Context Dependent Adaptation of Biting Behavior in Humans

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ABSTRACT

The focus of this thesis was to study an action that humans perform regularly, namely, to hold a morsel between the teeth and split it into smaller pieces. Three different issues related to this biting behavior were addressed: (1) the effect of reduced periodontal tissues on food holding and splitting behavior; (2) the behavioral consequences of performing different bite tasks with different functional requirements, i.e., to split a peanut half resting on a piece of chocolate or to split both the peanut and the chocolate; and (3) the reflex modulations resulting from such a change in the intended bite action. The main conclusions from the experimental studies were the following:

First, periodontitis, an inflammatory disease that destroys the periodontal ligaments and the embedded periodontal mechanoreceptors, causes significant impairments in the masticatory ability: the manipulative bite forces when holding a morsel are elevated compared to a matched control population and the bite force development prior to food split is altered. These changes are likely due to a combination of reduced sensory information from the damaged ligaments and to changes in the bite strategy secondary to the unstable oral situation.

Second, people exploit the anatomy of jaw-closing muscles to regulate the amount of bite force that dissipates following a sudden unloading of the jaw. Such control is necessary because without mechanisms that quickly halt jaw-closing movements after sudden unloading, the impact forces when the teeth collide could otherwise damage both the teeth and related soft tissues. Splitting a piece of chocolate, for instance, regularly requires >100N of bite force and the jaws collide within 5 ms of a split. On the other hand, when biting through heterogeneous food, the bite force needs to be kept high until the whole morsel is split. The required regulation is achieved by differentially engaging parts of the masseter muscles along the anteroposterior axis of the jaw to exploit differences between muscle portions in their bite force generating capacity and muscle shortening velocity.

Finally, the reflex evoked by suddenly unloading the jaw—apparent only after the initial bite force dissipation—is modulated according to the bite intention. That is, when the intention is to bite through food items with multiple layers, the reflex response in the jaw opening muscles following a split is small, thus minimizing the bite force reduction. In contrast, when the intention is to rapidly decrease the bite force once a split has occurred, the reflex response is high. This pattern of reflex modulation is functionally beneficial when biting through heterogeneous food in a smooth manner.

The presented studies show the significance of integrating cognitive, physiological and anatomical aspects when attempting to understand human masticatory control.
PUBLICATIONS ON WHICH THIS THESIS IS BASED

This thesis is based on the following published studies that will be referred to by their roman numerals.


INTRODUCTION

Background

Mastication is the first part of digestion where a series of jaw movements causes solid food to be handled, broken down and reassembled into a swallowable bolus. The masticatory motor behavior is usually divided into three main stages each comprising a series of characteristic opening and closing jaw movement cycles (Jean 2001; Lund 1991; Schwartz et al. 1989). In the first preparatory or manipulative stage food is brought to the mouth and split by the anterior teeth into smaller pieces. In the second grinding or reduction stage the food is mixed with saliva for softening and lubrication while it is further broken down by the action of premolar and molar teeth. The third pre-swallowing or oropharyngeal stage occurs at the end of mastication when the crushed food particles are reassembled into a cohesive paste “ready-to-be-swallowed” and transported towards the oropharynx by activity in the digastric, hyoidal, pterygoidal and tongue muscles (Jean 2001). Although a full range of functionality in the masticatory system might not be of vital importance from a nutritional viewpoint, adequate functionality promotes general well-being since both palatability of food and eating is recognized as an important component of life satisfaction (Brennan et al. 2008).

The anatomical and aesthetic outcomes of various oral therapies can usually be reliably evaluated. This is, however, not yet true for clinical outcomes in terms of masticatory function (Woda et al. 2006). A more detailed understanding of the human masticatory system and its control is required to develop effective clinical routines for assessing masticatory function. This thesis focuses on the control and regulation of the initial preparatory stage of mastication, during which food is manipulated in the mouth, positioned between the teeth and then split.

Neural control of biting

We regularly use the teeth for precision actions such as holding and manipulating objects and foods. The jaws also perform powerful actions when we break hard and dry foods that require high compressive stresses. In particular, during the manipulatory stage of mastication, we split food into smaller pieces with the anterior teeth. Depending on the size of the morsel, such splitting maneuvers require different forces and occur at different jaw gapes. Accordingly, the jaw muscles must be able to generate forces of various magnitudes at different jaw openings and at the same time balance the force vectors such that the food object remains between the teeth. But importantly, not only do the jaw muscles sometimes need to generate large
forces (>200N), they also need to quickly dissipate these forces. At the instance of split, when the reaction force provided by the food resistance suddenly disappear, the high muscle tension in the jaw closing muscles forcefully accelerates the lower jaw in the closing direction. If this force is not rapidly dissipated, potentially harmful collisions can occur between the dental elements.

For heuristic purposes, the bite act can be divided into three sub-stages according to the temporal sequence of bite force change: First, a morsel is explored and held between the teeth. Second, the bite force increases until the morsel splits, and third, during the post-split stage, the jaw quickly moves towards occlusion. Each of these sub-stages deserves a more detailed description.

During the first sub-stage, the properties of the food objects are determined by exploratory behaviors (Dan et al. 2007), e.g. to assess the magnitude of the force needed to overcome the physical resistance of the food. Furthermore, during the last part of this sub-stage the morsel is positioned and held optimally between the teeth to avoid object slip once the bite force is increased. Once a stable morsel position between the teeth has been achieved, the bite force increases. During this period the forces are controlled so the resultant force vectors pass through the object, thereby assuring a stable food holding situation. How this precise force increase is regulated is largely unknown, but experimental studies suggest that periodontal mechanoreceptors contribute. Indeed, by using an intraoral manipulation-and-split task, Svensson et al. (2013) showed that people having dental implants or local anesthesia of the periodontal ligament performed significantly worse and with higher failure rates compared to healthy controls. Furthermore, the bite force rate seems to be regulated depending on food properties (Svensson and Trulsson 2009) and periodontal status (Paper I, Johansson et al. 2006). That is, with more brittle food a lower rate of bite force increase is applied as compared with less brittle food and people lacking periodontal tissue support show a stuttering and hesitant behavior prior to the morsel split.

Once the object splits—often at an unpredictable bite force—the mandible accelerates in the closing direction. To split a chocolate piece ~5 mm thick with the incisors often requires >100N force, yet the teeth rarely collide forcefully when the chocolate suddenly fractures. Without mechanisms that quickly attenuate jaw movements after sudden unloading, impact forces would not only cause discomfort but could damage teeth as well as oral soft tissues. Indeed, the impact energy needed to split a raw carrot (~200 J/m²) is similar to that required to fracture healthy enamel (Rasmussen and Patchin 1984; Vincent 1990).
Three proposals have historically been forwarded to explain the fast attenuation of the jaw closing force once the object breaks:

i) **co-contraction** by the jaw opening muscles,

ii) **reflexes** elicited by the sudden unloading, and

iii) **intrinsic muscle properties** such as force-length-velocity relationship.

