REFLEX CONTROL OF SHOULDER GIRDLE MUSCLES IN HUMANS.

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ABSTRACT

Trapezius and serratus anterior are bilaterally located axial muscles. They work synergistically to rotate the scapula during movements of the arm. With its attachments onto the spine, trapezius has a role in the posture of the trunk. These functions require both independent and closely co-ordinated control, both between homologous muscle pairs and between each other.

The investigations presented here explore the reflexes of these muscles as well as the reflex control a) between the homologous muscle pairs, b) between trapezius and serratus anterior and c) between arm afferents and both muscles. How the reflexes between arm afferents and the shoulder girdle muscles differ in those individuals with various shoulder dysfunctions has also been investigated.

A mechanical tap to trapezius evoked a short latency reflex in the ipsilateral trapezius muscle. In addition, short latency facilitatory reflexes were also seen contralaterally. Electrical stimulation of the afferent nerve to trapezius also evoked short latency, facilitatory reflexes in both the ipsilateral and contralateral muscles. These reflexes would appear to be the equivalent of the Hoffmann reflex seen in the soleus muscle. Evidence is presented which suggests that muscle spindle afferents from the ipsilateral trapezius muscle monosynaptically activate the trapezius motoneurones contralaterally. The investigations of serratus anterior reveal contrasting results, reflexes in contralateral serratus anterior being of much longer latency.

Exploration of the reflex connections between the synergistic trapezius and serratus anterior revealed bi-directional short and long latency reflexes.

Electrical stimulation of the medial, ulnar and radial nerves of the arm, revealed long latency reflex connections from afferents originating as far distally as the hand to both trapezius and serratus anterior. Evidence is presented that suggests that these reflexes are transcortically mediated and that they are evoked by group I muscle afferents. These reflexes are delayed or absent in those subjects with shoulder dysfunctions.

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'The whole world is a narrow bridge; the important thing is not to be afraid.'

Nachman of Bratslav (1772-1810) from Chasing Shadows by Hugo and Naomi Gryn.

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1 INTRODUCTION

1.1 Anatomy and biomechanics of the shoulder complex.

The anatomy of the shoulder complex is well-understood (Culham & Peat, 1993; Donatelli, 1997; Kent, 1971; Paine & Voight, 1993; Peat, 1986; Williams *et al.*, 1989). The shoulder complex is a group of anatomical and physiological joints as illustrated in figure 1.

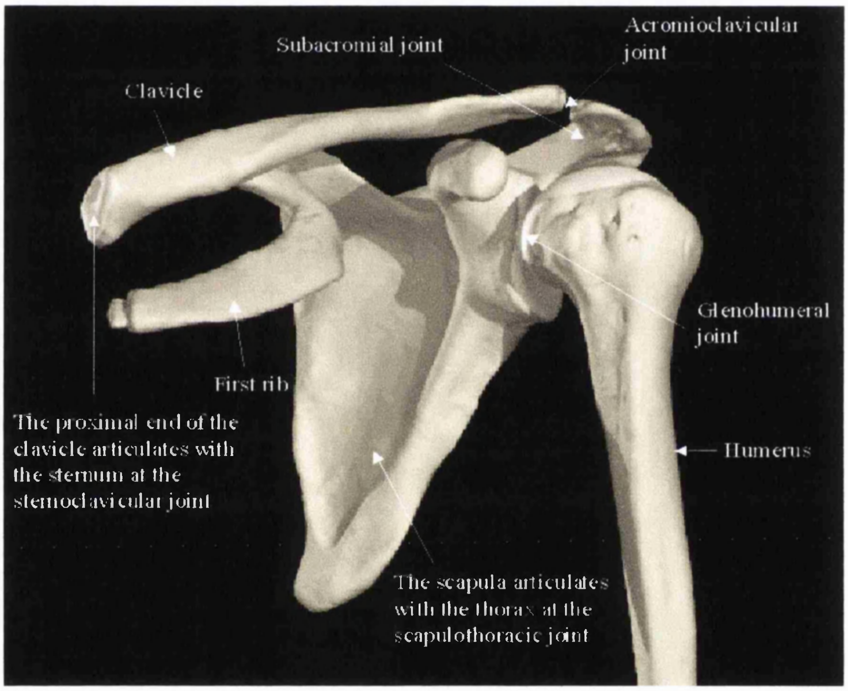


Figure 1. The three anatomical and two physiological joints of the shoulder girdle. The anatomical joints are the glenohumeral, acromioclavicular and sternoclavicular joints. The two physiological joints are articulations between the scapula and the thoracic cage - the scapulothoracic joint and between the acromion and the subacromial bursa with the rotator cuff muscles below - the subacromial joint. Adapted from Copeland *et al.* (2000).

Three of these joints form the base of support for the gleno-humeral joint and therefore the whole of the upper limb. These are the scapulothoracic, acromioclavicular and sternoclavicular joints, which together are called the shoulder girdle (Kapandji, 1986; Fromm, 2001; Paine & Voight, 1993).

At rest, the position of the scapula upon the chest wall defines the position of the rest of the shoulder complex (Kendall *et al.*, 1993). The position of the scapula is said to lie between the second and seventh ribs with the medial point of the spine of the scapula, otherwise called the root of the scapula or the deltoid tubercle, at the level of the third thoracic vertebra. The medial edge of the scapula is approximately 4cm to 6cm from the spinous processes, with the line of this edge at a mean of 91.3° from the horizontal. The under surface of the scapula is concave to allow for the alignment with a convex thoracic cage. To maintain contact with the thoracic cage, the scapula has a mean forward tilt of 9° and is at an angle of 50 to 60° with the clavicle (Culham & Peat, 1993; Kapandji, 1986). This positions the glenoid fossa, the socket of the gleno-humeral joint, at such an angle that it points laterally and anteriorly. Some suggest that the glenoid faces inferiorly and others that it faces superiorly. This angle affects the stability of the gleno-humeral joint, as if it is inferiorly positioned the head of the humerus would not be as well supported by the inferior lip of the glenoid labrum (Culham & Peat, 1993; Kapandji, 1986; Kent, 1971).

The scapula is able to move in a multitude of directions. The main functional movement is rotation. In upward rotation the glenoid moves to face superiorly following the humeral head in elevation of the arm. During this movement the scapula also tips posteriorly so that the acromion moves backwards and the inferior angle of the scapula moves into the body. This, along with lateral rotation of the humerus, allows the greater tubercle of the humerus to clear the acromion process (Peat, 1986; Ludewig *et al.*, 1996). Without the posterior rotation of the scapula, the rotator cuff muscles would become compressed within the subacromial space – an impingement syndrome.

The scapula also translates towards and away from the vertebral column. This is called protraction and retraction. To maintain the deep surface of the scapula in contact with the convex thoracic cage, during protraction the medial edge tips about a vertical axis – this is referred to as ‘winging’ – and the inferior angle tips about a horizontal axis. The scapula is also able to translate up and down the chest wall (Culham & Peat, 1993; Kapandji, 1986; Kent, 1971; Peat, 1986). All these movements demand concomitant rotation of the clavicle, which moves about a longitudinal axis at both the acromioclavicular and the sternoclavicular joints. The sternoclavicular joint is the only connection of the shoulder complex to the trunk. It has an interposed fibrocartilaginous disc. As the proximal end of the clavicle tips during superior inferior movement of the scapula, movement occurs between the clavicle and this disc. As the scapula protracts and retracts the anterior posterior movement of the clavicle promotes movement between the disc and the sternum (Kent, 1971; Kapandji, 1986).

Synchronous movement of these joints permit a large degree of multidirectional movement of the arm enabling the hand to have enormous freedom in terms of orientation and position in space (Peat, 1986). The timing and contribution of the movement of each joint allows for the correct orientation of the gleno-humeral joint. With a correct balance of movement, the head of the humerus remains in alignment with the glenoid. Without this, the range of shoulder movement is reduced or the head of the humerus is not centred on the glenoid (Dvir & Berme, 1978).

The co-ordination of the shoulder complex movement is termed the scapulohumeral rhythm. This has been most thoroughly examined during positioning of the arm overhead. Inconsistencies exist in the literature as to the contribution that each joint makes to shoulder movement. To examine scapulohumeral movement, elevation has been split into three phases of the movement of the arm, from the arm by the side to the position of the arm above the head (see figure 2).

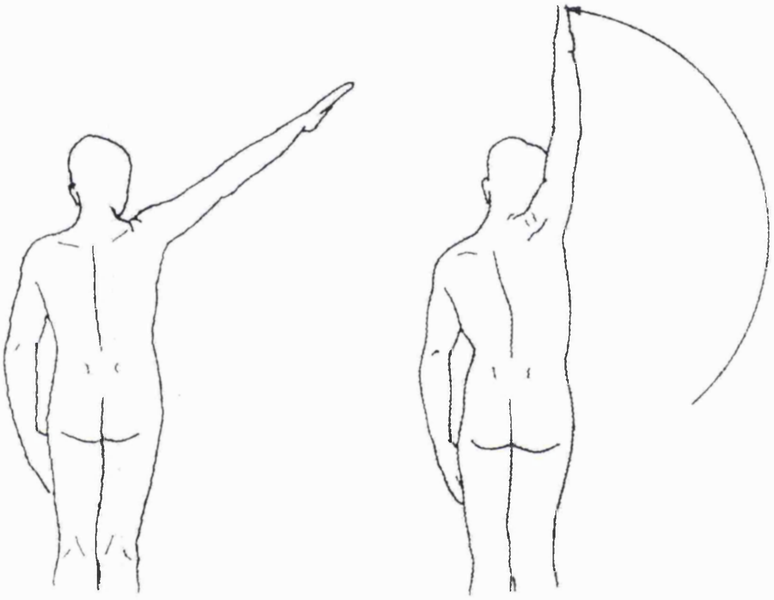


Figure 2. Side flexion of the spine in full ipsilateral elevation. The spine extends to achieve full bilateral elevation. This picture is adapted from Kapandji (1986).

The early phase corresponds to the first 60° of movement. During this phase the instantaneous centre of rotation of elevation of the arm stays within a small area near the medial end of the spine of the scapula (Donatelli, 1997; Dvir & Berme, 1978). The scapula rotates about this point whilst the humerus elevates. As the humerus elevates there is a slight superior shift of the humeral head in the glenoid (Liu *et al.*, 1997). The humerus contributes more to the movement than scapula rotation by a ratio of approximately 3.3:1, although some record 4.3:1 (Donatelli, 1997; Peat, 1986). As elevation continues to the second phase, between 60° and 100°, the axis of rotation migrates towards the acromioclavicular joint as ligamentous attachments between the thoracic cage and the clavicle become taut (see figure 3).

