill speeds differed significantly from values at the two higher speeds (Scheffe's tests, all $P < 0.01$). This corresponded to the speeds at which the gait changed from walking (0.7 and 1.4 $m.s^{-1}$) to running (2.1 and 2.8 $m.s^{-1}$). Differences in mandible relative acceleration or jaw opening were never significant for comparisons between speeds of walking (0.7 *vs.* 1.4 $m.s^{-1}$) or running (2.1 *vs.* 2.8 $m.s^{-1}$) at any slope (Scheffe's tests, all $P > 0.05$).

Mandible relative acceleration was smaller with uphill locomotion than both flat (Scheffe test, $P < 0.01$) and downhill (Scheffe test, $P < 0.001$) slopes. No significant differences were seen between flat and downhill slopes. The same pattern was observed for jaw opening, which was less with uphill locomotion compared with flat (Scheffe test, $P < 0.01$) and downhill (Scheffe test, $P < 0.001$) slopes. Jaw opening did not differ between flat and downhill slopes (Scheffe test, $P > 0.05$).

4.4. DISCUSSION

The active and passive mechanisms affecting the different postures of the mandible have recently been reviewed by Woda et al. (2001). The movements of the human mandible during tasks such as speech and mastication are well documented (Ostry and Flanagan, 1989; Plesh et al., 1993; Koolstra and van Eijden, 1997b; van Eijden, 2000) however, there is only one earlier description of the mandibular movements that occur during locomotion (Shiller et al., 2001). In that study, jaw movements were measured by a series of light-emitting diodes on dental appliances glued to the upper and lower teeth, and the focus was on the relationship of the jaw movements in speech. The present study extends the earlier study by measuring movements of the mandible relative to the head with special-purpose hardware that interferes minimally with normal jaw movements (Flavel et al., 2002), and by relating the movements to the parameters of locomotion under a variety of conditions.

The principal observations in this study are that the mandible moves vertically up and down relative to the maxilla during each step in all forms of locomotion, and that these movements increase on landing as the deceleration of the head increases.

At different speeds, and with different running patterns, the energy transferred from the foot to the skull and thence to the mandible varies markedly. There were marked differences in the amplitude of the acceleration measured at the skull for different speeds and styles of foot landing in walking and running (Fig. 4.3) as found by Rao and Jones (1975), Cappozzo (1981, 1982), Hirasaki et al. (1999) and Pozzo et al. (1990). Light et al. (1980) reported that the acceleration at the ankle increases linearly with speed. This was found also to be the case for both the head alone, and also for the movement of the mandible relative to the skull, whether running on a level or an inclined plane (Fig. 4.3). The acceleration is reduced about 2 to 5-fold from the ankle to the skull which compares with 3.5 fold as reported by Wosk and Voloshin (1981) and 3-fold by Light et al. (1980) and is then halved again from the skull to the mandible.

Heel-first landing in flat and downhill running causes a greater deceleration of the skull, and consequently a greater differential movement of the mandible relative to the maxilla, compared with the toe-first landing that occurs in uphill running (Fig. 4.3). This is presumably because landing on the toes allows some of the contact force to be cushioned by movement about the ankle (*cf.* acceleration measured just above the ankle in Fig. 4.3 for the three treadmill slopes). However, the resulting jaw movements in all forms of locomotion are relatively small in amplitude, and it should be noted that the teeth did not clash together, even during vigorous running.

The mechanisms that limit the extent of vertical jaw movements during locomotion are not clear. The mandible consists of a mass hinged to the skull by various soft tissues including muscles. Hence, passive elastic forces must play some role in limiting these movements. Lynn and Yemm (1971) and Yemm (1975, 1976) proposed a passive mandibular positioning control system in humans. Their model is based on elastic forces holding the mandible in a position that is the equilibrium point of opposing elastic soft-tissue elements and thereby dampening movements. The passive and active components of the masticatory system contributing to muscle contractile forces and corresponding mandible movements have more recently been modelled by Koolstra and van

Eijden (1997b). Their studies showed that all of the jaw-opening and jaw-closing muscles, whether by active contraction or by passive elasticity, together with the non-active biomechanical properties of the temporomandibular joints, contribute to the resting jaw-posture. Peck et al. (2002) have moved the human mandible passively at different velocities, and found that only low forces are required to open the jaw in relaxed humans. After modelling the system, they concluded that jaw muscle viscosity, not elasticity, provides the major resistance to downwards jaw motion in the absence of muscle activity.

It is also possible that reflex activation can contribute to the elevation of the jaw after it moves briskly downwards following landing. The jaw-closing muscles have strong stretch reflexes that work through both short-latency (Lund et al., 1983a) and long-latency pathways (Poliakov and Miles, 1994). Cooker et al. (1980) stretched human jaw-closing muscles sinusoidally and found that up to 50% of the measured stiffness was due to stretch reflex activation of muscle at frequencies between 1 to 8 Hz. However, while there is no direct evidence that reflexes act to maintain human jaw posture during locomotion, bursts of activity in the jaw-closing muscles have been seen with each step in the jaw-closing muscles of cats walking on a treadmill, which suggests that reflexes may contribute to active maintenance of jaw posture in this species (Lund et al., 1984). The present study suggests that increased muscle stiffness, most likely due to reflex muscle activation, reduces the relative mandible acceleration and jaw opening in all subjects tested at treadmill speeds greater than 2.1 ms^{-1}, irrespective of slope.

It is concluded that the human mandible moves vertically during locomotion in a manner that depends on the type and speed of gait. These movements occur over a small range, and the teeth do not normally touch. The mechanisms that are likely to limit the vertical movements include passive soft-tissue elasticity and viscosity and stretch reflexes in the jaw-closing muscles.

The non-linearity of the relationship between relative jaw opening and walking and running speed on the treadmill provides some evidence for active postural control and this will require further investigation.