Co-contraction is not a viable explanation because the jaw opening muscles cannot produce sufficient muscle force (van Willigen et al. 1997). Reflex mechanisms are also not viable because their latencies are far too long given that the force reduction is completed within 10 ms of the split event.

Accordingly, it was concluded that the main explanation for the rapid reduction of the jaw closing force is the force-velocity properties of the jaw closing muscles, i.e., the fact that the force generated by skeletal muscles decrease with increasing shortening velocities (Nagashima et al. 1997; Slager et al. 1997; van Willigen et al. 1997). But other factors do influence the residual forces including the bite force itself at the moment of split (Fig. 1A) and the jaw travel distance to impact following unloading (Fig. 1B). Note that at travel distances beyond ~3mm not much additional force is dissipated.

The very significant initial reduction in bite force following a sudden split of a food morsel are followed by bite force changes due to reflex mechanisms that come into play with latencies of ~10-15 ms, i.e., the so-called “sudden unloading reflex of the jaw” (Hannam et al. 1968; Karkazis et al. 1993; Miles and Wilkinson 1982; Turker and Jenkins 2000; Yamada and Haraguchi 1995; Yoshida 1998). These and other jaw-related reflexes are discussed in more detail below.

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**Figure 1. Influence of bite force and jaw travel distance on residual force.**

A, The bite force present before unloading influences the amount of residual force which is the epoch of force increase following unloading when the teeth contact an underlying surface. Colored lines represent different bite forces preceding the unloading and the corresponding residual forces. Gray sections in force traces represents the period when the jaw is unloaded. B, The residual force following an unloading of the jaw is also influenced by the travel distance of the jaw before it is arrested. Colored lines represents the residual force as a function of jaw travel distance at different bite force levels. Note at approximately 3mm of jaw travel the increase in residual force attenuates.
Motor programs

A series of motor commands – called a motor program – is executed to accomplish a biting maneuver. When executed, a motor program is presumed to be continuously updated via feedback from peripheral sensors, e.g. regarding bite force levels and vector alignments. Central pattern generators (CPGs), responsible for the motor program in grinding and pre-swallowing phases are located in the lower brainstem. The CPGs receive central and peripheral inputs and are engaged in both feed-forward and feed-back control (Lund 1991). However, for the manipulatory stage, which includes biting, direct control from higher centers, i.e. sensorimotor cortex, is more important (Enomoto et al. 1987).

There is a recognizable need for regulation of the oral motor system when performing a bite from the initial food contact to the breakage of the food piece and the subsequent post-split control of the jaw closing force. However, the precise mechanisms for this control are unknown (Türker 2002; van der Glas et al. 2007). Part of the reason for this is that behavioral experiments typically stimulate more than one receptor system at the time (Türker 2002). Nevertheless, it is believed that much of the oral motor control relies on multi-modal sensory information, i.e. parallel information from periodontal, cutaneous and mucosal mechanoreceptors, muscle spindles, and joint receptors in addition to auditory information (Johansson et al. 1988; Lobbezoo et al. 2006; Lund 1991; Türker 2002).

Muscles in general

Motor-units and fiber types

Skeletal muscle is the most common muscle type in the body and its characteristic cell type is myocytes, also known as muscle fibers.

The basic functional unit of a muscle is a motor unit. These consist of a single motoneuron with its cell body in the spinal cord and the muscle fibers that, in an adult, are exclusively innervated by this neuron. The motor units comprising a muscle typically vary significantly with respect to their force output, fatigability, and contraction speed (Burke 2011). A motor unit's ability to produce force is proportional to its cross-sectional area, which in turns depends on the number and cross-sectional areas of the constituent muscle fibers.

The biomechanical and functional properties of a specific muscle are highly dependent on the physiological properties of its motor units. Muscles used to control fine movements typically contain fewer muscle fibers per motor unit than muscles involved in coarser movements or those regularly generating large forces.
In short, muscle fibers can conveniently be classified into two main types: type I are slowly contracting and fatigue resistant whereas type II are fast contracting but fatigable. The type I fibers are commonly smaller and thus produce less force when activated and they are also the ones first recruited. The molecular basis for the differences between muscle fiber types are well known. The muscle fibers contain filaments whose interaction is the basis for force production. These filaments—myosin (thick) and actin (thin)—exist in several isoforms (i.e., proteins which have similar properties but are encoded by a different gene) in different muscle fibers that, in turn, gives rise to specific characteristics regarding ability to perform contraction. Accordingly, muscle fibers are often categorized by the speed of contraction and their ability to withstand repeated contraction (fatigability). The contraction speed of a motor unit is largely dependent on the specific myosin protein in the muscle fibers, because myosin isoforms differ in their rate of converting ATP into energy, which in turn determines the speed of actin-myosin detachment. There is a good correlation between the myosin isoforms and the maximum contraction velocity of fibers (Bottinelli et al. 1991). Small motor units are predominantly composed of myosin isoforms with less ability to convert ATP to energy than larger motor units (i.e. small motor units are often slow contracting motor units). The ability to resist fatigue is dependent on the metabolic properties of the fibers. Muscle fibers of fatigue resistant motor units contain a substantial amount of aerobic end-oxidation enzymes. In contrast, fibers of fatigable motor units are rich in glycolytic enzymes and low in enzymes of aerobic oxidative metabolism.

Motoneurons in the spinal cord are excited and inhibited via specialized connections between cells, called synapses. If a motoneuron is sufficiently excited (depolarized) it delivers action potentials that ultimately leads to activation of its associated muscles fibers and cause them to contract. Because the input resistance is larger in small than in large neurons, more current (i.e., stronger ‘activation’) is necessary to activate large neurons than small neurons and this is true for all neurons whether motoneurons or spinal interneurons. This give rise to the size principle (Henneman et al. 1965), i.e., that motor units are recruited in order of increasing size whatever measure of ‘size’ is used, e.g., motoneuron soma size, axon caliber and axonal conduction velocities. With everything else equal, motor units within a pool are recruited in a strict sequential order with increasing excitation to a pool and de-recruited in the reverse sequence. Accordingly, the smallest motor units are recruited first and they produce small forces and with increasing force demands, larger motor units join in. However, the largest motor units are rarely used and are recruited only during maximal effort for brief periods of time. It is this hierarchy of motor unit recruitment order that governs the
neural control of different fiber types within the same muscle, or muscle portions.

Important implications of the orderly recruitment of motor units are that slower fiber types are more frequently used than the faster ones, and that finer force modulation is possible at lower than at higher task intensities (Fig. 2). This finer modulation is due to the fact that small motor units produce less force than large motor units, and that there are more small than large motor units. It should be noted that muscle force is regulated not only by recruitment of motor units but by rate coding, i.e., by changing rate of motor unit activation. Both strategies are used, although their relative contributions differ (Korfage et al. 2005).