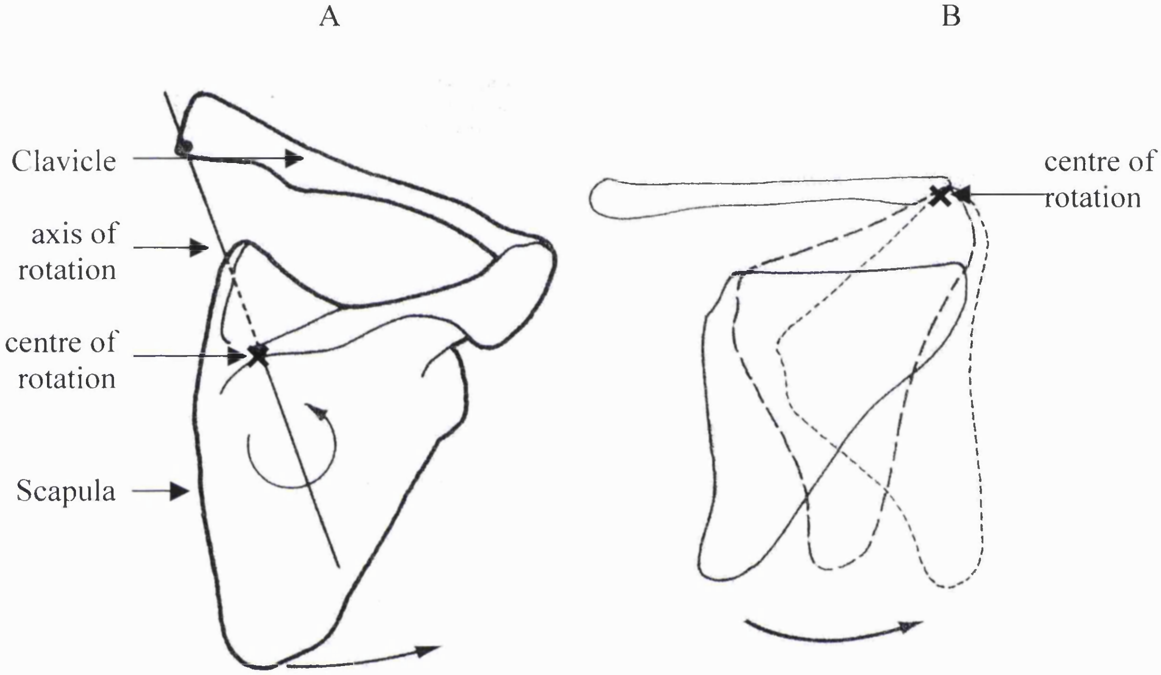


Figure 3. Phases of scapula rotation. A. During the first phase of shoulder abduction, the shoulder girdle rotates about the axis, which is centred upon the medial end of the spine of the scapula. B. The axis shifts to the acromioclavicular joint as the range increases above 60°. This picture is adapted from Kapandji (1986).

During this mid-phase of elevation, the contribution to elevation shifts from a predominant glenohumeral movement to a more balanced contribution with the ratio of glenohumeral to scapulothoracic rotation dropping to 0.7:1 (Donatelli, 1997). The humerus stays accurately centred in the glenoid, moving only about 3mm within the moving fossa by rolling and gliding (Liu *et al.*, 1997). In the last stage of elevation the axis of rotation is upon the acromioclavicular joint. The glenohumeral rotation now contributes most to the movement with the ratio rising to 3.5:1. Indeed, towards the end of range the scapula is relatively still. The spine side flexes or extends to achieve full elevation (see figure 2; Kapandji, 1986). If a load on the arm increases, the ratio of scapula to glenohumeral movement reduces. This reflects the increased need of the scapula to be stable to support a heavy load (Copeland *et al.*, 2000; Hess, 2000; Kent, 1971; Peat, 1986).

1.2 Muscles of the shoulder complex.

The function of the shoulder girdle is to act as a stable frame, which allows for movement of the upper limb. This involves balancing two concepts, stability and mobility (Dvir & Berme, 1978). The shoulder complex is the most mobile series of joints in the body (Dvir & Berme, 1978) yet remains stable with little passive restraint. This remains true for both the glenohumeral joint and the shoulder girdle. The glenohumeral socket is a moving flat fossa on the lateral aspect of the scapula. The movement of an incongruent round head of the humerus within the moving flat fossa allows for a large freedom of movement, but this lack of congruence and lack of a fixed base of support can also compromise shoulder stability (see figure 4; Peat, 1986).

Thus, the shoulder is particularly dependent upon the control of the surrounding muscles to ensure stability and yet allow mobility (Kent, 1971; Paine & Voight, 1993; Peat, 1986). Indeed, the stability provided by the shoulder complex muscles is such they can support up to 90% of body weight or nearly 10 times the weight of the limb through the glenohumeral joint. In other joints much of this force is taken up by passive structures, such as ligaments and the joint capsule. In the shoulder this is achieved through its musculature (Peat, 1986).

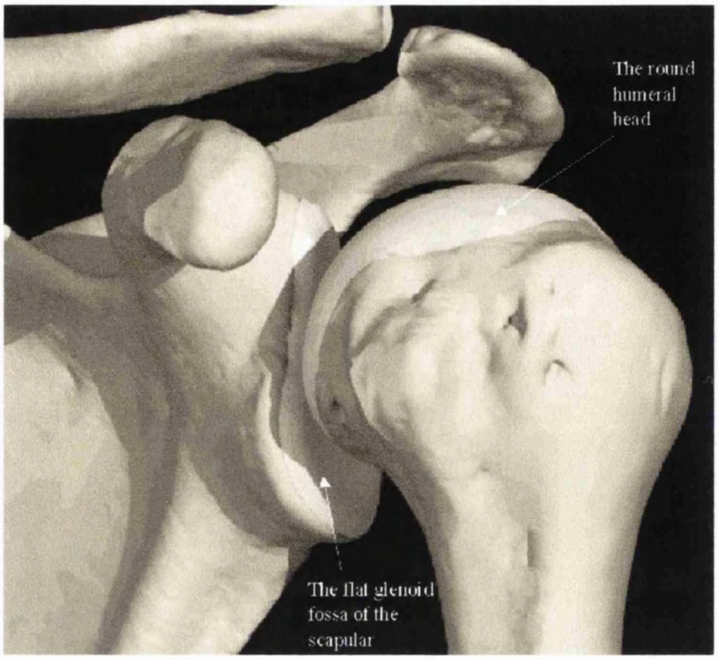


Figure 4. The glenohumeral joint. The shape of the articular facets of the glenohumeral joint contributes to the ability of the shoulder to move through a large, multidirectional range. Adapted from Copeland *et al.* (2000)

1.2.1 Muscles acting over the glenohumeral joint.

These muscles will be briefly discussed in terms of their role in movement and stability.

The middle and anterior deltoid and the supraspinatus abduct the arm (Dvir & Berme, 1978; Liu *et al.*, 1997). As they abduct, trapezius acts to counterbalance the pull of deltoid upon the scapula (Dvir & Berme, 1978). Indeed, the normal mechanics of the glenohumeral joint depends upon the co-ordinated control of the scapulothoracic muscles during scapula rotation to achieve the correct mechanical advantage for deltoid to work efficiently (Kent, 1971). At the start of elevation, the pull of deltoid and supraspinatus alone would sheer the humeral head upwards rather than move the arm effectively away from the chest (Halder *et al.*, 2001). The opposing force exerted by the other rotator cuff muscles through the glenohumeral joint prevents this superior sheer. So, at the start of elevation the rotators, teres minor, infraspinatus and subscapularis, pull the head downwards opposing this superior sheer (Peat, 1986; Pink, 2000). However, Liu *et al.* (1997) suggests that they also have a small abduction moment and so act as movers as well as stabilisers of the glenohumeral joint. As elevation continues these muscles, with supraspinatus, compress the head of the humerus into the glenoid, maintaining its centred position as the glenohumeral joint moves (Hess, 2000; Peat, 1986; Donatelli, 1997). Of the rotator cuff muscles, subscapularis is especially important. Subscapularis helps to prevent anterior displacement of the humeral head where the glenohumeral joint is particularly lacking in passive constraint (Peat, 1986; Arroyo *et al.*, 1997). Subscapularis also acts to stabilise the glenohumeral joint during internal and external rotation. Thus, as pectoralis major and latissimus dorsi contract, subscapularis helps to centre the joint (Pink, 2000).

The stabilising role of the rotator cuff is accentuated by the results of David *et al.* (2000). They investigated the onset of timing of these muscles with rotation of the glenohumeral joint. The rotator cuff was active before movement and before the onset of deltoid and pectoralis major activity. This suggests that feed forward mechanisms may act to stabilise the glenohumeral joint before the onset of movement (Hodges & Richardson, 1997a).

In addition to its role during elevation of the arm (Kent, 1971), the long head of biceps also has a role in stabilising the joint (Peat, 1986). If the shoulder is laterally rotated, the biceps is at such an angle to the shoulder that it is able to help in abduction of the arm (Kent, 1971; Peat, 1986). However, it also has a role in stabilising the joint. As the tendon runs superiorly over the glenohumeral joint, contraction of the muscle forces the tendon downwards upon the humeral head helping to maintain it in a centred position (Peat, 1986).

This is especially evident in subjects who have a shoulder stability dysfunction. Here, biceps activity increases, thus increasing the rigidity of the joint (Magarey *et al.*, 1996).

1.2.2 Scapulothoracic muscles.

Other than the sternoclavicular joint, the scapulothoracic muscles are the only attachment of the shoulder to the trunk. So, although these muscles are the prime movers of the scapula, they also anchor the shoulder girdle to the trunk (Dvir & Berme, 1978; Kent, 1971). In addition to trapezius and serratus anterior, these muscles are the rhomboids and levator scapulae (which elevate and retract the scapula) and pectoralis minor and subclavius (which connect the scapula to the anterior chest wall). However, trapezius and serratus anterior are the main two muscles controlling the scapula. Investigation of the control of these two muscles is the subject of this thesis. The co-ordinated contraction of all of these scapulothoracic muscles in controlling the scapula allows smooth movement and stability of the upper limb.

1.2.2.1 Trapezius.

Trapezius is a bilateral, flat triangular muscle that is divided into upper, middle and lower parts (figure 5; Williams, Jr. *et al.*, 1999; Johnson *et al.*, 1994). In the rat these parts are described as separate muscles (Kitamura & Sakai, 1982). In humans, the upper part (or upper fibres) originate from the superior nuchal line, the occipital protuberance and the ligamentum nuchae (Johnson *et al.*, 1994; Williams *et al.*, 1989). These upper fibres pass downwards and obliquely but most insert almost horizontally upon the distal end of the clavicle. Williams, Jr. *et al.* (1999) reports that some of the upper fibres also insert upon the acromioclavicular joint and the acromion. The middle part (or middle fibres) originates from the spinous processes and supraspinous ligaments of C7 and T1. These horizontal fibres attach along the whole length of the spine of the scapula from the acromion to the deltoid tubercle. A reduction in bulk of these middle fibres has occurred as man evolved from a quadrupedal to a bipedal stance. This suggests a greater importance of the upper and lower parts in the dynamic function of the muscle (Kent, 1971). The lower part (or lower fibres) originate from the spinous processes and supraspinous ligaments of T2 to T12 and insert upon the deltoid tubercle at the medial end of the spine of the scapula (Johnson *et al.*, 1994).