CHAPTER 5. POSTURAL STABILITY OF THE HUMAN MANDIBLE DURING HOPPING

5.1. INTRODUCTION

The human masticatory system includes the fixed maxilla and movable mandible, teeth, the trigeminally innervated masticatory muscles, and sensory nerves. The muscles are used in the daily activities of mastication, drinking, swallowing, biting and both verbal and non-verbal communication. At rest, and with the head still, the position of the mandible relative to the maxilla remains remarkably constant. This concept of resting jaw posture and the various controlling factors was reviewed by Atwood (1968) and more recently by Woda et al. (2001).

From personal experience we are aware that our teeth do not clash together when we undergo activities such as walking, running and jumping. Systems of control and compensation for movement of linked body segments have been described (Pozzo et al., 1990; Winter et al., 1993; Eng et al., 1995). The nature and magnitude of the forces acting on the skull when undergoing whole body movements have been reported (Grossman et al., 1988; Grossman et al., 1989). However the motions of the mandible and control mechanisms acting to minimise displacement of the mandible during these normal activities have not been described previously in humans due to the lack of suitable techniques available for non-invasive measurements. I have developed a novel, non-invasive technique to measure non-masticatory jaw movements in humans (as described in Chapter 3) to address these issues.

The first aim of the present study was to characterise the movements of the mandible during a natural movement in which there was rapid deceleration of the head. Hopping was selected as a natural task allowing a wide range of head accelerations depending on whether the subject lands on their heel (a hard landing) or their toes (a soft landing). Two general mechanisms may contribute to the maintenance of jaw position in this situation. Control may be neurogenic (either anticipatory or reflex) (Møller, 1976; Taylor, 1976) or non-neurogenic due to the viscoelastic properties of the structures supporting and moving the mandible (Lynn and Yemm, 1971; Yemm, 1975; Yemm, 1976). The second aim of the present study was to determine whether reflexes were elicited in the jaw-closing muscles following the landing, and whether these may help to stabilise mandibular position. Possibilities include stretch reflexes evoked by muscle spindles in the jaw-closer muscles (Matthews, 1964; Matthews, 1976; Møller, 1976; Cooker et., 1980; Lund et al., 1983; Poliakov and Miles, 1994), or vestibular reflexes (Jones, 1992, Tolu and Pugliatti, 1993, Tolu et al., 1994; Deriu et al., 2000) or vestibuloocular reflexes (Grossman et al., 1989).

5.2. METHODS

The study was approved by the University of Adelaide Human Research Ethics Committee and conformed to the standards of the Declaration of Helsinki (1996). The subjects were eight healthy males aged 21 - 51 years with normal dental occlusion and no identifiable neurologic disorders. All gave informed written consent.