**Moment arm and muscles**

The relationship between the force generated by individual muscle fibers and the action of their parent muscles is complex for several reasons. The long axis of muscle fibers does not typically co-align with their parent muscles. Furthermore, the bones that the parent muscles are attached to rotate around joints. When such rotation is present the angular equivalent to force—torque—is a better measure of a muscle’s action than force. Torque is calculated by multiplying force by the moment arm, which is the perpendicular distance from the axis of rotation to the straight line of pull of the muscle (Fig. 3). The moment arm typically varies with the degree of joint rotation and accordingly so does the torque resulting from the contraction of motor units. Moreover, if muscles with different moment arms act together, these muscles will experience different amount of length change as the movement occur.

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**Figure 2.** Cumulative muscle force vs. number of recruited motor units. The recruitment of motor units follows the size principle. Accordingly, the smallest motor units are recruited first resulting in relatively small force output. Consequently, when a muscle produces small forces a relatively large number of motor units are activated. When the force output from the muscle increases, the larger units join in and each of them increase the force output more than compared to a small motor unit. As a consequence of the size principle, a finer modulation of muscle force is possible at lower than at higher muscle forces.
Muscles of the oral system

Commonly, the jaw muscles are categorized as jaw opening and jaw closing muscle depending on their main action. The jaw closing muscles are the temporal muscle, masseter muscle, the superior head of the lateral pterygoid and the medial pterygoid muscle but among these, the masseter muscle is the dominant one (Farella et al. 2008; Raadsheer et al. 1999). The jaw opening muscles are the inferior head of the lateral pterygoid and the digastric muscle. In addition to these jaw opening muscles an anatomically complex set of muscles also assist in jaw opening: known as the supra- and infrahyoidal muscles.

Masseter muscle

The human masseter muscle is a complex anatomical structure. Internal tendinous septa divide the muscle into portions. These portions are stacked in deep and superficial layers and side-by-side along the anteroposterior axis of the muscle (McMillan and Hannam 1991). The human masseter consists mainly of Type I fibers and they make up 62–72% of the muscle’s total fiber content (Eriksson and Thornell 1983; Vignon et al. 1980). However the proportion of other fiber types is not equally distributed throughout the muscle (Eriksson 1982; Eriksson and Thornell 1983; Korfage et al. 2000; Stal et al. 1994). In fact the presence of the faster type II fibers increases in the more posterior regions of the muscle. Nor are muscle spindles homogenously distributed in this muscle but most are found in the deep parts of the muscle (Eriksson and Thornell 1987). In summary, the human masseter shows regional differences in both fiber type composition and muscle spindle distribution. The organization of motor units along the anteroposterior axis of the muscle allows for a unique control scheme where groups of motor units potentially can act with different moment arms relative the temporomandibular joint (Turkawski and van Eijden 2001).

Figure 3. Schematic illustration of the forces and corresponding moment arms in the jaw system. Illustration shows the force (blue arrows) generated by the masseter muscle when contracting ($F_M$) and the corresponding reaction forces from the joint ($F_J$) and the food ($F_F$). The green dashed lines represent the moment arms (perpendicular distance between the force vector and the point of rotation, i.e. joint, indicated by black circle) for the force generated by the masseter muscle ($M_M$) and the reaction force from the food ($M_F$). The torque around the temporomandibular joint is calculated by adding the product from the forces acting in the system and their corresponding moment arms, e.g. $(F_M \times M_M) + (F_F \times M_F)$. Note that the reaction force from the joint ($F_J$) is not a part in this calculation since the force vector passes through the pivot point, i.e. the moment arm is zero.
**Digastric muscle**

Compared to the masseter muscle the internal organization of the digastric muscle is less complex. As the name indicates this muscle has two bellies, one anterior and one posterior. It has been claimed that the two bellies contract simultaneously (Munro 1974; 1972) but non-synchronous activity has also been observed (Munro 1974; Widmalm et al. 1988). The bellies show similar fiber type composition (Eriksson et al. 1982), i.e., approximately one third type I fibers and two thirds type II fibers evenly distributed in the cross section plane of the muscle. Moreover, the motor units containing type I fibers are of smaller size compared to those with type II fibers and an orderly recruitment of the fibers have been documented (Mimura 1989). Interestingly, the human digastric muscles seems to be devoid of, or very sparsely populated with, muscle spindles (Lennartsson 1979).

**Sensors in the masticatory system**

The CNS receives afferent information from different sensors in the oral system much in the same way the CNS receives information from the rest of the body (Eriksson and Thornell 1987; Johansson et al. 1988; Klineberg 1980; Kubota and Masegi 1977; Lennartsson 1979; Lund 1991). However, there is one mechanoreceptor that is unique for the oral system and that is the periodontal mechanoreceptor from which periodontal afferents (PMAs) originate. Since these afferents are of interest in this thesis they deserve some special attention.

**Periodontal mechanoreceptors**

The root of a tooth is anchored to the jaw by the periodontal ligament. It is composed of collagen fibers that stretch from the alveolar bone to the surface cement on the root. Nerve endings — the PMAs — making up the periodontal mechanoreceptors are tangled between these collagen fibers in such way that they respond to forces acting on the tooth (Byers 1985; Cash and Linden 1982). The role of PMAs in controlling jaw muscles during biting and chewing have been well documented (Lund 1991; Lund and Kolta 2006; Trulsson 2006; Türker 2002). For example, Trulsson and Johansson (1996) demonstrated the importance of PMAs in connection with sensorimotor regulation of the forces exerted during manipulative actions involved in mastication, i.e., food positioning and holding.

PMAs adapt slowly to tooth loads in a manner similar to slowly adapting type II afferents (Ruffini endings) from the skin and provide temporal, spatial and magnitude information about tooth loads (Trulsson 2006). About 80% of PMAs have a pronounced sensitivity to low forces (below 1 N for anterior teeth and 3 N for posterior teeth) but saturate at higher forces and the remaining 20% show discharge rates that increase almost pro-
portionally to increased force over a wide range of forces (Johnsen and Trulsson 2005; Trulsson and Johansson 1994).

The PMAs are myelinated and have their cell bodies in the trigeminal ganglion or in the trigeminal mesencephalic nucleus of the brainstem (Beaudreau and Jerge 1968; Gottlieb et al. 1984; Heasman and Beynon 1986). Sensory neurons originating from these two different regions innervate different but overlapping areas in the periodontal ligament. Although the afferents originating in the ganglion are distributed throughout the ligament, the density of innervation is highest close to the mid-axial point of the root. The mesencephalic nucleus fibers are distributed from the mid-axial point to the apex of the root and their innervation density is highest near the apex (Byers and Dong 1989). This organization suggests that their inputs serve different not yet known functions (Olsson and Westberg 1989).

Reflexes
A reflex is a motor behavior that does not require voluntary initiation, but occurs automatically under appropriate conditions. All reflexes depend on some kind of afferent signal. The term ‘appropriate stimulus’ is used for the modality that evokes a response with the smallest stimulus strength.