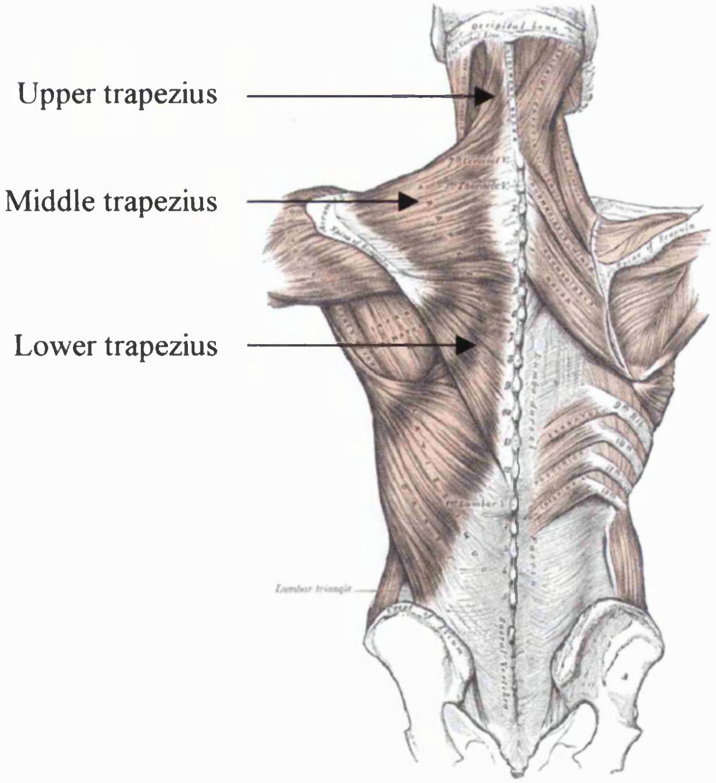


Figure 5. The location and attachments of trapezius. The upper fibres of trapezius attach upon the distal end of the clavicle. The middle fibres attach along the length of the spine of the scapula. The lower fibres attach upon the medial end of the spine of the scapula (the deltoid tubercle). Adapted from Williams *et al.* (1989).

The course of the nerve supply to trapezius is controversial and is not typical of peripheral nerves. Williams *et al.* (1989) detail the motor supply as arising from the spinal accessory nerve and the afferent supply travelling separately via the cervical nerves of C3 and C4 in humans. The spinal accessory nerve also provides the motor supply to the sternocleidomastoid muscle, which has its afferent supply via the cervical nerves of C2 and C3. This separation of the afferent and efferent nerve supply is mirrored in other species such as the cat and the rat (Richmond *et al.*, 1999; Fitzgerald *et al.*, 1982). The spinal accessory nerve forms from laterally placed nuclei in the anterior grey column of the spinal cord i.e. it has a spinal rather than cranial origin (see figure 6).

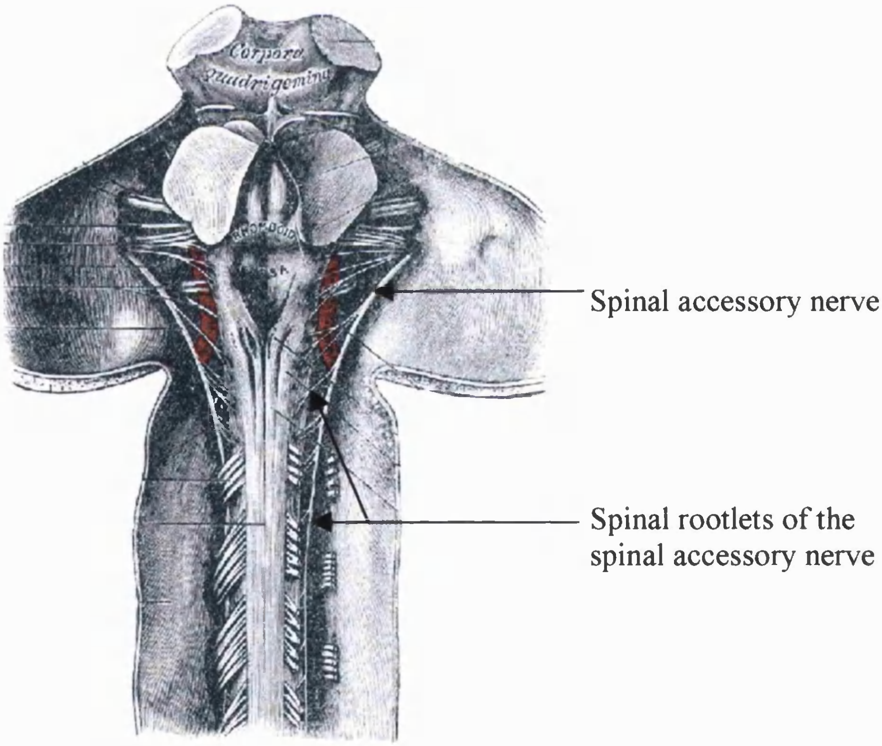


Figure 6. The origin of the spinal accessory nerve. The rootlets emerge from C1 to C5/6 segmental levels and merge to ascend as the spinal accessory nerve. This passes through the foramen magnum and out of the skull at the jugular foramen. Adapted from Williams *et al.* (1989).

In addition there is the cranial accessory nerve, which can be easily differentiated from the spinal accessory nerve, as they are functionally and anatomically distinct. The cranial accessory nerve arises from the nucleus ambiguus. It is closely associated with the vagal nerve and can be adherent to it. It supplies the soft palate, the recurrent laryngeal nerve and some fibres go to cardiac muscle.

Motoneurone location

The details of the location and morphology of the motoneurones in humans is sparse. In embryos, the position of motoneurones from the spinal accessory nerve has been identified and the cell column has been seen to extend from the very start of the spinal cord to the sixth cervical segment (Pearson, 1938). Pearson (1938) also described the position of the motoneurones at C1 to be laterally placed within the ventral horn. However, from animal work, it appears that in the cat these C1 motoneurones are more medially positioned (Vanner & Rose, 1984). The column of motor nuclei is located laterally in the ventral horn although, in the lower segments they are more medially and dorsally positioned as the lateral ventral horn enlarges. In the rat, the motoneurones supplying the upper, middle and lower muscles are rostro-caudally arranged (Kitamura & Sakai, 1982). In the cat, the motoneurones supplying the different parts of the muscle are somewhat intermingled along the length of the motoneurone pool (Liinamaa *et al.*, 1997; Vanner & Rose, 1984).

It is evident in the cat that the trapezius motoneurone pool is comprised of cells with two differently projecting dendritic trees (Vanner & Rose, 1984). The first project densely in a rostro-caudal direction generally projecting within the spinal accessory nucleus. To a lesser extent they project laterally into the white matter and dorsally as far as lamina VI. The second type of motoneurone has a more widespread dendritic tree, which project away from the spinal accessory nucleus. These are situated at the rostral and caudal ends of the column of motoneurones. Although the dendrites project in a rostral and caudal direction, they also project both laterally and ventrally into the white matter, dorsally as far as lamina VI and medially as far as the midline (Vanner & Rose, 1984).

The axons arising from these nuclei converge into bundles and emerge as rootlets from the lateral cord at irregular intervals. The largest rootlets were seen to emerge from the higher levels (see figure 6; Pearson, 1938). The fibres travel superiorly entering the skull through the foramen magnum. The nerve exits the skull through the jugular foramen and then passes downwards and laterally through or behind sternocleidomastoid (which it supplies) and across the posterior triangle of the neck, in the deep fascia (Williams *et al.*, 1989; Kent, 1971). Here it becomes superficial. Soo *et al.* (1986) described how the spinal accessory nerve is then joined in a plexus by the cervical nerves of C3 and C4 on the under surface of the upper portion of trapezius before supplying it. In the cat, the nerve branches to separately supply the different parts of the muscle (Richmond *et al.*, 1999). This branching was also seen in human cadavers, although these are my unpublished observations in four cadavers examined in the Department of Anatomy and Developmental Biology at UCL.

Stacey *et al.* (1996) described what they thought to be an anomalous case where trapezius had no supply from the spinal accessory nerve and therefore its motor and sensory innervation was through the cervical nerves only. Krause *et al.* (1991) explored the nerve supply in greater detail. They wanted to explain why after a radical neck dissection for metastatic disease, some patients developed problems with the motor control of the scapula and others did not. They demonstrated that Stacey's anomaly existed in 6.4% of those studied. In 71.1% their findings agreed with Soo *et al.* (1986), demonstrating communication between the cervical and spinal accessory nerve supply just before its innervation. In the final 22.4% the two supplies remained separate before innervation of the muscle. A cervical innervation into the lower portion of the trapezius muscle was also demonstrated. As this is not lost in radical neck surgery, this innervation is able to provide some motor input to the muscle. Indeed, in 10% of patients it innervates the whole muscle, in 43% it innervates part of the muscle and in 47% the cervical branch provides only a minor motor innervation (Krause *et al.*, 1993). In summary, trapezius has a motor supply from the spinal accessory nerve and an afferent supply from the cervical nerve but this may also provide a varying motor supply although it is inconsistent (Nori *et al.*, 1997; Fahrer *et al.*, 1974).

Given that a cervical motor supply exists in humans, it is relevant to consider the location of motoneurones with axons in this nerve. In rats and sheep these cervical motoneurones have been located using horseradish peroxidase (Kitamura & Sakai, 1982; Clavenzani *et al.*, 1994). In the rat, motoneurones were found to be positioned medially to those of the spinal accessory nerve and lying between C3 and C5 (Kitamura & Sakai, 1982). A medial location also recurs in sheep but the motoneurones are found at two distinct levels of C1 and C4 (Clavenzani *et al.*, 1994).

Function of trapezius

Trapezius has different actions depending upon the task. Its anatomy is such that different fascicles will pull in different directions upon different structures. This leads to contrasting functions of the different parts of the muscle. So, in elevation of the scapula, the upper fibres are active (Bull *et al.*, 1985) and the lower fibres are inactive (Guazzelli *et al.*, 1994). In depression of the scapula, the lower fibres are active and the upper fibres remain inactive

(Guazzelli *et al.*, 1994). Even during rotation of the scapula, the different muscle parts are imparting different actions. The upper fibres pull upon the distal end of the clavicle to create a moment of upward rotation. This compresses the clavicle through the sternoclavicular joint so that the pull of trapezius does not pull strongly through the more delicate cervical spine (Johnson *et al.*, 1994). Through the clavicle's attachment to the scapula, the upper fibres of trapezius act as part of a force couple to upwardly rotate the scapula during elevation of the arm. Meanwhile, the lower fibres pull directly upon the initially stable axis of rotation of the scapula (Dvir & Berme, 1978). This suggests that the lower fibres initially stabilise the axis, rather than move the scapula during rotation. This is true not only because these fibres attach right upon the axis of rotation, but also because at this early stage of elevation these fibres do not change length. Thus, the position of the axis of rotation is maintained so that the scapula rotates about a stable axis (Johnson *et al.*, 1994). Once the instantaneous centre of axis of rotation shifts laterally (see section 1.1, p.20), the lower fibres help to rotate the scapula by a downward pull upon the deltoid tubercle (see p.39).