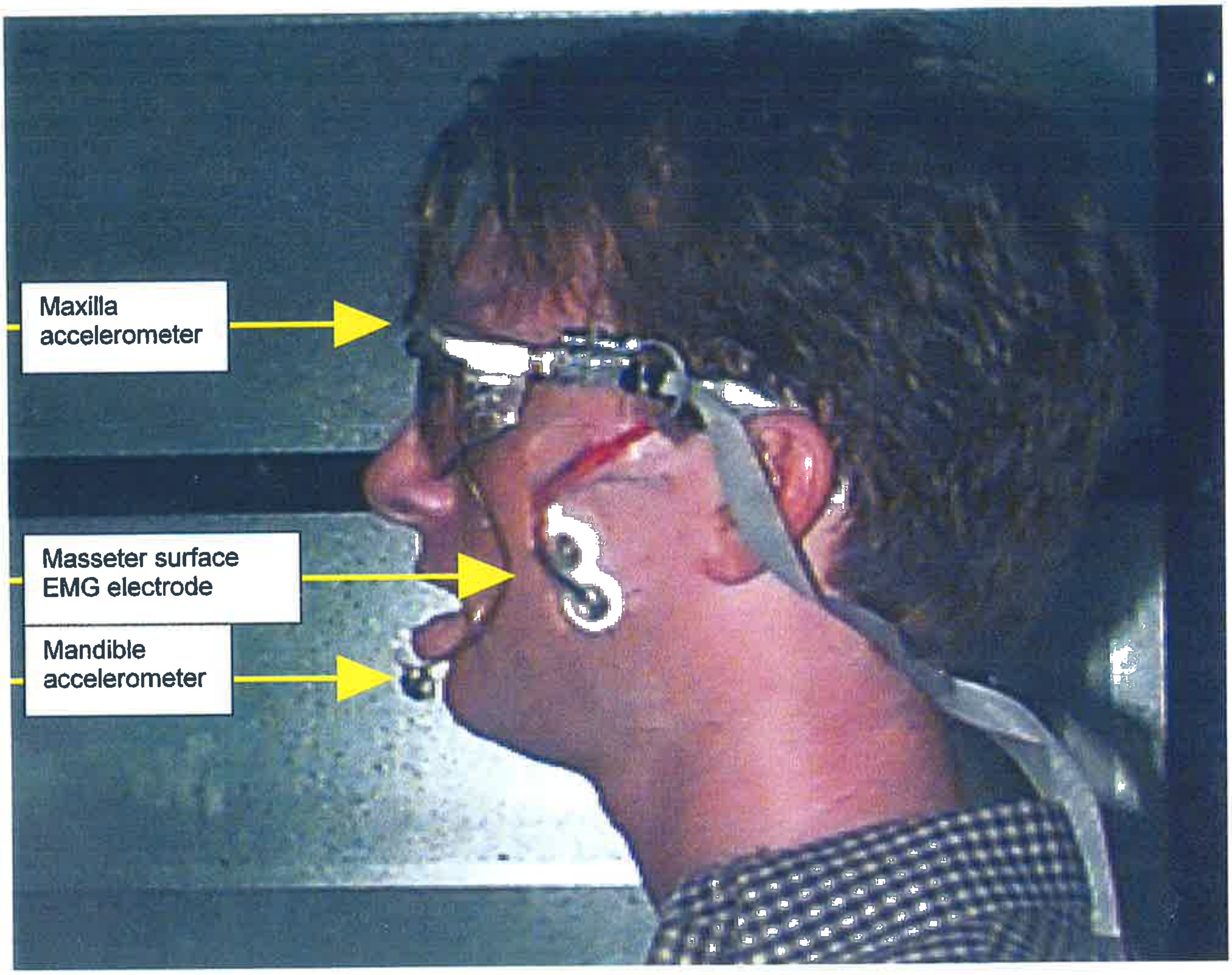

Figure 5.1. ...Subject with instrumentation for recording masseter surface EMG and maxillary and mandibular acceleration.
Adhesive EMG electrode pair (Ag/AgCl, Duotrode) positioned securely on prepared skin aligned with palpated axis of the masseter muscle. Maxilla accelerometer is glued onto the frame of spectacles that fitted the subject's head firmly. Mandible accelerometer is glued to incisor teeth of the mandible.

5.2.1. Acceleration

As described in Chapter 3, the use of miniature accelerometers provided the means of non-invasively detecting the vertical forces acting on the maxilla and mandible. To measure the vertical acceleration of the maxilla in this series of experiments, the subjects wore a pair of close-fitting safety spectacles with an accelerometer firmly attached to the nose-bridge (Fig. 5.1). Mandibular acceleration was detected using an identical accelerometer fixed to a small metal bracket glued to a lower incisor tooth. The sensitive axes of the two accelerometers were aligned vertically and the electrical outputs band-pass filtered (10 to 500 Hz), to remove slow gravitational and body movement artefacts.

Once mounted, the accelerometers were checked for relative alignment and differences in output by having the subjects perform vigorous vertical shaking of the head with the molar teeth occluded. Under these conditions, there should be no relative movement between the two accelerometers and the difference signal (maxilla - mandibular acceleration) should be zero volts. A typical example of raw acceleration records during head shaking, and the difference between the sensor outputs prior to filtering is shown in Figure 5.2.

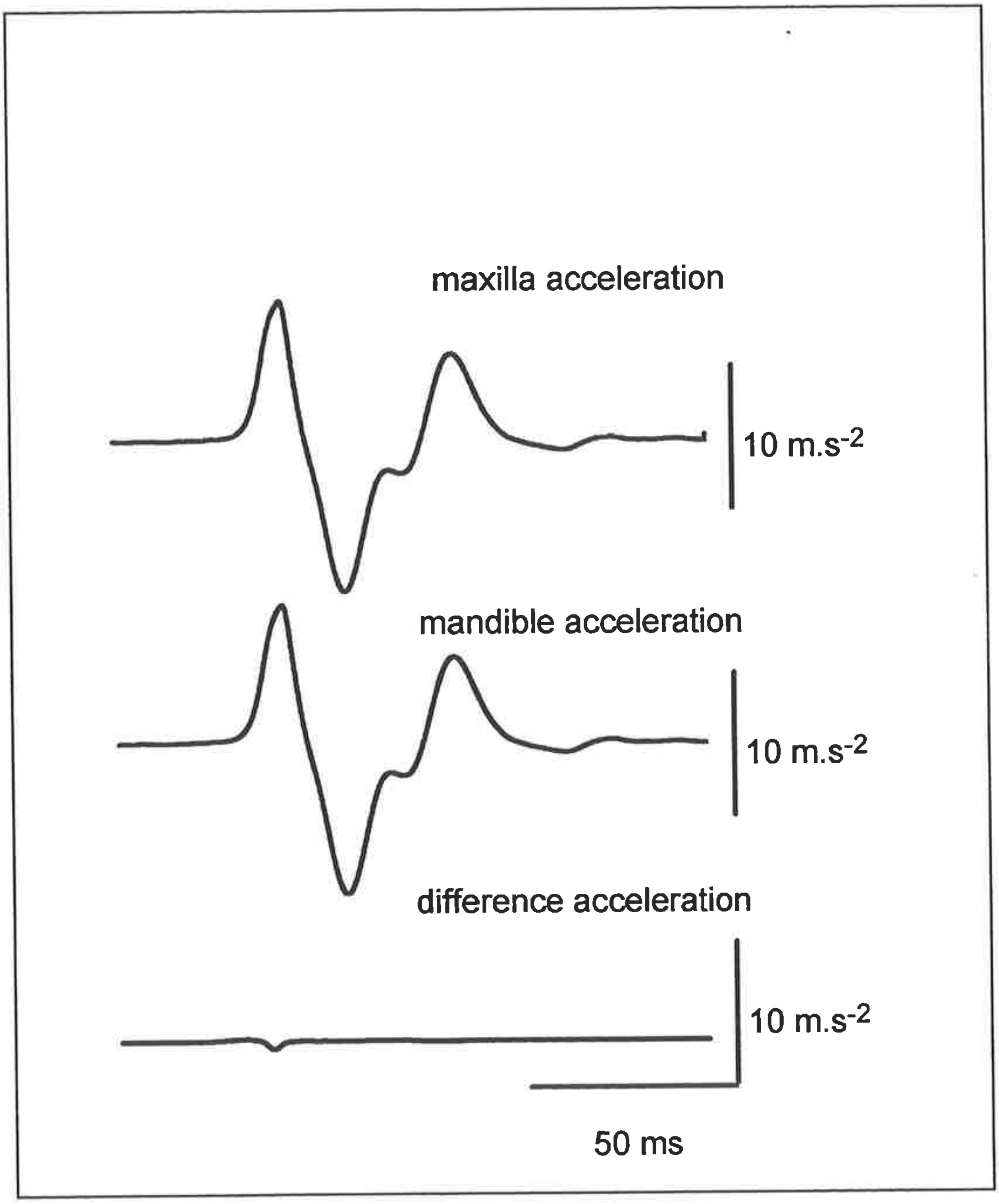

Figure 5.2. Raw accelerometer traces for a pair of matched accelerometers while the subject vigorously nodded the head with the teeth firmly occluded.