Oral reflexes
Among the first well documented descriptions of oral reflexes were authored by Sherrington: “Reflexes elicitable in the cat from pinna vibrissae and jaws” (Sherrington 1917). He described in decerebrated cats both the jaw closing reflex and the jaw opening reflex along with their appropriate stimuli. Since then extensive research in the field of oral reflexes has been conducted. Apparent in that work is the lack of common nomenclature for the different reflexes, i.e. the naming of oral reflexes has been done on the basis of the involved neural pathways, the motor actions evoked or the stimulus modality (Türker 2002). There are therefore several, similar reflexes described for the oral system which all have the same end effect, i.e. jaw opening or jaw closing. Jaw reflexes have been extensively reviewed (Lobbezoo et al. 2006; Türker 2002; van der Glas et al. 2007). Below I provide some short, general comments on the jaw closing and jaw opening reflexes, followed by a more detailed description of the sudden unloading reflex.

Jaw closing reflex
When we are awake and in supine position, the jaw is kept closed by the jaw closing reflex, counteracting the effects of gravity. If we fall asleep in an upright position (e.g. sitting position) the neural control of jaw position is disturbed, with the result that the mouth may fall open. The stretch on the muscle spindles caused by the jaw bouncing up and down as we move causes
the jaw-closing muscles to stiffen at the right time to keep the jaw elevated. The jaw closing reflex is a monosynaptic stretch reflex (Goodwin and Luschei 1974). A sudden tap on the chin stretches the muscle spindles and causes a fairly synchronous activation of the closing muscles. The latency of the response, from stimulus to contraction, is about 10ms.

**Jaw opening reflex**

The digastric muscle is likely devoid of muscle spindles, which is in contrast to the jaw closing muscles. Consequently the reflex control of these antagonistic muscles require different central organization. Kidokoro et al. (1968) addressed this and showed that the jaw opening reflex was disynaptic, as opposed to the mono-synaptic jaw closing reflex. When an appropriate stimulus enters the brainstem it is relayed via two groups of pre-motor interneurons that disynaptically inhibit jaw closing and activate jaw opening motoneurons (Kidokoro et al. 1968; Olsson and Westberg 1991).

There are several appropriate stimuli for eliciting a jaw opening reflex and the gain of the reflex can be modulated according to different parameters. For instance, injuries to oral or perioral tissues activate nociceptors which elicits a jaw-opening reflex that quickly stops further jaw closure (Lund and Olsson 1983). During mastication, this protective response is modulated according to jaw movement phase, such that it is largest when the jaw is closing and the oral tissues are most susceptible to damage (Lobbezoo et al. 2009; Lund and Olsson 1983). Also non-noxious stimuli such as a tooth tap or weak electrical stimulation of the oral mucosa can elicit reflexive jaw opening (Lobbezoo et al. 2009; Lund and Olsson 1983; Sherrington 1917; Turker and Jenkins 2000; Yemm 1972). This response is also sensitive to the movement phase but, in contrast to the protective jaw opening response, it is largest during the opening phase (Lobbezoo et al. 2009; Lund and Olsson 1983). Moreover, the non-noxious response is sensitive to masticatory stage such that it is strongly suppressed throughout the pre-swallowing stage but not during the preparatory and grinding stages (Mostafeezur et al. 2009; Yamada and Haraguchi 1995; Yamamura et al. 1998). Reflexive jaw opening can also be modulated for different motor behaviors, such as rhythmic jaw closing and clenching, even when accounting for jaw gape and muscle state at the time of stimulation (Huck et al. 2005). Taken together, many studies have shown that reflexive jaw opening is modulated as a function of stimulus intensity, masticatory stage, movement phase and motor behavior.

**Sudden unloading reflex of the jaw**

Interestingly, an appropriate stimulus to evoke a jaw opening reflex response is to suddenly unload the jaw when generating bite force. This response has been given its own name: The sudden unloading reflex of the jaw.
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The unloading of the jaw has been experimentally studied primarily by introducing a load between the jaws and then suddenly removing it. In response to such stimuli, reflexes have been recorded in both jaw-opening and jaw-closing muscles (Lamarre and Lund 1975; Miles and Wilkinson 1982). The most pertinent component of the jaw-unloading reflex is an increase in the EMG of the anterior digastric muscle at a latency of approximately 20 ms. This burst of activity is preceded by a reduction in the EMG of the masseter muscle (latency 10-20ms) (Hannam et al. 1968; Lamarre and Lund 1975; Miles and Wilkinson 1982). While the functional role of the unloading reflex remains unclear, several suggestions have been forwarded (Türker 2002). Importantly, the jaw opening muscles are not strong enough to significantly affect the immediate force reduction (<10ms) seen when suddenly unloading the jaw (van Willigen et al. 1997). However, in the time window of 40-60ms after an unloading event, the jaw opening muscles are active while the jaw closing muscles are not, and they may then reduce the bite force present and increase jaw impedance.

Several receptors are affected by the unloading and thus could be responsible for initiating this reflex but conclusive evidence is lacking. For example, blocking periodontal input by infiltration of local anesthetics around the roots of the teeth failed to alter the unloading reflex (Lamarre and Lund 1975; Miles et al. 1995; Poliakov and Miles 1994). However, this view has been challenged in studies using orthogonal loading of the teeth, which seem to demonstrate a contribution from PMAs to the reflex response (Turker and Jenkins 2000).

It has also been suggested that muscle spindles are the principal contributors to the unloading reflex, primarily because the latency of the onset of surface EMG reduction is consistent with a monosynaptic pathway, but also because muscle spindles are thought to be responsible for the unloading reflex in the limbs (Angel et al. 1965; Lamarre and Lund 1975; Miles et al. 1995; Miles and Wilkinson 1982; Poliakov and Miles 1994). However, Goodwin and Luschei (1974) showed that destruction of cell bodies of muscle spindle afferents in the trigeminal mesencephalic nucleus in monkeys did not alter their jaw-unloading reflex. Sound stimuli has also been proposed to contribute to the reflex (Duncan et al. 1992; Türkert 2002), but to the best of my knowledge this issue has never been directly addressed. Interestingly, Yoshida (1998) reports reduction in the reflex response following anesthesia of the temporomandibular joint capsule.
LIST OF AIMS

Aim addressed in Paper I:
... to determine whether an altered mechanoreceptive innervation of the teeth, due to periodontitis, affects the masticatory behavior during holding and splitting foods.

Aim addressed in Paper II:
... to investigate if the rapid decline in jaw closing force, occurring after sudden unloading of the jaw can be regulated and, if so, what possible mechanisms could underlie such regulation.

Aim addressed in Paper III:
... to determine if the reflexive jaw opening response that occurs after sudden unloading of the jaw is modulated by the intention of a bite.
BRIEF METHODOLOGICAL ACCOUNT

Experimental paradigm and apparatus

First experimental series

In the first experimental series (Paper I), we used the paradigm and measuring devices developed by Trulsson and Johansson (1996). In this paradigm, participants are instructed to manually hold a bite force measuring device with a morsel plate upon which a peanut half rested and to use their incisor teeth to split the peanut (Fig. 4A).