So, the trapezius muscle can be functionally sub-divided into different parts. One of those parts has been further sub-divided. Jensen & Westgaard (1997) recorded from the anterior, middle and posterior parts (bordering on the middle part of trapezius) of the upper fibres and demonstrated differential activation during maximal isometric contraction whilst the arm was placed in different positions. They also recorded differential activation of these parts during three different tasks, abduction, arm circling and shoulder girdle elevation. Westgaard & De Luca (2001) went on to record from the upper fibres during slow and fast elevation. They concluded that there are different control mechanisms within this one sub-unit of the muscle. With fast contractions, the earliest recruited units had the greatest firing rate. During slow, postural contractions, this was reversed with the high threshold units having the greatest firing rate. They suggested that Renshaw cell activity, activated by the newly recruited units, inhibit those first recruited low threshold units. They concluded that postural units are differently controlled to those recruited during fast activity. Westgaard & De Luca (2001) suggested that the functional implication of this is to protect the low threshold postural units from fatigue.

The reaction of the upper part of trapezius to fatigue has been investigated by Kleine *et al.* (2000). They also demonstrated a sub-division of the upper trapezius by showing that these fibres have a greater ability to compensate for fatigue by the recruitment of additional motor units. This is in contrast to the lower fibres of the upper trapezius, in which in similar situations additional motor units are not recruited. Therefore, these authors demonstrate that the upper part of trapezius is sub-divided with some separation of the controlling mechanisms acting upon these different sub-units.

This varying control of sub-divisions within trapezius has been demonstrated in other muscles. Like trapezius, the sub-divisions of other muscles have different actions due to their widespread insertion upon the skeleton. For example, the cat biceps femoris has three compartments. The anterior compartment has fibres that attach above and below the hip and so are involved in hip extension, the middle and posterior compartments attach below the knee and are involved in a different proportion of hip extension and knee flexion. The posterior compartment also inserts upon the crural fascia which, when pulled, acts upon the ankle. These sub-units are active at different times and during different tasks such as locomotion, scratching and paw shaking (Carrasco & English, 1999; Chanaud *et al.*, 1991a). The human deltoid is another good example. This muscle has seven compartments, which attach around the shoulder from an anterior to posterior position. Together they abduct the arm. However, they are also involved in the contrasting actions of flexion and extension (Wickham & Brown, 1998). These different muscular subdivisions have also been demonstrated in gracilis, semimembranosus, tensor fasciae latae, sartorius, serratus anterior and tibialis anterior in the cat and rat (Carrasco & English, 1999; Chanaud *et al.*, 1991a; Chanaud *et al.*, 1991b; Grow *et al.*, 1996; Pratt *et al.*, 1991; Pratt & Loeb, 1991). They have also been described in the biceps brachii, pectoralis major, the first dorsal interosseous and masseter in humans (Carrasco & English, 1999; Jensen & Westgaard, 1997). That these muscle sub-units impart different actions suggest that their control can be separated. There are three mechanisms by which this differential control might occur.

The first is due to the grouping of fibre types within the muscle. Chanaud *et al.* (1991b) investigated the grouping of muscle fibre type in semimembranosus and tibialis anterior. They have a non-uniform distribution of slow and fast motor units within different sub-sections of the muscle. These sub-sections act independently during slow locomotion but with vigorous action the muscle acts homogeneously. Chanaud *et al.* (1991b) suggest that the differential action is due to the orderly recruitment of different sized motor neurones (Henneman *et al.*, 1965). In this aspect, trapezius is a border line case. Its distribution of slow and fast fibre types has been described as being relatively even throughout the muscle. However, there are more slow fibres within the lower section of upper, middle and lower parts (Lindman *et al.*, 1991). Thus, this suggests that each part of trapezius may be further sub-divided and these sub-divisions could be separately controlled.

The second mechanism of differential control between the sub-units of muscle is through a separate nerve supply. For example, the cat sartorius and biceps femoris have branched innervation to their different sub-units (Chanaud *et al.*, 1991b; Pratt & Loeb, 1991). This innervation is discrete and compartmentalised (Chanaud *et al.*, 1991b). As previously described the innervation of trapezius is varying and complex. Although, the dissection of the spinal accessory nerve as it enters trapezius does suggest that there are separate branches to the upper, middle and lower parts (personal observations on four human cadavers). This anatomical division might correspond to the three functional divisions of trapezius.

The third mechanism described is the differential input upon different parts of a muscle's motoneurone pool. Pratt *et al.* (1991) investigated the low threshold, cutaneous afferent input upon different simple and complex, compartmentalised muscles. They demonstrated varying reflex effects upon different sub-units of the complex muscles that were not apparent within the simple muscles. Chanaud *et al.* (1991b) and Chanaud & Macpherson (1991) demonstrated 'non synchronous activation of different muscle regions' of the cat biceps, during different tasks which were unrelated to fibre type distribution. Once more, this method of differential control may be relevant to the control of trapezius. Indeed, anatomically trapezius has several possibilities to allow for such differential control. There are two motoneurone pools (Krammer *et al.*, 1987; Clavenzani *et al.*, 1994); those motoneurones that course in the spinal accessory nerve and those that course in the cervical spinal nerve, leaving open the possibility of different inputs upon these different motoneurone pools. Trapezius also has two different motoneurone dendritic projections at different spinal levels (Vanner & Rose, 1984). The widespread and different dendritic projections open the possibility of a variety of different connections at different segmental levels. The independent activation of the upper trapezius described earlier and demonstrated by Jensen & Westgaard (1997), may be an example of this varying input upon different parts of the motoneurone pool.

During unilateral shoulder movements the two trapezii seem to work independently from each other. Indeed, the right and left muscles also work independently during rotation of the cervical spine (Bernhardt *et al.*, 1999). However, the bilateral trapezii work together during extension of the cervical spine and as an accessory muscle to respiration (Williams *et al.*, 1989; Charlton *et al.*, 1988). They also function together when demands are imposed that require head stabilisation (Keshner *et al.*, 1989). Although Keshner *et al.* (1989) recorded upper trapezius activity during head stability tasks, they suggest that the trapezii are functioning to stabilise the scapulae rather than stabilise the head. This may allow other scapulothoracic muscles to act more efficiently upon the cervical spine.

As described earlier, trapezius acts to stabilise the scapula. This is true for shoulder elevation but it is also true during hand activities without arm movement. Many authors have recorded trapezius activity during various hand tasks (Kitahara *et al.*, 2000; Roman-Liu *et al.*, 2001; Schnoz *et al.*, 2000; Sporrong *et al.*, 1995). Both Kitahara *et al.* (2000) and Schnoz *et al.* (2000) have recorded from the upper, middle and lower fibres of trapezius. They investigated the trapezius activity during a non-complex task of finger tapping at various rates. All parts of trapezius showed significant increases in activity with increased rate of tapping, although this did not occur in every subject. The activity was not synchronised with the tap. This lack of synchrony suggests that trapezius is controlling a different task to the hand muscles such that it may be stabilising the scapula whilst the hand task is completed. Roman-Liu *et al.* (2001) recorded from lower trapezius whilst the subject performed a complex task over a 25 minute period. The subject had to press a button at varying speeds and pressures which was indicated by sound and visual feedback. As the precision of the task became more complex, the tension within the lower trapezius increased. This suggests that mental complexity also increases trapezius activity. These findings corroborate observations made in the upper trapezius. Waersted *et al.* (1996) recorded an increase in upper trapezius activity whilst subjects were asked to press buttons in response to a visual stimulus. This required the subject to say whether two types of data upon a screen were the same and this was done with a time constraint. They demonstrated that the attention-demanding task increased upper trapezius activity.

To summarise, trapezius is a sub-divided muscle, which has a variety of different functions. The differential control of its sub-divisions may be controlled by anatomical and physiological means.

1.2.2.2 Serratus anterior.

The serratus anterior muscle is divided into two parts, both of which originate from the medial border of the scapula (Kent, 1971; Paine & Voight, 1993). The fibres traverse around the thoracic cage to insert as individual digitations upon the ribs. The number of digitations vary between seven and ten with the majority having eight digitations to the first eight ribs (Cuadros *et al.,* 1995; see figure 7).

The upper part originates from the superior angle and the medial border of the scapula where its tendon blends with the tendinous insertion of levator scapulae and the rhomboids (Williams *et al.*, 1999). This upper part inserts upon the first to the fourth ribs (Paine & Voight, 1993; see figure 7).

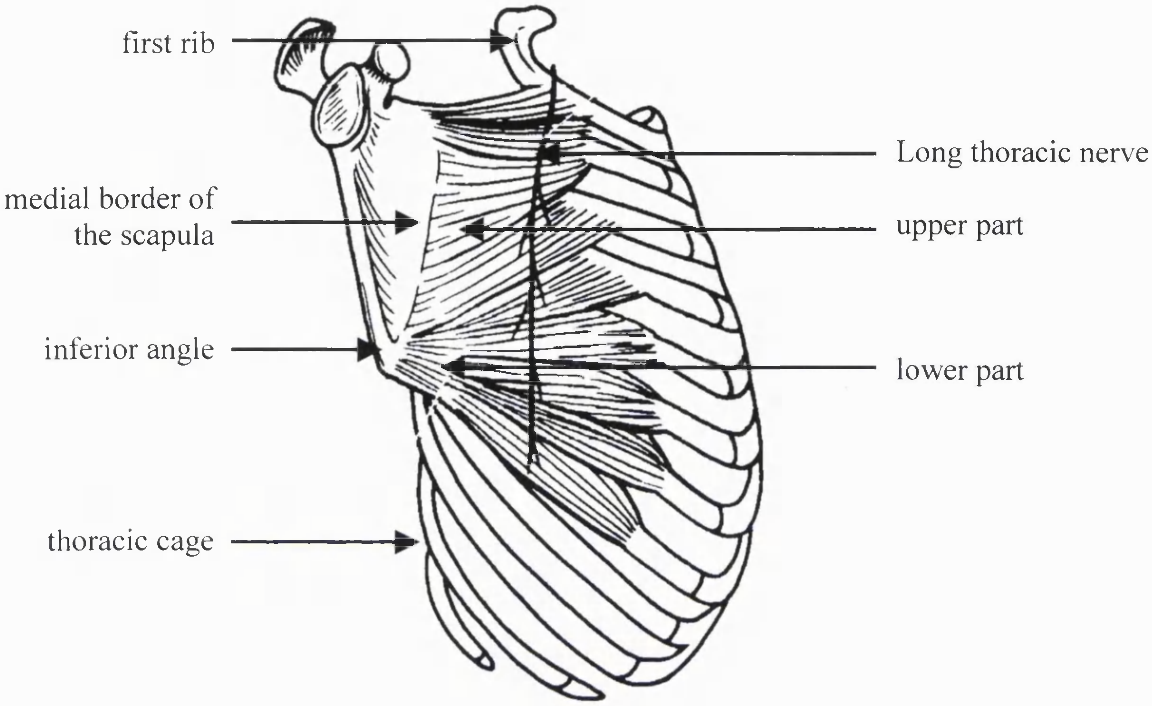


Figure 7. The location and attachments of serratus anterior. The thoracic cage with the scapula showing the origin and insertion of the upper and lower parts of the serratus anterior muscle. The nerve supply, the long thoracic nerve, is also illustrated. Adapted from Fromm (2001).