This produced brisk acceleration of the maxilla (top) and mandible (middle). The difference acceleration signal shows the relative acceleration of the mandible with respect to the maxilla, obtained by subtracting mandibular from maxillary signals. Under these conditions the difference acceleration was negligible, indicating that the acceleration signals from maxilla and mandible provided a good measure of the relative acceleration of the mandible with respect to the maxilla.

Electromyography

To detect the surface electromyogram (EMG) of masseter muscles, pairs of Ag-AgCl electrodes (Duotrode, Myotronics, California, USA) were placed on the skin overlying the long axis of the masseter muscle and 20 mm apart (Figure 5.1). Fine, lightweight leads from the electrodes were taped to the skin and combined into a low-capacitance multi-stranded lead connecting to remote amplifiers. Signals were amplified (10,000 X) and filtered (sixth order Butterworth, bandwidth 50 to 500 Hz).

The subject was grounded using conductive pads held above both ears by the spectacle arms and connected to the common instrument earth point.

Experiments were conducted within a ventilated and electrically shielded room.

Ground Reaction Forces

Dynamic contact forces generated at the time of foot-strike were detected with a purpose-built force transducer. This was constructed from a one metre long coil of piezo-electric cable (part number 256-809, Radiospares Components, Sydney, Australia) sandwiched between two 10 mm thick steel plates 350 mm x 350 mm. The metal assembly was mounted on a hardwood base. Reference weights dropped from fixed heights were used to calculate the contact forces and to calibrate the electrical output. The electrical output was linearly related to dynamic contact force and was recorded on one channel of the data recorder.

5.2.4. Data Recording

The six analog signals were recorded on a six-channel Pulse Code Modulated/Frequency Modulated data recorder (Model 402, AR Vetter Company, Rebersburg, PA, USA). Surface EMG from both masseter muscles were recorded on the two FM channels (channels 5 and 6; DC to 10 kHz bandwidth) and the four other signals from the forceplate, maxilla accelerometer, mandible accelerometer and difference acceleration on the PCM channels (Channels 1-4; DC to 10kHz bandwidth sampling interval 50 microseconds for each channel).

5.2.5. Validation

Initial experiments were conducted to optimise mounting and positioning of sensors, electrodes and leads connecting to signal conditioning and recording devices. High and low impedance sources to the recording electrodes were simulated using insulating plastic and prepared skin surfaces, respectively. With the recording electrodes in place the subject underwent a range of jumping and nodding procedures and manipulations to subject the electrodes, connections and the skin surface to mechanical stresses. Interference or artefacts caused by the movement of the overlying fleshy skin over the masseter muscle body (resistance change) and/or inductive or capacitive coupling between electrode wires leading to the amplification and recording apparatus were not observed. This follows a method previously described by Miles et al., (1982).

5.2.6. Experimental Protocol

Jaw-jerk Reflex

The jaw-jerk reflex was elicited in the masseter muscle using a tendon hammer to tap briskly downwards on a finger placed on the chin. The responses to 25 trials were recorded with the jaw in the normal resting position and repeated for 25 trials with the jaw closing muscles clenched to approximately 20% of maximum. The timing and delivery of force from the tendon hammer was judged from the output of the mandible accelerometer.

Hopping

Subjects were trained to hop on one leg and land on the force plate. The head was held erect with a forward gaze to a wall-mounted target 2 m in front. Three hopping tasks were performed in a randomised order. For each task, the rate of hopping was maintained at one hop per two seconds using a metronome to provide an auditory cue, for a total of 100 trials. Subjects were rested, and alternate legs used after every 25 hops, to avoid fatigue.

For the first hopping task, subjects were instructed to keep the jaw-closing muscles relaxed and to land on their heel (Heel Landing).

For the second hopping task, subjects were instructed to keep the jaw-closing muscles relaxed and to land on their toes (Toe Landing).

For the third task, subjects landed on their heel while the teeth were clenched together by voluntary activation of jaw-closing muscles including the masseter muscles on both sides (Heel-Landing with clenched teeth). The masseter EMG was approximately 20% of that produced by a maximal voluntary clench and was calculated at the beginning of the trial. No feedback on clench strength was given to the subjects during the trials.

The maintenance of a standard hopping height of 100 mm along with head posture and landing style was visually monitored and errors minimised by verbal feedback given to subjects.

Analysis

At the completion of the experiment, the recorded tapes were replayed and all channels were digitised at the rate of 5,000 samples per second (CED 1401plus computer interface, Cambridge Electronic Design, Cambridge, UK). Resolution of signals was maintained at 13-bit throughout the recording and analysis procedures. Data were stored and analysed in a computer workstation with proprietary software (*Signal* version 1.81, Cambridge Electronic Design, Cambridge, UK). Digitised EMG signals from both masseter muscles were processed to produce full-wave rectified and integrated EMG records.

The distinct negative peak seen in the relative mandible acceleration signal, occurring 10 to 20 ms after toe or heel contact (e.g., Fig. 5.4), was selected as representing a rapid downward (opening) jaw movement. The rapid onset of this jaw movement triggered the averaging process, by which events occurring 300 ms before and after the trigger were ensemble averaged. Each trial was reviewed visually and those containing landing artefacts such as wobble or multiple toe-strike, as evidenced by multiple smaller peak accelerations, were manually excluded from the average.

Latency and peak amplitude of EMG reflex properties were measured by cursors using the Signal analysis program from the averaged waveforms. Data are reported as mean ± SD unless otherwise indicated.

5.3. RESULTS

A short latency jaw-jerk reflex was readily evoked in the masseter muscles of all subjects following a tap on the chin from a tendon hammer. The onset latencies of the masseteric reflex for each subject are reported in Table 5.1. When clenching at a level of 20% MVC the tap of the tendon hammer produced only a small difference acceleration and no evidence of an transient increase in muscular electrical activity above baseline.