Using a natural food morsel such as a peanut is favorable for several reasons. First, peanuts break in a crisp way, i.e., they typically splits in two

![Figure 4. Methods. A. Apparatus used in Paper I. The force exerted by the incisors was sampled by an instrumented 9-cm-long bar-shaped handle (26g). A nut was placed on the rubber coated small plate on one end of the handle. A strain-gauge force transducer (FT) measured the force (0–200 Hz) compressing this and the lower plate in contact with the mandibular incisors. The distance between the parallel surfaces contacted by the teeth was 10 mm, and the stiffness of the instrument in the direction of the applied bite force was 50 N/mm. B. Apparatus used in papers II–III. The force and position measuring system consisted of two parts: a mouthpiece and a headpiece. The mouthpiece, weighing 26 g, consisted of two horizontal beams attached perpendicularly to a vertical beam. The upper horizontal beam had a rectangular morsel plate on which a peanut-half was stacked on a rectangular chocolate piece. The lower horizontal beam was attached to the mandibular incisors by means of impression paste applied in a milled pocket. The bite force was measured by strain gauges integrated in the upper horizontal beam (0–1 kHz; range: -10 to 150 N; r.m.s. noise 0.006 N). The stiffness of the mouthpiece in the direction of biting was 250 N/mm and the unloaded resonance frequency of the system was 1.5 kHz. The wooden headpiece was fixed to the head by straps of hook-and-loop fabric and used to measure the distance between the incisors in the lower and upper jaw. This distance was measured by means of two three-axis magnetometers attached to the headpiece 170 mm apart; they sensed the magnetic field of two cubic nickel-plated permanent magnets integrated in the mouthpiece (0–1.5 kHz; range 60 mm; r.m.s. noise 0.014mm).]
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pieces, unloading the jaw with minimal disturbance and lag. Second, the peanut is a naturally occurring food that practically everyone is familiar with. In previous studies related to the current thesis (Nagashima et al. 1997; Nordström et al. 1990; Slager et al. 1997; Turker et al. 1997; van Willigen et al. 1997) people have been asked to bite on a mechanical device (e.g., a metal bar). This could conceivably affect people’s behavior because they may be afraid of damaging their teeth or simply find it unpleasant to bite hard onto metal objects. Furthermore, for mechanical unloading devices methodological issues have been raised concerning the speed of unloading the jaw (Nagashima et al. 1997).

Second experimental series
In the second experimental series (Paper II and Paper III), we focused on the unloading event (split of the peanut) instead of holding and manipulating the peanut. To achieve this, several changes in the experimental setup were needed. First, we introduced an additional task. Second, we eliminated the manual hand support of the force-measuring device. Third, we redesigned the apparatus so additional measuring parameters could be included as well as provide for a substantially increased bandwidth of the measurements (Fig. 4B).

The main hypotheses we aimed to test was if people—without training or special instructions—could regulate the dissipation of bite force following unloading. We designed two tasks to stress the behavior of the participants in such a way that regulating the force dissipation would be beneficial for task completion. The first task was similar to the one in paper I, that is, to hold a peanut and to split it when requested (single-split task). In this new experimental setup, however, the peanut rested on a piece of chocolate and the instructions to the participants included that they should not damage the chocolate piece. In the second task, using the same setup, the participants were instead instructed to split both the peanut and the chocolate piece in one biting action (double-split task). Thus, when splitting the peanut half only, substantial bite force dissipation would be beneficial since the risk of breaking the chocolate piece would be reduced. In the other case, when instructed to bite through both the peanut and the chocolate, maintaining high bite force would be beneficial as to overcome the resistance of the chocolate.

From the data in first experimental series it was evident that the split event triggered rapid force transients. Since our intent was to study these transients, we eliminated the possible interaction of manually holding the measuring device. Furthermore, the original force transducer had an insufficient bandwidth (0—200Hz) to resolve the transient force events. To that end, the apparatus was re-designed and, by increasing the mechanical stiffness in the loading direction, the bandwidth also increased. We also
introduced permanent magnets in the mouth piece which could be sensed by a device fastened to the head. This allowed us to measure the position of the mandible relative to the maxilla (Fig. 4B).

RESULTS

Paper I

Background and hypothesis

Periodontitis is an inflammatory disease, characterized by a progressive breakdown of the periodontal ligament as well as other structures surrounding the teeth. Thus, information originating from the PMA population within the periodontal ligament is likely altered when the tissue is destroyed. Since previous work has showed that lack of this information reduces the ability to finely tune low bite forces we hypothesized that changes following periodontitis also would affect the ability to regulate and control low bite forces.

Furthermore, the split phase of the hold-and-split task is characterized by a vigorous increase in the bite force lasting a fraction of a second until the bite force falls instantly when the morsel breaks up. The force development immediately before the split phase does not appear to depend on signals from periodontal mechanoreceptors (Trulsson and Gunne 1998; Trulsson and Johansson 1996). This observation and results from the measurement of maximum bite forces (Kleinfelder and Ludwig 2002) predict that the split-phase behavior in subjects with reduced periodontal tissue support would be similar to that in healthy control subjects. However, individuals with advanced periodontitis may have learned (implicitly or explicitly) about the reduced periodontal tooth support and, as a result, have developed a more cautious biting strategy compared to healthy individuals.

Results

The test group, consisting of patients with advanced periodontitis in opposing central incisors was compared to a sex and age matched control group with intact and healthy periodontal tissue. The test group used on average higher bite forces to hold and control the peanut half and showed a greater variability in the hold force between trials. Moreover, the within trial variability was significantly higher in the patient group compared to the healthy control group. However, for both the test and control group, the variance (between and within trials) in hold force increased with increased hold force. A multiple linear regression analysis with the between-trial variance as a dependent variable indicated a significant correlation between the hold force and its variability. A corresponding analysis for the within-
trial variability provided similar results. Thus, the hold force variance was approximately proportional to the level of bite force.

The patients showed a more cautious and variable behavior when splitting the peanut, manifested primarily as differences in bite force rates before the split (Fig. 4A-D in Paper I). That is, patients, when compared to the test group, increased their bite force less vigorously before the split.

Paper II

Background and hypothesis

Splitting food items between the incisors often requires high bite forces but rarely do the teeth harmfully collide when the jaw quickly closes after food split. The prompt dissipation of the jaw closing force—literally within a few milliseconds—that is required to prevent harmful collisions has in previous studies been explained by the force-velocity relationship of the jaw closing muscles, influenced primarily by the bite force present at the unloading moment and the jaw travel distance following unloading (Fig. 1) (Nagashima et al. 1997; Slager et al. 1997; van Willigen et al. 1997). If this was the only mechanism, however, biting through heterogeneous materials would likely be carried out in a stuttering manner but this is contradicted by everyday experiences. It still remains unknown, however, if bite force dissipation can be regulated in a task dependent manner when performing, e.g., smooth vs. stopping actions when biting. Furthermore, the human masseter muscle is organized in multiple anatomically discrete portions that contain different neuromuscular compartments (English et al. 1993; Widmer et al. 2007). From an anatomical point of view, muscle portions and thus neuromuscular compartments have different origins and insertions along the anteroposterior axis (Hannam and McMillan 1994; Tonndorf and Hannam 1994; van Eijden and Raadsheer 1992) and thus can differ with respect to their moment arms relative to the temporomandibular joint (reviewed in Korfage et al. 2005). The moment arm length determines muscle shortening velocity during jaw closing and therefore, recruiting motor units with different moment arms allows for various levels of jaw closing force dissipation.