The lower and largest part of the muscle originates from the inferior angle of the scapula. The fibres insert upon the fifth to eighth ribs (although 13% have digitations up to and including the tenth rib; Cuadros *et al.,* 1995). The external oblique muscle attaches upon the lower eight ribs, so where these muscles share rib attachments their fibres interdigitate (Williams *et al.*, 1989; see figure 8).

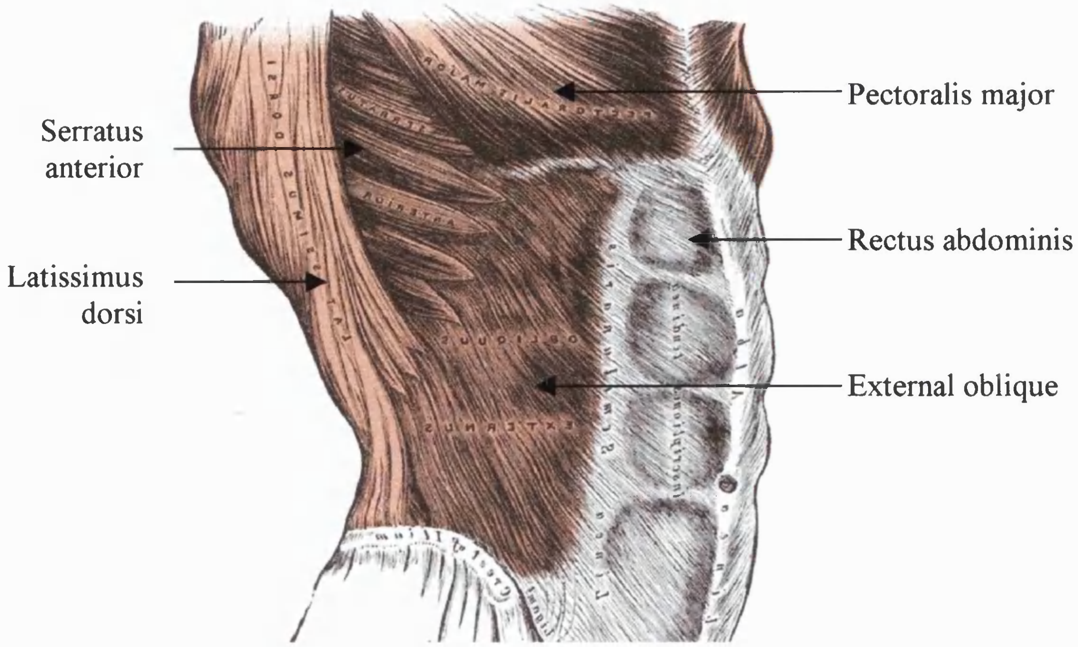


Figure 8. The lateral torso illustrating that both the serratus anterior and latissimus dorsi muscles interdigitate with the external oblique. Adapted from Williams *et al.* (1989).

Little is known about the fibre types in serratus anterior. Grow *et al.* (1996) investigated the fibre types of this muscle in rats. They showed that the proportion of slow muscle was greater at the lower digitations. When Grow *et al.* (1996) denervated the muscle sparing the lower supply to reinnervate it, a greater proportion of slow muscle was found. They concluded that the slow fibre type was dependent upon its lower segmental supply.

The nerve supply to serratus anterior is the long thoracic nerve, a mixed nerve from C5, C6 ± C7. The roots from C5 and C6 merge within scalenus medius in the neck. This nerve then tracks in a caudal direction where it is medial, anterior and inferior to the spinal accessory nerve. It is joined by the root from C7 (if present) and then turns laterally to pass over the first rib. It tracks over serratus anterior in the mid axillary line, supplying each digitation of the muscle as it goes (see figure 7; Williams *et al.*, 1989; Kaplan, 1980). The efferent fibre conduction velocity of the long thoracic nerve has been recorded in man at a range of velocities from 50 to 67m/s (Alfonsi *et al.*, 1986; Lo Monaco *et al.*, 1983; Petrera & Trojaborg, 1984).

The serratus anterior muscle functions to stabilise and rotate the scapula during movements of the arm (Bull *et al.*, 1990; Paine & Voight, 1993). Its activity maintains the medial edge of the scapula in contact with the chest wall at rest and during arm movement (Kent, 1971). Serratus anterior also protracts the scapula such that it is active during pushing, punching, push-ups and throwing (Glousman *et al.*, 1988; Lear & Gross, 1998; Paine & Voight, 1993; Bull *et al.*, 1989).

In relation to elevation of the arm, serratus anterior acts to rotate the scapula. At the start of rotation, the pull of the rotator cuff and the upper part of serratus anterior upon the scapula are counterbalanced by the action of the lower trapezius, the rhomboids and levator scapulae (Dvir & Berme, 1978; Peat, 1986). In this way the upper serratus anterior helps to stabilise the centre of rotation of the scapula during the first phase of arm elevation. With its long moment arm, the lower part of serratus anterior pulls upon the lower medial border of the scapula, externally rotating it about both the deltoid tubercle and then the acromioclavicular joint (see figure 9; Peat, 1986; Dvir & Berme, 1978).

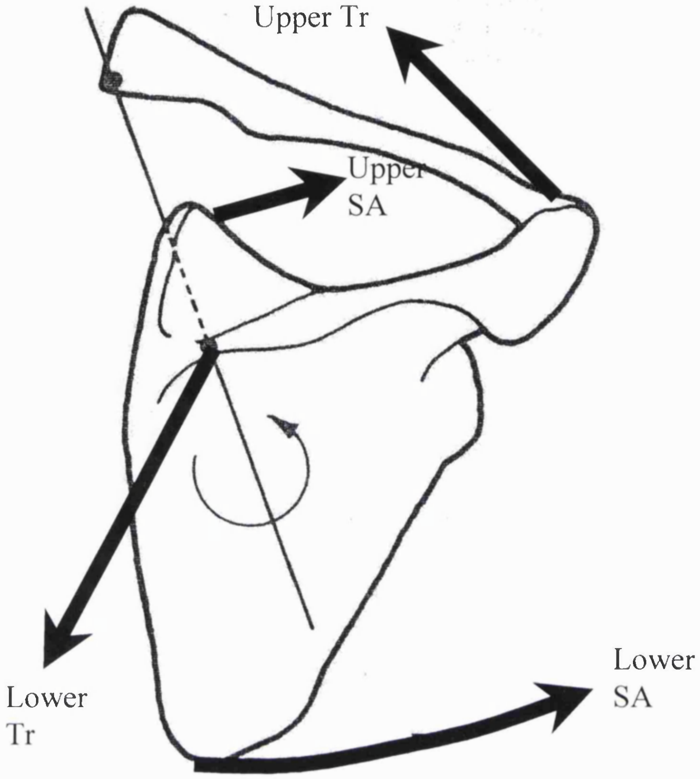


Figure 9. The direction of force produced by the trapezius and serratus anterior muscles. The upper serratus anterior (SA) and lower trapezius (Tr) helps to stabilise the centre of rotation. Upper trapezius pulls the lateral clavicle upwards, whilst the lower serratus anterior pulls the inferior angle laterally externally rotating the scapula. Adapted from Kapandji (1986).

1.3 Reflex connections between synergists.

The preceding section indicates that trapezius and serratus anterior are synergists. However, the mechanisms that help to co-ordinate their co-contraction are unknown. Examples exist of reflex connections between other synergists, which play a part in the control of their co-ordinated action. Although there is extensive detail in relation to reflex connections between synergists in animals, there is more limited detail in relation to humans. However, there has been a recent explosion of information regarding human reflexes. This has been brought about, at least partly, by better technology and more sophisticated computational methods.

The reflex connections of various afferent fibres and the patterns of convergence of various reflex and descending pathways can now be studied using a variety of indirect means. For example, the probability of a single motor unit firing as a result of a particular input can be recorded as a post stimulus time histogram. The timing of any increase or decrease in probability of firing can be used to give an indication of the central processing. Thus, one can estimate the number of interneuronal connections that are interposed between the stimulated afferent and the motoneurone pool under examination. If a mixed peripheral nerve is electrically stimulated, one can also try to identify the origin of the afferents that are involved in the generation of a reflex response. The largest diameter axons in a given nerve (and also the fast conducting afferents) have the lowest threshold to electrical stimulation. So, using soleus afferents as an example, the fastest group II afferents have a threshold which is 2.1 times that of the fastest group I afferents (Simonetta-Moreau *et al.*, 1999). Thus, low stimulation intensities can be used to specifically evoke a group I response. In addition, one way a group II response may be differentiated from a group I response is by investigating the effect of cooling of the nerve, as cooling will slow the smaller afferents to a greater degree (Schieppati & Nardone, 1997). Other common methods of investigating reflexes between synergistic muscles in humans are to evoke the Hoffmann reflex (H reflex) or the tendon jerk and use a test-condition paradigm. A typical test-condition paradigm involves recording a change in amplitude of a test reflex by the stimulation of a conditioning stimulus at appropriate test-condition intervals. This can be used to infer a reflex or descending input to the motoneurone pool (Pierrot-Deseilligny & Mazevet, 2000; Mazevet & Pierrot-Deseilligny, 1994).

1.3.1 Methodological considerations.

The H reflex and tendon jerk are used in the investigations of the reflex connections presented in this thesis. The H reflex was named after Paul Hoffmann who, in 1918 demonstrated that stimulation of the tibial nerve evoked a soleus reflex. The latency of this reflex resembled that of the stretch reflex evoked by a mechanical tap. This suggested that these reflexes were mediated by the same fast conducting afferents (Hoffmann, 1918). The central pathway of these Ia afferents was described by Lloyd (1943) in the cat. Lloyd (1943) demonstrated that the Ia afferents responding to a muscle stretch, monosynaptically facilitate the motoneurone pool of the homonymous muscle. Later, electrophysiological evidence corroborated this (Mendell & Henneman; 1971). Anatomical evidence was presented by Iles (1976), who stained primary afferents with their boutons terminating upon motoneurones in the cat spinal cord. That the H reflex in humans activated this same pathway was confirmed by Magladery & McDougal, (1950). Thus, both the H reflex and the tendon jerk were thought to evoke a Ia facilitatory monosynaptic reflex.

Although both the H reflex and the tendon jerk were both thought to evoke similar central pathways, it is recognised that the H reflex is not the electrical equivalent of the tendon jerk (Burke *et al.*, 1983; Van Boxtel, 1986). They differ in a number of ways; one important difference is that they do not evoke an identical afferent response. Matthews (1972) and Burke *et al.* (1983) have described the afferent contribution to the brief percussion of a tendon. The major contribution to this afferent barrage is from the group Ia afferents. Few discharges of the group Ib afferents from golgi tendon organs or the group II muscle spindle afferents have been recorded (Burke *et al.*, 1983). However, the tendon jerk does activate mechanoreceptors in the skin evoking cutaneous afferent input (Burke *et al.*, 1983).