	Latency of reflex (ms)	
Subject	Jaw-jerk	Hopping
A	7.3	7.4
B	7.5	7.8
C	7.3	7.6
D	7.6	8.1
E	7.6	7.8
F	7.3	7.6
G	7.9	7.7
H	7.2	7.9
Mean	7.4	7.7*
SEM	0.24	0.84

*indicates significant difference (paired t-test, $P < 0.02$, 7df.).

Table 5.1 .....Latencies of reflexes evoked in the masseter muscles of 8 subjects.

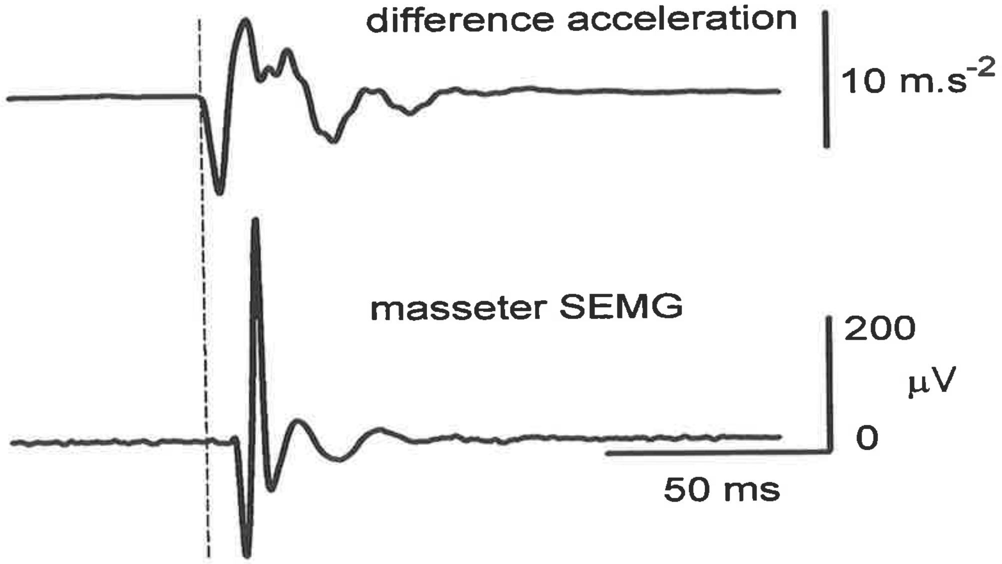

Figure 5.3 Jaw-jerk reflex in masseter.
The averaged (n = 25) mandible difference acceleration and masseter surface electromyogram (SEMG) are shown for one subject. Traces aligned to onset of the mandibular acceleration. A jaw-jerk reflex in masseter was evoked in this subject with a latency of 7.5 ms.