We thus hypothesized (1) that people indeed can regulate jaw closing force dissipation in a task dependent manner and independent of the force level at the moment of unloading (cf. Fig. 1A), and (2) that people can accomplish this regulation by taking advantage of the anatomical organization of the masseter muscle along its anteroposterior axis.

Results

All participants (n=12) regulated the jaw closing force dissipation according to task. We assessed this by quantifying the rate of bite force increase when the teeth hit the chocolate following peanut split. This measure, termed
impact intensity, differed significantly depending on the task. However, there were several other measured parameters that also exhibited task dependent differences, e.g. the rate of force increase before the split of the peanut (Fig. 4A and C in paper II).

A linear model was used to determine if task itself influenced the impact intensity or if it was a function of some other parameter. The model, which accounted for 58% of the variance in impact intensity, showed that task per se significantly affected the impact intensity as did the rate of bite force increase prior to the split event. To better understand what mechanisms could make up the task effect we turned to the EMG data. From those signals we could show a differential activation depending on task, i.e. a higher activation in the posterior part as compared to the anterior during the double split task. These EMG findings were further validated using ultrasonography in three additional participants. Indeed the ultrasound

![Force rate (N/s)](image)

![EMG](image)

**Figure 5. Temporal activation pattern of masseter muscle in single-split trials.** Averaged data across all participants from single-split trials. Top traces represents bite fore rate and bottom traces EMG. All trials from each participant with the largest EMG peak occurring in 10 ms time bins from -60 ms to +20 ms were averaged together as was the corresponding bite force rates (96% of all trials were included in the bins; no trials appeared in the bin ranging 10-20 ms after split. The number of trials in each bin is shown to the left in the EMG traces). Vertical arrows indicates the center of each bin in the corresponding average tracing. Color-shaded areas denotes the SEM for each mean trace. Dashed black line, overlaying the EMG traces depict the instance of peanut split.
analysis was congruent with the EMG findings, indicating a higher activity in the posterior part of the masseter muscle during double-split compared to single-split task.

The above summarizes the main finding of paper II, however in the process of analyzing the results we found that the averaged signals from the EMG declined prior to the split event, especially in single-split trials (Fig. 3 and 7 in Paper II). This invites speculation that the participants accurately predicted the split force and in anticipation decreased the muscle drive. However, after analysis of the EMG data we found a temporal pattern of muscular activation. When averaged across trials, this pattern, gave rise to a deceptive decrease in the EMG signal before the split. The underlying mechanism being the pulsatile outflow from the motor units in combination with the muscular electromechanical delay (Fig. 5).

**Paper III**

*Background and hypothesis*

As previously described, a reflex is evoked after the sudden unloading of the jaw. It consists of a temporary suppression of the masseter muscle activity and an activation of the digastric muscle activity at latencies of ~15-20ms after the split event.

One possible role for this change in muscle activity may be to stiffen the jaw system, another may be to modulate the bite force in the period later than 20 ms following an unloading event. This could aid the execution of a successful bite if the reflex gain can be modulated. For example, when biting through heterogeneous materials it would seem appropriate to have low reflex gain so that the bite force can be maintained high; the opposite would apply when a morsel is brittle or homogenous. Interestingly, jaw reflexes—including the unloading reflex—has been shown in both humans and animals to be subject to modulation. The nature of this modulation depends on masticatory stage, whether the jaw is opening or closing, stimulus modality (non-noxious vs. noxious stimuli) as well as motor behavior (rhythmical chewing vs. clenching). However, it is still unknown if the reflex response in the jaw opening muscles is modulated according to the intention of a bite.

In summary, in addition to mechanical and stiffening factors, the elicitation of the unloading reflex may have an important role in preventing further jaw closing from occurring after the initial slowing of the jaw when an object fractures. And vice versa, i.e., the absence of an unloading reflex might enable a better ability to maintain bite force production and thus enable the execution of a smooth biting motor behavior. To that end we hypothesized that depending on the task requirements this reflex response is subject to modulation.
Results

The data set analyzed is the same as in Paper II and accordingly, the tasks were same, i.e., to split only the peanut while preserving the chocolate vs. to split both the peanut and the chocolate in one bite action.

In all participants we demonstrated the expected reflex modulation as hypothesized: the reflex was strong when splitting only the peanut compared to when splitting both the peanut and the chocolate. However, as in Paper II, there were other parameters that also, on a group level, varied depending on the task (e.g., bite force rate before split and masseter EMG) as well as parameters that did not vary, e.g. digastric EMG level before split. Of specific interest was the level of digastric EMG activity before split because from previous work it is known that reflex gains are sensitive to the pre-perturbation excitation level of the motor-pool, i.e., so-called gain-scaling of reflexes (Matthews 1986; Pruszynski et al. 2009). To further elucidate what possible factors that could influence the gain of the jaw opening response on a single trial level, a linear model was applied to predict the jaw opening response with measured bite parameters. The model accounted for ~34% of the variance and the main contributing factors were task and the pre-split EMG level of the digastric muscle (Table 1, Paper III).
DISCUSSION

The experimental setup and measurements

Task
Although all participants were given exactly the same instructions it can be argued if the two tasks—splitting only a peanut vs. splitting both a peanut and a piece of chocolate—in Paper II and III were indeed interpreted as different tasks. Nevertheless, completing these two tasks challenged bite force control regardless of how a given individual interpreted the instructions.

Even if it was possible to precisely control how the participants understood the instructions, only speculations could be offered regarding the true neural networks controlling the behavior. This is because activity in the presumed circuits cannot easily be measured in humans. Registrations of neural activity at cortical and brainstem levels are mainly limited to animal models where complex instructions to elicit specific behaviors are difficult.

Devices
Applying intraoral devices is necessary if one want to measure bite forces with high accuracy. Other possible techniques to assess muscle activity lack accuracy; for instance, surface EMG of jaw closing muscles is poorly correlated with bite force (Farella et al. 2008). That said, measuring bite forces by intraoral appliances can be done in a variety of ways, the one used in this thesis being one. The force measuring devices used are maybe, less obtrusive compared with other published methods addressing bite force regulation in relation to unloading of the jaw (e.g. Türker et al. 1997; Türker et al. 2004; van Willigen et al. 1997) and allow near-to-natural biting behaviors: the incisors acted on a natural piece of food and both head and jaw movements were possible and only minimally constrained.