The afferent response from the electrical stimulation that evokes an H reflex is dependent upon the distribution of the size of the afferent nerve fibres and the stimulation intensity. However, whatever the size of the afferent axons and the stimulation intensity used to evoke the response, both the H reflex and the tendon jerk evoke a Ia monosynaptic facilitatory reflex. In addition, it is possible that other pathways contribute to these reflex responses. Burke *et al.* (1984) demonstrated that there is time for other temporally dispersed input to contribute to the rising phase of a composite EPSP before the motoneurones discharge. Thus, the activity of motoneurones discharging in the later stage of the rising phase of a composite EPSP may have been activated or modified by other oligosynaptic inputs (Burke *et al.*, 1984). In summary, the H reflex and tendon jerk are not simply Ia facilitatory monosynaptic reflexes. The composition of the afferent profile activated must be taken into account in the analysis of any experimentation of H reflexes and tendon jerks.

1.3.2 Monosynaptic Ia reflexes between synergists.

The reflexes relevant to this study are mainly those evoked from group Ia afferents. Some other Ia reflexes contributing to muscle synergy are therefore discussed here. As described in the previous section, Ia afferents project monosynaptically to the motoneurone pool of the homonymous muscle (Lloyd, 1943). In addition, these Ia afferents project monosynaptically to heteronymous muscles that function as synergists (Baldissera *et al.*, 1981; Schomburg, 1990). The common function of these muscles seems to be reflected in the pattern of projections of their Ia afferents. The Ia projections of close synergists have been described in both animals and humans. Thus, in the cat, such reflexes are evoked between muscles that generate single movements, for example between biceps and brachialis which together act to produce flexion of the elbow (Caicoya *et al.*, 1999). In humans, an example of this simple functional pattern of Ia projection exists between the wrist flexors, flexor carpi ulnaris and radialis (Chalmers & Bawa, 1997). Interestingly, monosynaptic reflex connections do not always exist between muscle synergists. Chalmers & Bawa (1997) revealed that the wrist extensors, extensor carpi radialis and ulnaris do not have monosynaptic Ia reflex connections between each other even though they co-contract in wrist extension. Instead, each muscle makes a heteronymous connection to extensor digitorum, another wrist extensor.

Group Ia reflexes are also evident between muscles that act over a single joint but do not necessarily act to produce movement in the same direction. An example might be the reflexes that project across the shoulder from biceps to the rotator cuff muscles. These muscles work together to help stabilise the glenohumeral joint during the positioning of the forelimb in the cat (Caicoya *et al.*, 1999). So, although their line of pull is differently directed these muscles are also monosynaptically connected.

The balance of Ia reflexes varies across muscle groups. Indeed, Ia connections can evoke larger EPSPs heteronymously than homonymously (Baldissera *et al.*, 1981). Of the heteronymous connections, those between synergistic muscles may be stronger in one direction than the other; that is, they can be skewed or even unidirectional. Caicoya *et al.* (1999) and Fritz *et al.* (1989) suggest that these skewed or unidirectional reflexes tend to connect from the proximal muscles to the distal muscles. They suggest that this enables the repositioning of distal segments with proximal movement. In summary, bi-directional, monosynaptic Ia reflex connections between synergists have been described in both human and animal studies (Cavallari & Katz, 1989; Cavallari *et al.*, 1992; Caicoya *et al.*, 1999;

Fritz *et al.*, 1989). In addition, closely balanced Ia bi-directional reflexes seem to exist between those muscles that act together to produce movement in a single direction (Caicoya *et al.*, 1999).

1.3.3 Some other Ia reflexes evoked between synergists.

Group Ia facilitatory reflexes connecting synergists are not necessarily monosynaptically mediated. Indeed, di- and tri-synaptic Ia facilitation has also been demonstrated between synergists. For example, Jankowska *et al.* (1981) recorded EPSPs consistent with both di- and tri-synaptic connections between Ia afferents from ankle and toe extensors to the motoneurone pool of the hamstrings in the cat. In addition to these oligosynaptic reflexes, Ia afferents also input to the cervical propriospinal system. In the cat, a propriospinal system has been identified, using electrophysiological and staining techniques, at C3 and C4 (Alstermark *et al.*, 1987; Alstermark *et al.*, 1990). This system may be a point of relay and modulation for Ia and other afferent and descending information upon upper limb motoneurones. These C3/4 propriospinal neurones project to muscles throughout the whole of the forelimb. That is, to muscles acting over the shoulder, the elbow, wrist and digits or indeed, a combination of these muscles which control several of these joints. So, this system helps to co-ordinate the stability of the shoulder whilst the forelimb is reaching (Tantisira *et al.*, 1996).

Whether a propriospinal system exists in man is yet to be clearly established. Indeed, Nakajima *et al.* (2000) demonstrated a decreasing influence of the C3-4 propriospinal tract in progressively higher species. The New World squirrel monkey species, with its weak monosynaptic corticospinal projections to cervical motoneurones, have a relatively strong projection to the propriospinal system. In contrast, the macaque monkey, with a stronger monosynaptic corticospinal projection to cervical motoneurones, has a weaker projection to the propriospinal system. So, Nakajima *et al.* (2000) predicts in man, where the monosynaptic corticospinal tract is particularly strong, the C3-4 propriospinal system will not significantly input upon the upper limb motoneurones.

On the other hand, there is a body of work that suggests a role for the propriospinal system in man. For example, Burke *et al.* (1992) revealed a pattern of converging inputs upon flexor carpi radialis motoneurones at test-condition intervals that are compatible with mediation through a propriospinal system. This included weak, low threshold facilitatory afferent input, which is suggestive of a group I effect. Also, Pauvert *et al.* (1998) demonstrated that low threshold afferents from the musculocutaneous nerve facilitate flexor carpi radialis at test-condition intervals that are again consistent with their mediation through a propriospinal system. Interestingly, Pierrot-Deseilligny (1996) suggests that this propriospinal system is utilised to a greater degree than normal when the corticospinal tract is damaged by stroke.

Polysynaptic, long latency reflex activity evoked by a muscle tap has also been demonstrated between synergists. Some of these long latency reflexes are thought to be transcortical (Taylor *et al.*, 1995). Dimitrijevic *et al.* (1980) evoked long latency reflexes in both ipsilateral and contralateral paraspinal muscles in humans. These muscles work synergistically in extension of the trunk. Also, Myriknas *et al.* (2000) evoked these long latency reflexes between other truncal muscles. The reflexes were evoked bilaterally in rectus abdominis, which work together in flexion of the trunk. However, that long latency reflexes evoked by a mechanical tap to a muscle, are evoked by Ia activity has been challenged by Corden *et al.* (2000). They evoked the stretch reflex in the first dorsal interosseous muscle by tapping the lateral edge of the distal interphalangeal joint. Corden *et al.* (2000) then immobilised the index finger in the belief that this would prevent the muscle stretch and then tapped in the same location so evoking the same cutaneous input. The early stretch reflex of the first dorsal interosseous muscle was obliterated leaving the long latency response. Thus, Corden *et al.* (2000) evoked these reflexes independently of a muscle stretch but not without cutaneous input. They conclude that rather than these long latency reflexes being mediated by Ia afferent input, the mechanical tap drives a reflex that is cutaneous in origin.

In summary, group Ia facilitation between synergistic muscles can be investigated in humans using indirect means. These investigations often evoke the H reflex and tendon jerk by using an electrical stimulus or a mechanical tap to activate Ia afferents. Such investigations have demonstrated the existence of Ia facilitatory connections between muscles acting synergistically. These reflexes are believed to be processed both at spinal and supraspinal levels. However, there is still controversy as to the contribution of the Ia afferents to these longer latency responses.

1.4 Aim of study.

This introduction establishes that the trapezius and serratus anterior muscles act together to rotate and stabilise the scapula during arm movement. However, little is understood of their homonymous and heteronymous reflex control. The aims of these investigations were three fold. Firstly, to explore the reflex control mechanisms that assists the co-ordination of these bilateral muscle pairs. Secondly, to explore the reflex mechanisms that assists the synergistic action of trapezius and serratus anterior. Finally, to explore the heteronymous projections from upper limb afferents to both trapezius and serratus anterior that might assist in arm movement and to investigate how these might change in those individuals with shoulder dysfunctions.

2 IPSILATERAL AND CROSSED REFLEXES IN TRAPEZIUS

2.1 Introduction

As described in section 1.2.2.1, the trapezius muscles are axial and bilaterally located. The independent control of each of these two muscles is necessary in the rotation and stability of the scapula during movements of each arm (Culham & Peat, 1993; Peat, 1986). However, both trapezii co-contract in movements of the head and neck (Bernhardt *et al.*, 1999; Williams *et al.*, 1989) and when acting as an accessory muscle to respiration (Charlton *et al.*, 1988). This bilateral control must demand close links between the two trapezius muscles. Indeed, as figure 10 illustrates, even when trapezius acts to move one arm, it is closely linked to the contralateral muscle presumably to help with postural alignment and the maintenance of balance and stability of the trunk.

Despite the requirement for both independent control and the co-ordination of the two muscles, the underlying neural circuitry controlling trapezius is only partially understood. Short latency reflexes have been revealed by tapping the spinous processes or the acromion (Lundh & Rosen, 1979; Shimizu *et al.*, 1993). Similarly, tapping various parts of the head and wrist evoke reflex activity in trapezius which is altered in disorders such as stroke and Parkinson's disease (Lisy, 1989). All of these results have been interpreted in terms of afferent action on the ipsilateral trapezius. On the other hand, the reflex control of the contralateral trapezius and how the two trapezius muscles are controlled together has not been explored. Thus, the purpose of this study was to investigate the neural circuitry of the trapezius muscle with particular attention to its bilateral control.