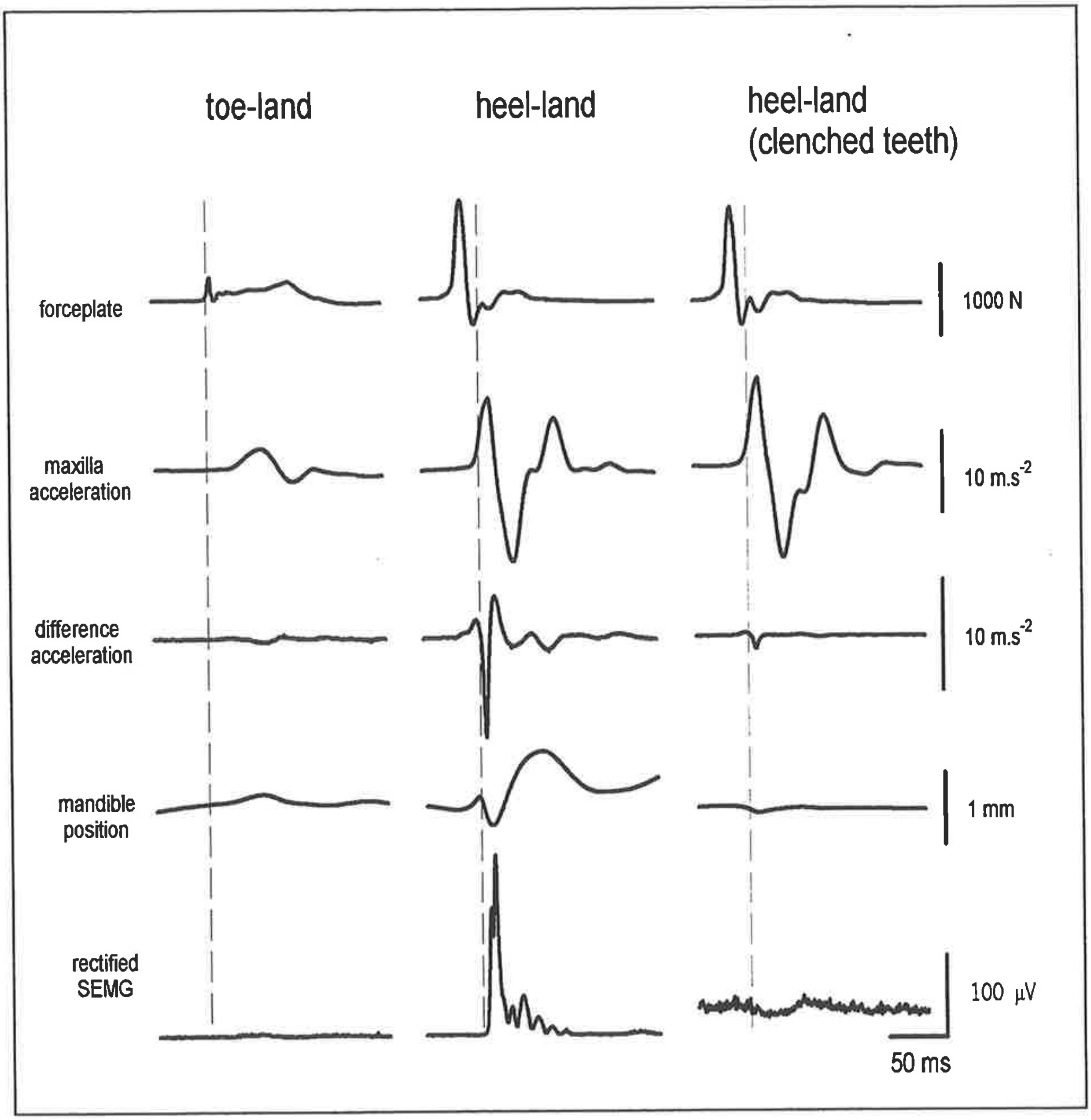

Figure 5.4 Representative examples of the kinematic and EMG data obtained from one subject during the three hopping tasks.
Typical averages obtained from 100 hops. Vertical dotted line shows trigger point for ensemble averaging.

During Heel Landing with masseter muscle relaxed (Fig. 5.4 centre panel) there was a large reaction force measured at the forceplate as the heel struck the ground. This force propagates through the body to be measured by the accelerometer on the maxilla. The mandible difference acceleration shows a slight upward movement of the jaw, followed by a rapid acceleration downward (opening). This rapid downwards acceleration was used to trigger the ensemble average (vertical dashed lines) by setting an amplitude threshold crossing by visual inspection of single trials. In this subject, the mandible relative position undergoes an initial closing of 0.15 mm, then a jerk open (downwards after dotted line) of 0.3 mm followed by a closing movement of 0.95 mm peaking approximately 50 ms after the onset of the brisk downwards acceleration of the mandible.

In this subject, and all others tested, heel landing with the masseter muscles relaxed elicited a synchronous EMG reflex response in masseter that was time-locked to the brisk downwards acceleration of the mandible relative to the maxilla following landing. For the subject shown in Fig. 5.4 the latency of this reflex was 7.5 ms after the first detectable difference in downwards acceleration of the mandible with respect to the maxilla (dashed vertical line).

The peak to peak amplitude of the reflex responses for all subjects with Heel Landing was between 40 and 270 μV and lasted 10 to 50 ms as seen by the envelope of the rectified EMG signal. The mean onset latency of the reflex was 7.7 ± 0.8 ms (Table 5.1), which was slightly but significantly longer than the latency of the jaw-jerk reflex in these subjects (paired t-test; $P < 0.02$).

The peak activation of masseter muscle (measured from rectified EMG records) causing jaw closing (mandible elevation) occurred 50 ± 10 ms from the start of the reflex. The mandible moved upward in response to the jaw-closing muscle contraction and then returned to a similar resting position 50 to 100 ms later. There was often a small hysteresis in position.

The responses to heel-landing with the teeth clenched are shown in the right hand panel of Fig. 5.4. The force-plate and maxilla accelerations are comparable with the heel landing with the jaw muscles relaxed. With the masseter muscle active, however, there is greatly reduced mandible difference acceleration after landing. The mandible position shows a small opening movement (downwards) of 0.05 mm from the clenched position. The mean rectified surface EMG remains constant (35 to 40 μV) before and after landing, with no evidence of any anticipatory increase prior to landing, or synchronous reflex activity after landing. These data indicate that the masseter EMG response after landing is related to mandibular difference acceleration (which would stimulate muscle spindles in masseter), and not acceleration of the head (which would stimulate vestibular afferents).

The data obtained with toe-landing and relaxed jaw muscles are shown in the left panel of Fig. 5.4. The ground reaction force and maxilla acceleration is attenuated by landing on the toes compared with the heels. There is a negligible mandible difference acceleration following toe-landing. Because of this, the trigger used for the ensemble average with toe landing was the foot striking the force-plate (dashed vertical line). The mandible shows a small (0.1mm) closing (upward movement) of jaw followed by a small (0.15 mm), slow opening (downward movement). The mandible returns to pre-landing position within 100 ms. Landing on the toes during hopping produced no short or long latency reflex activity in the masseter muscle (Fig. 5.4 - left, bottom trace).

5.4. DISCUSSION

In this study each subject was displaced bi-directionally along their vertical axis by jumping and landing on the spot. The acceleration and deceleration measured before and after landing show that the suspended mandible decelerates more slowly than the skull that it is suspended from. The result is that the mandible rotates at the temporomandibular joint and the tissues supporting the jaw are stretched. The elongation is relatively small (less than 1mm displacement of the lower incisors from the maxilla) and transient, lasting typically less than 50 milliseconds for all subjects. The relative movement of the mandible is greater when landing on the heel than landing on the toe or when landing on the heel with the teeth mildly clenched together. There was an associated transient increase in electrical activity in both right and left masseter muscles in situations where the jaw-closing muscles were sufficiently stretched and this occurred within 10 milliseconds of the downward acceleration of the mandible. The evidence suggests that this is a stretch reflex helping to arrest the downward movement of the mandible and return it to the pre-landing position. There was no evidence for anticipatory adjustment of jaw muscle activity, or vestibular reflexes, in the maintenance of mandibular position during hopping.

There are no previously reported techniques to measure the small movements of the mandible in a freely moving human with sufficient time and spatial resolution to track the reaction forces from the foot to rapid mandible movements and associated changes in masseter muscle surface electromyograms. Unlike data obtained from the maxillary accelerometer in earlier experiments (Chapter 4) in these earlier experiments the measuring transducer device was firmly fixed to goggles rather than as a direct connection to a maxillary tooth. Although this could have been a potential source of errors if slip occurred between goggles and face, valid records of the difference acceleration were obtained (Fig. 5.2), indicating that the technique was reliable.