One unresolved issue and difference between the two force measuring devices used is the effect of manual hand support when manipulating objects with the teeth. Comparing the two hold forces reported for the different experimental series indicate a difference, i.e., lower hold forces were applied by the participants in the first study where the force measuring device was manually supported. Off course there can be several reasons for such difference. For example, in the first experimental series specific instructions relating to the holding of the peanut were given—“hold the peanut carefully while waiting for the order to split it”—which was not the case in the second experimental series. Another reason, we cannot rule out, is an effect on the hold force by the manual hand support of the force measuring device. This is a very interesting issue to further investigate since interaction between hand and mouth with or without a tool is very common, e.g., when eating using forks, spoons and chopsticks.
Ultrasonography
The use of the ultrasound technique to evaluate the spatiotemporal contraction pattern of the masseter muscle is novel. Previous efforts in documenting the masseter muscle using ultrasound technology has mainly focused on comparing static conditions, i.e., volumetric comparisons between relaxed and contracted muscles (Bakke et al. 1992; Benington et al. 1999; Kiliaridis and Kälebo 1991). However, for other muscles in the body ultrasound is a well described technique to study spatiotemporal contraction patterns (Wells and Liang 2011).

A sufficiently high spatial and temporal resolution to follow the pattern of muscle contraction was achieved by focusing on a cross sectional area of the muscle. The strain (percentile change in length) was measured between two endpoints of the muscle, i.e., the superficial aponeurotic sheet and the ramus part of the mandible. This measure is an indication of the averaged strain developed in the muscle over the measured region. In the future however, it might be possible to develop techniques allowing assessments of the strain in whole muscular subportions while the masseter muscle contracts. One promising and interesting approach for facial muscles, including jaw muscles, is to calculate strain based on the raw ultrasound signal (RF-signal) which allow high spatial and temporal resolution (Lopata et al. 2009). Importantly, the technique described in Paper II to assess the spatiotemporal development of masseter contraction is based on some assumptions that can be presumed to hold water: (1) that the actual change in length between the ramus and aponeurotic sheet is because of contraction of the muscle fibers along the imaginary line, and (2) that the cross section image is acquired at an approximate midpoint of the muscle belly.

Ultrasound techniques—once matured—can be developed to an important clinical tool when assessing dynamic functionality and when objectively evaluating the functional outcome of various therapies.

Experimental measures
There are several reasons to believe that the impact intensity provides a valid measure of jaw closing force dissipation; e.g., it is very well correlated to other measures of force dissipation in trials that allowed such comparisons. Other measures, such as the jaw closing velocity at impact and residual force, previously described were not applicable in Paper II–III. This is because of both the morsel used (i.e. peanut half) and the introduction of the double split paradigm. That is, the velocity at impact saturates at approximately 3 mm travel distance (Fig. 1B) (Nagashima et al. 1997; van Willigen et al. 1997), but the thickness of the peanut halves ranged well above that. The residual bite force (Slager et al. 1997; van Willigen et al. 1997), which is the epoch of bite force increase following the split event (Fig 1A), is masked in...
the double-split task because of the superimposed bite force drive needed to overcome the resistance of the chocolate (Fig. 3C and D in Paper II).

The reflexive response when unloading the jaw comprises of both inhibition and excitation of masseter and digastric muscles, respectively. Quantifying the early response in the masseter muscle is difficult if not impossible, given the inhibited state of the muscle. Instead we quantified the gain of this reflex by measuring the excitatory digastric muscle response. The digastric activity is well correlated with the jaw opening muscle complex and thus provides a good window in to the group of jaw opening muscles responding to sudden unloading (Ahlgren et al. 1978; Pancherz et al. 1986; Winnberg and Pancherz 1983).

There are several ways to quantify an EMG response, e.g. the peak activity level, integral during the reflex response, mean value during response, etc. Several such measures were evaluated during the elaboration of the results, and they all yielded qualitatively similar outcomes. We reported the mean value for two main reasons: it is easier to communicate than the integral and it had less variance than peak EMG level.

**Functional consequences of periodontitis**

The main finding in Paper I was that masticatory behavior is impaired in participants with reduced periodontal tissue support. Specifically, the forces by which participants in the patient group held the food before splitting were higher than for controls. Altered mechanoreceptive innervation of the periodontal ligament can explain these elevated hold forces. These results are in accordance with other published data showing the importance of PMAs when regulating and controlling low bite forces (Trulsson 2006). Furthermore, during the increase in bite force preceding food split the participants applied a lower bite force rate compared to controls, and the overall behavior was more inept. The origin of this change in biting strategy is unclear but can perhaps be explained by weaker tooth support, which may induce a more cautious food-splitting strategy. The fact that periodontitis not only causes alterations in masticatory ability by the physical changes in the oral cavity (e.g. number of teeth, tooth mobility) but also on a perceived subjective level has been shown (Borges Tde et al. 2013; Pereira et al. 2012; Pereira et al. 2011). However, recent work, based on the results from Paper I show that PMAs are of importance to regulate the bite force increase leading to a morsel split (Svensson and Trulsson 2009). That is, applying local anaesthesia to the periodontal ligament reduces the rates of bite force increase when splitting peanuts.

PMAs are of great importance for regulating the low bite forces used to hold and control morsels between the teeth. It may appear tempting to suggest that the reduced periodontal ligament was subjected to greater stress
at a given force than in healthy people and therefore caused more efficient excitation of the PMAs. This would promote finer force control but the results, in fact, points to the contrary: the reduction of periodontal tissue, was associated with a reduced ability to regulate low bite forces.

Periodontitis cause a gradual loss of tooth supporting tissues. It typically starts marginally and advances in apical directions, and if left untreated, leading to the loss of the affected tooth. Over the time course of periodontitis, the PMAs with their cell bodies in the trigeminal ganglion will almost certainly be affected first since they are situated anatomically more marginally compared to those with their cell bodies in the trigeminal mesencephalic nucleus (Byers and Dong 1989). There are studies suggesting differential function for the different PMAs (Turker et al. 1997) but the precise reason or difference in functions remains unclear (Westberg and Olsson 1991). However, teeth affected by periodontitis also show increased mobility and most patients that participated in the study presumably were aware of their unstable oral situation. This may, in turn, activate complex neural strategies that alter the biting behavior, for instance, to apply higher hold forces than what is normally used because the teeth are wobbly at low forces and stabilize first at higher force levels. Interestingly, following treatment of periodontitis both a decrease in tooth mobility is observed (Lindhe and Nyman 1975) and an improvement in masticatory function (Pereira et al. 2012; Pereira et al. 2011). However, it is still unclear if and how these two factors relate.

**Muscle organization and recruitment**

The central advance in Paper II was the finding that humans regulate the dissipation of the jaw closing force following food splitting and that the biological basis for this ability, at least in part, is a differential recruitment of the masseter muscle along its anteroposterior axis.

**Model to account for differences in force dissipation**

The results from Paper II inspired a simplified model that accounts for the regulation of jaw closing force dissipation (Fig. 6). In short, regulation of the closing force dissipation is possible by differential recruitment of muscle portions with different length in their moment arms relative to the temporomandibular joint. By skewing the distribution along the anteroposterior axis of engaged muscle portions the overall mean moment arm relative the temporomandibular joint will shift and thus the force dissipation will be different.