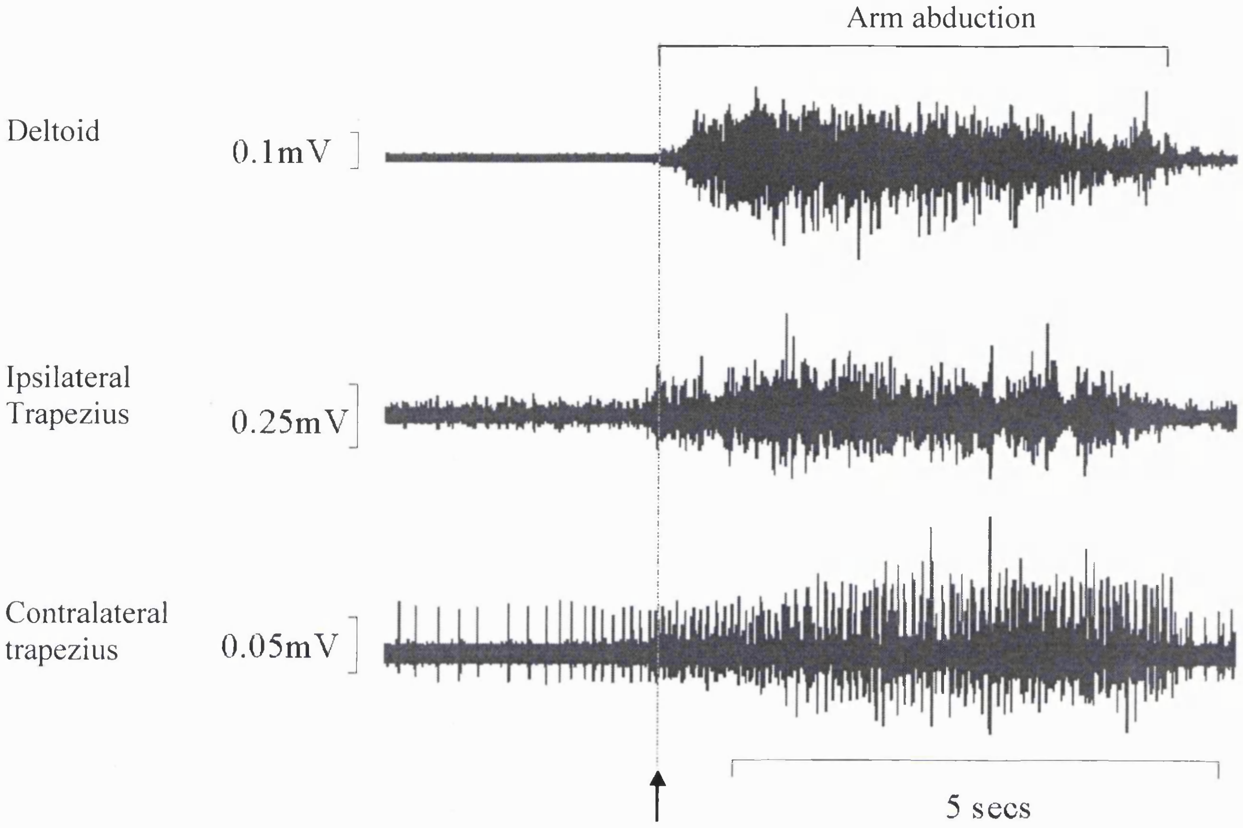


Figure 10. EMG of deltoid and trapezius muscles during abduction of the arm. EMG of ipsilateral deltoid (top), the ipsilateral lower trapezius (middle) and the contralateral lower trapezius (bottom) before, during and after abduction of the ipsilateral shoulder. EMG activity of the contralateral lower trapezius (recorded using a concentric needle) illustrates that this muscle is active during ipsilateral abduction. The arrow and dotted line mark the onset of abduction.

2.2 Methods

Recordings were made, with local ethical approval and informed consent, from a core group of eighteen healthy subjects aged between 20 and 51years.

2.2.1 Reflex activity evoked by a mechanical tap to the trapezius muscle.

Whilst the subjects were sitting, reflexes were evoked by (a) tapping the lower fibres of trapezius as they insert into the medial end of the spine of the scapula and (b) tapping the upper fibres as they attach into the distal end of the clavicle. A specially designed tapping device delivered a minimum of 10 taps at constant amplitude and at a rate of between 0.33 and 1Hz. The tapping device was constructed from a powered Ling vibrator, extended by a probe, with a moulded plastic tip with a rounded end of approximately 4mm. A digital pulse controlled the timing of the tap (using a CED 1401). Surface EMG was recorded bilaterally using adhesive electrodes (Blue Sensor) placed edge to edge with the recording area 3cm apart. When recording from the upper fibres of trapezius, the electrodes were positioned mid way between C6 and the acromion process (Jensen & Westgaard, 1997). When recording from the lower fibres, the electrodes were positioned in line with these fibres at the level of T6/7 (see figure 11). The electrodes recording the lower fibres of trapezius were placed close to the mid-line. Such a location presents the possibility that the trapezius recordings could be contaminated by activity from the contralateral side. Indeed, that the lower trapezius is thin and that the rhomboid major lies directly beneath these fibres suggests that trapezius activity could also be contaminated by the activity of rhomboid major. These factors have been examined and the considerations presented in Appendix I suggest that this was not the case.

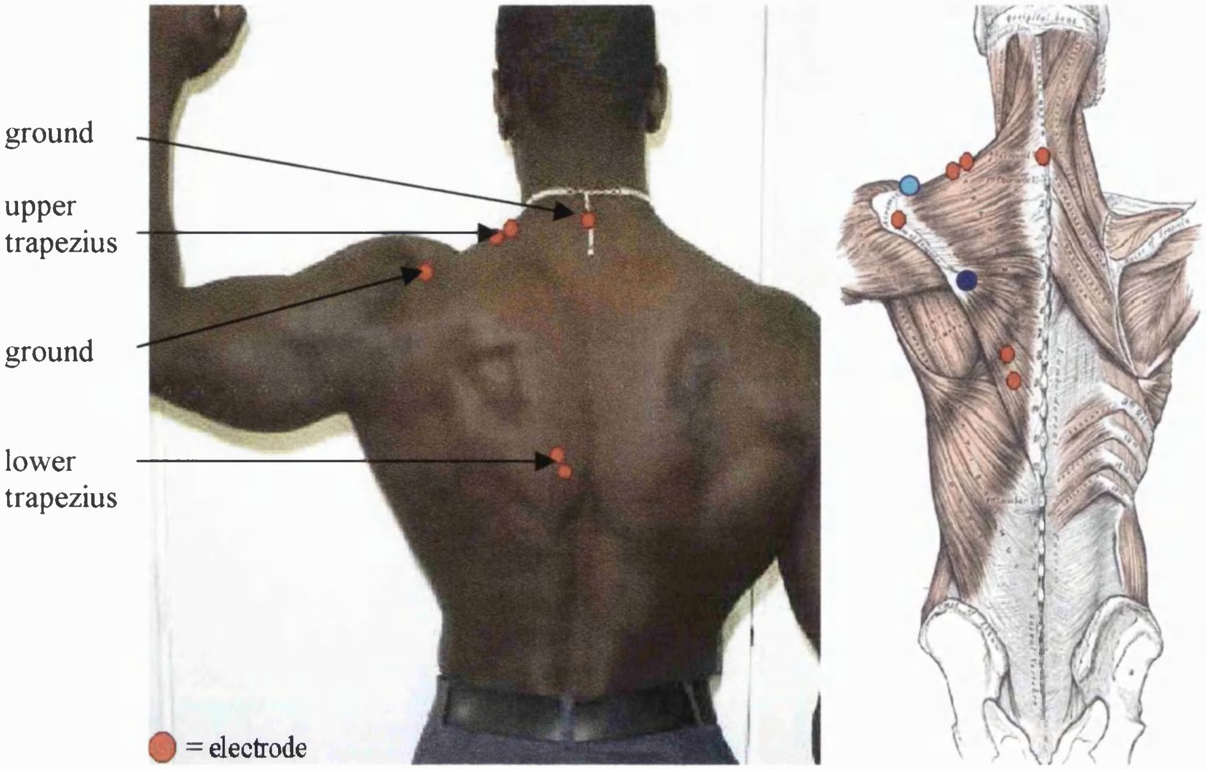


Figure 11. The location of electrodes used to record trapezius EMG. The positions of the electrodes overlying the upper and lower fibres of the trapezius are marked in red. Those recording the upper fibres were grounded using an electrode positioned over the spinous process of T1. Those recording the lower fibres were grounded using an electrode positioned over the acromion process. ◉ Indicates the anterior tapping point of the upper trapezius. The● indicates the tapping point of the lower trapezius. The diagram of the posterior torso is adapted from Williams *et al.* (1989).

The EMG was amplified (Digitimer NL824) and filtered (Neurolog NL125) with a bandwidth of 30 to 3KHz. The data was converted from an analogue to a digital signal at a sampling frequency of 4 to 20KHz, (CED 1401) and stored for later analysis by CED Signal software. The EMG activity was averaged. The latency (measured to the nearest 0.25ms) and peak to peak amplitude of the resulting reflex was measured. The latency was taken to be the first clear deflection from baseline. The EMG was also rectified and averaged. The amplitude of any late reflex was also recorded. The maximum amplitude was measured and the percentage increase above the pre-stimulus mean activity was calculated. The procedure was repeated on some subjects, in which case each subject's mean latency was used in the calculation of the population results.

The experiments were carried out with the subject sitting with the arms and shoulders relaxed. Maximum voluntary contraction (MVC) was determined and particular levels of contraction were controlled with the aid of a visual feedback device. The experiments were also performed whilst the subject contracted the lower fibres of the ipsilateral trapezius by a combined retraction and depression of the shoulder girdle at 10 to 20% of MVC (twelve subjects, n=19). The resulting reflexes were averaged. The amplitude (measured from peak to peak) was compared to the amplitude of the reflex with the subject at rest. Differences in amplitude were analysed using a paired Student's t-test.

To ensure that any response of the contralateral trapezius was indeed as a result of ipsilateral afferent input and not due to mechanical transmission of the tap resulting in a local reflex in the contralateral muscle, an accelerometer was used to examine the transmission of the tap across the body. The accelerometer measured movement of the shoulder girdle in a superior/inferior direction by positioning it upon the ipsilateral superior surface of the acromion in three subjects. The tap was delivered and the reflexes were evoked and recorded as described above. The accelerometer was then positioned contralaterally and the taps were again delivered ipsilaterally in the same way. The average reflexes and the average amplitude of the superior / inferior movement was recorded and stored for later analysis.

2.2.2 Reflex activity evoked by electrical stimulation of the afferent nerve to trapezius.

Reflex responses of trapezius were also evoked by a 1ms square wave electrical stimulus applied to the cervical nerve of C3/4, with an inter-stimulus interval of 3 seconds. (See Appendix II, section 8.1 and section 8.2 for discussion of pulse width and inter-stimulus interval chosen.) A digital pulse (CED 1401) triggered the stimulus. The anode, a gauze covered metal plate, was positioned just below the clavicle. The cathode, a roving, gauze covered probe was used to locate the cervical nerve of C3/4. This is superficially located on the anterior surface of the upper fibres of trapezius above the clavicle (see figure 12). The cathode position was identified as the correct position by the resulting contraction of the trapezius muscle. The cathode was then replaced with a self-adhesive Ag /AgCl electrode.

EMG recordings were collected as detailed above. A sub-maximal reflex was evoked for data collection. A series of at least 10 stimuli were delivered. The EMG activity was averaged and the latency (measured to the nearest 0.25ms) and peak to peak amplitude of the resulting reflex was measured. The procedure was repeated with some subjects, in which case each subject's mean latency was used in the calculation of the population results (nine subjects, n=15). The experiments were carried out with the subject sitting with the arms and shoulders relaxed. The experiments were then repeated whilst the subject contracted the lower fibres of the ipsilateral trapezius at between 10 and 20% of MVC by a combined retraction and depression of the shoulder girdle (twelve subjects). The reflex responses were analysed as detailed above.