The magnitude of accelerative forces measured at the foot (30 to 50 $m.s^{-2}$) and head (10 to 35 $m.s^{-2}$) during hopping are greater than the findings of Cappozzo (1981, 1982), Le Pellec and Maton (1999) and Shiller et al. (2001) who studied these forces during stepping and walking. Transmission time of the foot reaction forces through the body to the skull was constant for each subject, at 10 to 15 ms and varied less than 2 ms between hops. These data are comparable with previous findings and indicative of a constant path of the forces and the attenuating anatomical elements (Rao and Jones, 1975; Cavanagh and Lafortune, 1980; Light et al., 1980; Wosk and Voloshin, 1981; Pozzo et al., 1989; Pozzo et al., 1990). There is limited published information on human jaw movements whilst hopping or walking, however lower precision optical methods have been used to record jaw movement variation during speech whilst treadmill walking (Shiller et al., 2001) or seated (Zafar et al., 2002). Studies on the vibration transmission to the jaw in seated humans using accelerometers

(Hashimoto and Clark, 2001) and jaw kinetics using magnetic sensors (Christensen and McKay, 2000) have been reported.

When not being actively used for chewing and speech the human mandible remains suspended in a stable resting position such that the teeth are not in contact. The nature of the forces acting to keep the mandible in a stable resting position has been greatly debated with evidence of two mechanisms for controlling jaw posture.

Active mechanisms

Møller (1976) proposed a reflex driven, active, servo-system using muscle spindle based feedback. It was proposed that spindles are sensitive to small stretch displacements and load variations and that their afferents would excite alpha motoneurons supplying the jaw-closing muscles (Lund et al., 1983). This active mechanism would support the mandibular position against gravity using continuous modulation of low levels of muscular electrical activity. This is consistent with the observation that jaw-elevator muscles continually show small amounts of asynchronous muscle activity in the order of 5 to 20 μV from surface EMG recordings under moderate perturbations of gravity and vertical movement (Michelotti et al., 1997). A comprehensive review by Watkinson (1987) concludes that the mandibular rest position representing minimal muscle activity has a greater occlusal distance of 4.5 to 7 mm, compared to the conventional clinical rest position with average 2 to 6 mm occlusion.

Passive mechanisms

Lynn and Yemm (1971) described a passive mandibular positioning control system in humans. They postulated a system based on elastic forces dampening movement and holding the mandible in a position that is the equilibrium point of opposing elastic elements in muscle and tissue. The evidence supporting this idea comes from three observations. The first is that the elastic properties of inactive jaw-closing muscles can lift the jaw as the jaw opening muscles are gradually relaxed (Lynn and Yemm, 1971; Yemm, 1975). The second is that jaw opening can only occur by activation of jaw-opener muscles while the much stronger jaw-closers are almost completely inactivated (Yemm, 1976, Yemm and Nordstrom, 1974). Third, in studies of jaw-opening and closing muscles, disabled by lesions or anaesthetics, a considerable force is still required to move the mandible in either direction from the resting position. (Yemm and Nordstrom, 1974)

The regulatory mechanisms and clinical implications of mandibular posture have been extensively reviewed by (Woda et al., 2001) who concluded that the variability of mandibular position is due to both active and passive forces acting with head posture being of great importance.

The components of the masticatory system and corresponding mandible movements have been modelled to show that resting jaw posture is the result of both the cumulative active contractile and passive elastic forces of all of the jaw-opening and jaw-closing muscles (Koolstra and van Eijden, 1997a, b).

There is much published work on the movement of the mandible and elaborate models of the kinematics and biomechanics of the jaw during speech and mastication have been developed (Ostry and Flanagan, 1989; Hannam and McMillan, 1994; Koolstra and van Eijden, 1997b, 1999).

In humans, tapping on the mandible with a tendon hammer elicits a short-latency excitatory reflex in both the masseter and temporalis muscles. This monosynaptic reflex, although analogous to the limb stretch reflex, has a latency of 7 to 12 ms due to the short conduction distance (Lamarre and Lund, 1975; Aramideh and Ongerboer de Visser, 2002).

Short-latency reflexes and rapid muscle twitch activation may be sufficient to arrest downward movement of the mandible and actively return the mandible to close to the former resting position after landing from the hop (Lamarre and Lund, 1975). This may be compared with the findings of Cooker et al. (1980) who, using sinusoidal stretches applied to human masseter muscles, found that up to 50% of the measured stiffness was due to stretch reflex activation of muscle for stimuli between 1 to 8 Hz. The slight error in muscle returning to a prior position seen in the present study has been reported after lateral stretches by Rugh et al. (1989).

The position record shows that active lifting (elevation) of the mandible occurs but without teeth contact. The upward mandibular movement following landing is not the result of purely elastic forces, which would rather show a symmetrical and damped oscillation. The lack of tooth contact would exclude periodontal mechanoreceptor excitation as a stimulus for the masseter reflex activity (Brodin et al., 1993).

Eriksson et al. (1998) and Zafar et al. (2002) demonstrated that slow head movements had a concomitant steady jaw opening and closing. In this experiment there was minimal head movement except in the vertical axis which would preclude trigemino-cervical coupling.

The difference in SEMG activity after hopping with teeth occluded vs. apart (Fig. 5.4) must exclude the involvement of oculo-vestibular and vestibular reflexes because in both cases the vertical forces acting on the maxilla and mandible were identical and the reflex was present with the teeth apart (when the mandible was free to move downwards), and not seen with the teeth clenched. In any event the measured latencies are much shorter (7.7 ± 0.8 ms, this report) than sternocleidomastoid reflexes (24 ± 0.7 ms) (Aoki et al., 2001), vestibular reflexes (67 to 78 ms) (Bishop et al., 1984; Hickenbottom et al., 1985; Rodenburg et al., 1985), vestibulo-cortical reflexes (60 ±3 ms) (Deriu et al., 2000, Deriu et al., 2002). Similarly the corneo-mandibular reflex (73.3 ± 7.4ms), corneal reflex (36 to 64 ms) and vestibulo-ocular reflex (9 to 20ms) all reported by Aramideh and Ongerboer de Visser (2002) are of significantly longer duration.