The underlying mechanism for this is the force-velocity properties of the muscle fiber, i.e., that the ability to maintain force production decreases as the shortening velocity increases (Fig. 6B). Hence, a long moment arm,
which is the case when shifting the mean moment arm anteriorly, will yield higher shortening velocities and thereby also greater jaw closing force dissipation (Fig. 6C and D). The opposite occurs when the mean moment arm is shifted posteriorly because of the shorter moment arm, i.e., the muscle will shorten slower and thus better maintain its force.

The model is based on a couple of assumptions. First, an orderly recruitment of the motor units in the masseter muscle is assumed along the anteroposterior axis of the muscle. In other words, when the central drive to the masseter motor neuron pool increases the mean moment arm decreases

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**Figure 6. Model for interpreting the masseter control.**

A, For illustration purpose, the masseter muscles was divided in four portions along the anteroposterior axis (colored areas, consequently, each portion had a different moment arm relative to the temporomandibular joint (black arrows) which is the mandibular pivoting point. B, All muscle portions in panel A are assumed to have the same force-velocity relationship. C, The activation level of each portion required to produce a certain bite force (velocity=0) and the corresponding force-velocity curve. D, The velocity of muscle shortening is also affected by the difference in moment arms. The portions with long moment arms are subject to higher velocities than those with short moment arms. E, When the same force-velocity curves as in C are shown as jaw closing force—incisal closing velocity relationships, the dissipation of the jaw closing force clearly depends on the muscle portion responsible for generating the bite force. By letting the different portions contribute to different degrees, an uncountable number of jaw closing force—incisal closing velocity curves within the area depicted by the most posterior (orange) and the most anterior (blue) curves could be generated and give rise to a range of jaw closing force dissipations.
because the motor neurons innervating the posterior masseter requires stronger activation because of higher input resistance. Indeed, previous work has shown that the motor units of the human masseter muscle are subject to orderly recruitment (Desmedt and Godaux 1979; Yemm 1977) and that motor units align vertically and are distributed along the anteroposterior axis (McMillan and Hannam 1991). A second assumption is that the actual shortening velocity of the sarcomeres in the masseter muscle does not cancel any effects of differences in moment arms. Off course, given the complex anatomy of the masseter muscle and inter-subject variation in anatomy (e.g. Cioffi et al. 2012) we cannot control for this. However, the results from studies that have addressed changes in sarcomere length as a function of jaw gape indicate that the actual change in length, as the jaw gape increases, is smaller in the posterior regions as compared to the anterior regions (Goto et al. 2001; van Eijden and Raadsheer 1992). Thus, if anything this would further enhance the effect of differences in moments arm by a nonlinear relationship.

In the light of the results and the proposed model from Paper II the food splitting behavior of the participants affected by periodontitis in Paper I becomes more interesting. Importantly, in Paper I we did not record any EMG activity from the masseter muscles, which makes post hoc analysis of the behavior speculative. However, the participants suffering from reduced periodontal tissue support applied lower force rates to accomplish peanut split (Fig. 4A-D in Paper I). According to the proposed model in Paper II this could be a good strategy to minimize the impact forces following peanut split. That is, by applying low force rates the mean moment arm relative to the mandibular joint would be long because, according to the orderly recruitment, motor units in the anterior masseter would contribute more to the bite force development. Once the peanut splits, the muscle fibers would shorten with high velocity and thus lose the ability to maintain force production and consequently, the jaw closing force dissipates quickly.

**Pulsatile motor command mimicking predictions**

The motor-output to the muscles, assessed by EMG, was of a pulsatile nature. Such activation of the jaw closing muscles has been observed in other tasks (Jaberzadeh et al. 2003; Junge et al. 1998; Sowman et al. 2008; van Willigen et al. 1997; Wilding and Shaikh 1997), but neither the underlying physiological mechanism, nor its functional role has been fully determined. The decline in the average EMG prior to the split events gave the impression of a predictive behavior by the participants. However, more detailed analyses revealed that these observation could be explained entirely by pulsatile jaw muscle commands in conjunction with electro-mechanical delays, i.e., the intervals between the EMG bursts were short enough to maintain an increase in the bite force of the masseter muscle. In fact, the food split for the...
majority of trials occurred during an epoch of low EMG activity and this explained the decline in the average EMG amplitude before the peanut split (c.f. Fig. 3 in Paper II). Previous work has speculated on the origin of the pulsatile activation of the jaw muscles has been put forward. One suggestion is that the pulsations are the consequence of centrally generated, alternating bursts of activity in the jaw-opening and jaw-closing muscles (Jaberzadeh et al. 2003). Another theory claims that the pulsations mainly result from motor unit synchronization (Nordstrom et al. 1990). Interestingly, the motor unit synchronization is more apparent in low threshold than in high threshold motor units, which may imply that pulsations would be more evident during slow contractions as compared to faster, more forceful ones.

**Reflex control**

The main finding of paper III is that reflexive jaw opening following sudden unloading of the jaw is modulated according to how a participant intends to bite through a food morsel. A larger response occurred when the task was to split one part of the morsel (i.e. the peanut) without damaging the other part of the morsel (i.e. the chocolate) as compared to when they were instructed to split both parts of the morsel in a single action.

The functional role of the digastric response following unloading of the jaw is unclear. Importantly, this reflexive response occurs too late to play a role for the rapid breaking of jaw closing movement and the dissipation of the jaw closing force (Miles and Wilkinson 1982; van Willigen et al. 1997). The consensus today is that the reflex response seen in the digastric muscle serves to increase the stiffness of the jaw system (Türker 2002). However, the jaw opening muscles are very weak as compared to the jaw closing muscles and the overall effect of co-contraction might be negligible. In fact, van Willigen et al. (1997) did not find any relationship between the magnitude of the residual force and the amount of co-contraction, thus emphasizing the unequal relationship in force producing ability between the jaw opening and closing muscles.
The results of this thesis furthers the knowledge of masticatory motor control mechanisms in humans as well as emphasizing the importance of integrating cognitive, functional and anatomical aspects when attempting to understand human masticatory control.

According to the International Research Group on Reconstructive Preprosthetic Surgery (IRGRPS), “the overall goals of oral and facial rehabilitation are to restore function and aesthetics, preserve the associated structures and contribute to the patient’s perception of improved quality of life” (Cawood and Stoelinga 2006). Satisfactory esthetic aims can usually be reached. However, the goal of restored masticatory functions is generally more difficult to assess due to lack of consensus regarding the selection of suitable evaluation methods (Feine and Lund 2006; Woda et al. 2006). The development of new methods for evaluating the degree of handicap and therapeutic outcomes in oral rehabilitation programs depends critically on our ability to understand the natural healthy behavior. The increased knowledge of masticatory motor behavior this thesis presents advances the possibility for new assessment tools in clinical dentistry.
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