In the same manner the masseter reflex latency is also too short for it to be the consequence of stretch reflexes occurring in lower limbs as a result of the landing, which are in the range 70 to 100 ms (Melvill Jones and Watt, 1971a; Melvill Jones and Watt, 1971b; Greenwood and Hopkins, 1976a ; Greenwood and Hopkins, 1976b)

The reflex from the downward acceleration of the mandible relative to the skull has a latency of 7.7± 0.8 ms which is slightly larger than the standard jaw jerk reflex (7.4 ± 0.2 ms), elicited in these subjects with the tendon hammer (Table 5.1). A paired t-test shows this difference to be significant ($p < 0.02$, df = 7).

Latency differences are statistically significant yet this may be not be indicative of different excitatory pathways. The delivery of the tendon hammer stretch stimulus is more rapid and synchronised to all spindles within the masseter muscle, and this could provide slightly shorter response in masseter motoneurons due to the faster rise of the compound excitatory post-synaptic potential.

The nature of this reflex (fig 5.4 and Table 5.1) strongly suggests that it is a monosynaptic stretch reflex caused by brief, rapid downward displacement of the mandible stretching the masseter muscle. Poliakov and Miles (1994) reported displacement speeds in the order of 20 to 50 mm s^{-1} were required to produce a short-latency reflex in the masseter. Thus mandibular velocities resulting from heel landing (12 to 45 mm. s^{-1}) are in the right range to activate spindles and produce masseteric stretch reflex whereas the recorded velocity range of 2 - 20 mm .s^{-1} from toe-landing is below the threshold for spindle activation of a stretch reflex reported by Poliakov and Miles (1984).

Controlled stretches applied to human jaw muscles have demonstrated both short- and long-latency reflex activities in jaw-closing muscles. Marsden et al. (1976) first showed long latency (35 to 80 ms) reflexes in jaw closing muscles, evoked by slow mechanical stretches. A transcortical, polysynaptic pathway is a proposed reason for the longer latency component, although studies of the masseter LLSR find no evidence supporting this hypothesis (Luschei and Goldberg, 1981; Pearce et al., 2003). Poliakov and Miles (1994) showed that smooth, slow stretches reliably evoke long-latency (35 to 50 ms) stretch reflexes while rapid stretches evoke primarily short-latency (7 to 10 ms) reflexes in human jaw-closing muscles. In this study there is no evidence of longer-latency stretch reflexes in any of the three types of landing.

When a subject lands heel-first with the mandible held in a mild clench, the downward vertical forces acting on the mandible are the same as those on the passively supported mandible. The stiffness of the voluntarily contracted jaw-closing muscle is sufficient to abolish or minimise downward movement of the mandible. The reduced stretch on jaw-closing muscles produces no evidence of short- or long-latency reflex activity. This is in contrast with the findings of Lobbezoo et al. (1993) who showed that various clenching tasks increased the reflex amplitude of temporal muscles in man when subjected to mechanical jaw jerks. motoneuronIt was shown by Godaux and Desmedt (1975a, 1975b) that the amplitude of the jaw stretch reflex as measured by surface electromyography, increases in partially contracted jaw elevator muscles but actually decreases if the jaw opening muscles are fully contracted prior to the tap. The amplitude of this reflex is proportional to the strength of stimulus and to any tonic stretch applied to the muscle. The size of the reflex is proportional to the excitability of the motoneuron pool, as has been demonstrated in a number of studies (Matthews, 1976; Lund et al., 1979; Lund et al., 1983a; Miles et al., 1995).

In the present study the force of the clench was about 20% of maximal voluntary clench EMG which prevented mandible displacement on landing and no stretch reflex was recorded.

5.5. CONCLUSION

Short-latency stretch reflexes were reliably and consistently elicited in masseter muscle when human subjects performed movements that involved a rapid vertical displacement of the mandible. These stretch reflexes are capable of evoking a rapid muscle twitch causing a rapid elevation of the mandible. The position records show no evidence of actual tooth contact and the mandible returns close to its resting position within 200 milliseconds.

The novel techniques developed for this study may prove important in aiding our understanding of other complex, whole-body movements such as running and jumping. In the sense that the body is continually protecting sensitive components from the hard impacts of landing, it is now possible to monitor the dynamic effects of different running styles and footwear on head and jaw posture.

CHAPTER 6. SUMMARY AND CONCLUSION

These studies have investigated some of the effects of whole body movements such as one leg hopping and treadmill walking and running at positive, negative and neutral slopes. Movement records from the head and mandible demonstrate a remarkable ability of the masticatory muscle to maintain a stable mandibular position relative to the maxilla (Chapter 4). These findings are supportive of the hypothesis that the mandibular posture is maintained by a combination of passive forces during slow non-jarring actions such as soft landing on the toes at slow movement speeds. As harder landings from hopping or as speed over-ground increases the increased reaction forces jolt and jerk the mandible and thereby stretch the masseter. This results in short latency (7.7 ms) stretch reflexes in the masseter surface EMG. This observations suggests that that stretch reflexes participate in maintaining a stable mandibular position during whole body movements. (Chapter 5).

These investigations were made possible by the development of a novel system for measuring acceleration of the head and jaws, and relative displacement of the mandible from the maxilla in a freely moving human (Chapter 3). Longer term and overnight studies on jaw movement during bruxism and apnoea events are now possible.

Further study is warranted to investigate the involvement of other masticatory muscles (e.g. temporalis and medial pterygoid) in jaw postural stability. Likewise the effects of a wider range of whole body activities including sporting, jumping and acrobatic activities may be investigated with the techniques and equipment I have developed.

The impacts of different footwear and running styles is of importance in the attainment of superior and more competitive running styles with the potential for detecting extreme forces and thus indicating preventative measures to minimise long-term damage to the skeleton, spine and head.

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