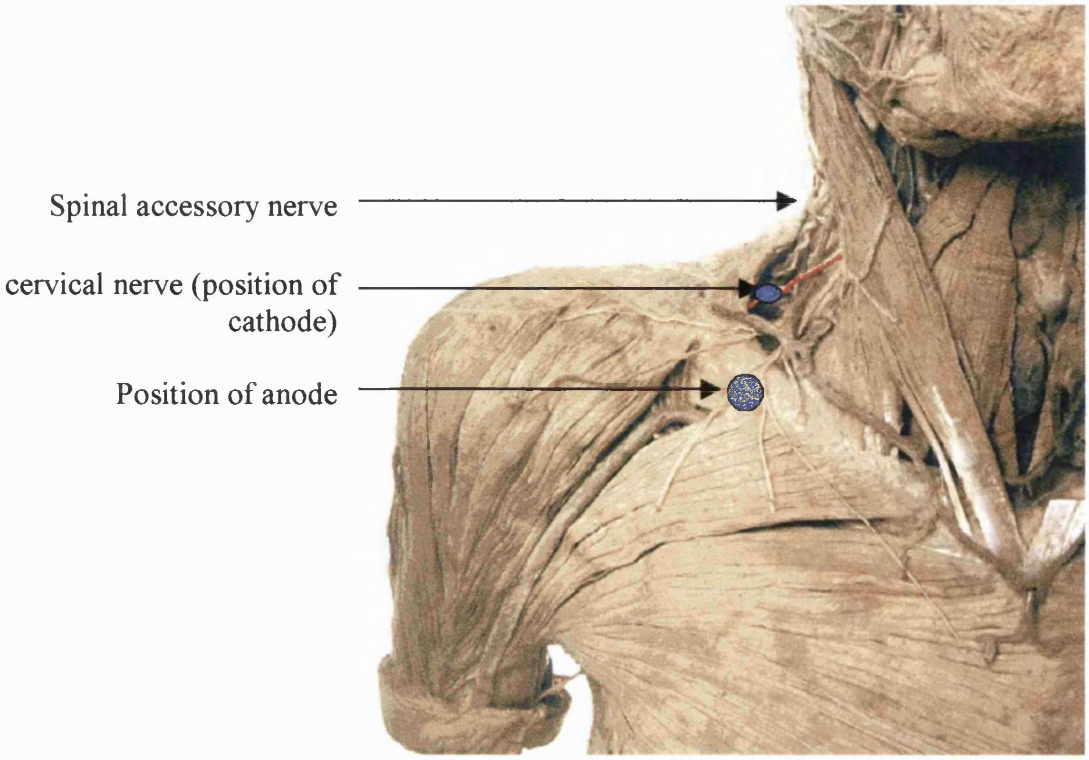


Figure 12. The location of electrodes used to stimulate the cervical nerve of C3/4. The dissection of the anterior upper quadrant shows the cervical nerve of C3/4 in red and the spinal accessory nerve as it spirals above it. The cathode is positioned over the cervical nerve and the anode is positioned just inferior to the clavicle. This picture is adapted from Copeland *et al.* (2000).

Recruitment curves for the lower trapezius reflexes was constructed as follows. Recordings were made from ten healthy subjects aged between 21 and 41. Reflex responses of the lower trapezius were evoked by an electrical stimulus applied to the cervical nerve of C3/4 and recorded bilaterally as previously described. The stimulus intensity was varied and the peak to peak amplitude of ipsilateral and crossed lower trapezius reflexes were measured for each level of stimulus intensity. The peak to peak amplitude for the ipsilateral and crossed reflexes were then plotted against stimulus intensity.

2.2.3 Comparison of the behaviour of the ipsilateral and crossed trapezius muscles.

2.2.3.1 The effect of muscle vibration on reflex amplitude.

Recordings were made from eight healthy subjects aged between 21 and 46 years of age. The ipsilateral and crossed lower trapezius reflexes were evoked by a) an electrical stimulus applied to the cervical nerve of C3/4 and by b) a mechanical tap to the insertion of the lower fibres as previously described. Vibration was applied to the ipsilateral muscle at 50 or 100Hz. The peak to peak amplitude of the average reflexes evoked before and during vibration was compared using paired Student's t-tests. Recruitment curves for the ipsilateral and crossed trapezius H reflexes were also constructed both before and whilst vibrating the muscle.

2.2.3.2 Cross correlation of EMG from bilateral trapezii.

Recordings were made from trapezius muscle pairs: the left and right lower fibres, the left and right upper fibres and the ipsilateral upper and lower fibres of trapezius. Ten subjects were asked to maintain a weak contraction of trapezius by abducting the arms to approximately 90°. This was aided by visual and auditory feedback of the EMG signal. Surface EMG recordings were collected as detailed above and stored on a PC using CED Spike software. Large amplitude spikes (approximately 3700) were selected from the EMG of both muscles using level detectors (Neurolog NL200). These trigger pulses were also converted to a digital signal (CED 1401) and stored on the PC using Spike software. Cross correlograms were constructed from the spikes using a 1ms bin width and a recording period of 100ms before and after the triggered period. The size of any peak within the correlogram was measured in terms of peak bin count divided by the mean bin count (κ), the number of extra bins above the mean divided by the mean (E/M) and the duration of the peak. To ensure an accurate reflection of the mean, the mean bin count was measured away from any central feature. A peak was significant if it was more than two standard deviations above the mean bin count. The standard deviation was calculated as the square root of the product of the number of extra spikes above the mean and the inter-spike interval (Davey *et al.*, 1986). Any differences in the size and duration of the peak between the three muscle pairs were analysed using a two-factor analysis of variance without replication.

2.2.3.3 Magnetic stimulation of the trapezius motor cortex.

To investigate the corticospinal input upon trapezius motoneurones, EMG recordings were made during magnetic stimulation of the motor cortex. The motor cortex activating trapezius was found 3-4cms lateral to the mid-line and 1-2cms anterior to the biauricular line (Berardelli *et al.*, 1991). EMG was recorded bilaterally from four subjects using surface electrodes as previously described. A 70mm double coil from the magnetic stimulator (The Magstim Co, Magstim 200) centred over an area of the motor cortex found to activate trapezius (henceforth referred to as the trapezius motor cortex) and the coil was held in place using a series of clamps. 25 stimuli were delivered with the coil orientated in a posterior anterior direction. This was repeated at different stimulus intensities. The stimulus intensities used generally ranged from 40% to 70% of the stimulator's output. The procedure was repeated with each subject, in which case each subject's mean latency was used in the calculation of the final results.

2.3 Results

2.3.1 Reflex activity evoked by a mechanical tap to the trapezius muscle.

As might be expected, a homonymous, short latency stretch reflex was evoked in trapezius by a brief tap to the muscle (see figure 13). A priori, one might expect this to be evoked monosynaptically. The latency of the reflex in the upper fibres of trapezius was 12.2 ± 1.1ms (n=9); when tapping the lower fibres the latency of the reflex in the lower fibres of trapezius was 11.9 ± 1.4ms (n=16) which is compatible with a monosynaptic reflex (see Discussion, section 2.4.1). The latency of the upper trapezius reflex is not significantly different from the lower trapezius reflex (Student's unpaired t-test, p=0.50). Long latency reflexes were not evident.

Figure 13. Examples of trapezius reflexes. A. Examples of average upper trapezius reflexes each evoked by single mechanical taps repeated 30 times to the insertion of the upper fibres. B. Examples of average lower trapezius reflexes each evoked by a mechanical tap repeated 30 times to the insertion of the lower trapezius fibres. The stimulus occurred at the onset of each trace.

In addition, and perhaps surprisingly, a short latency reflex was also evoked in the crossed trapezii (see figure 14). On tapping the upper fibres this crossed reflex in the upper fibres was evoked at 13.5 ± 1.3ms (n=9) and on tapping the lower fibres the latency of the crossed reflex in the lower fibres was 14.3 ± 1.7ms (n=16); the crossed reflex latency being 1.3 ± 1.4 and 2.4 ± 2.0ms significantly longer respectively (p = 0.04 & 0.0004 respectively). Again, long latency crossed reflexes were not evident.

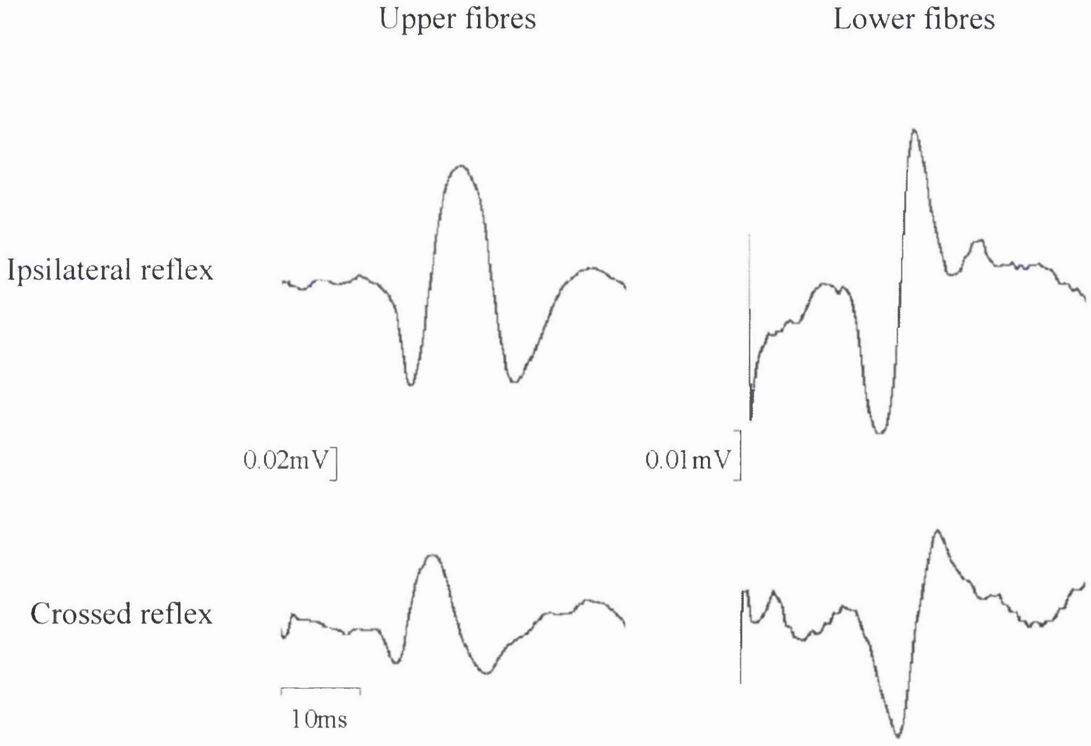


Figure 14. Average ipsilateral and crossed trapezius reflexes constructed from the result of 30 stimuli. A mechanical tap to the insertion of the upper fibres evoked the upper trapezius reflexes. A mechanical tap to the insertion of the lower fibres evoked the lower trapezius reflexes. The stimulus occurred at the onset of each trace.

While 30 sweeps were typically averaged, a clear discernible response was often evident with only 10 sweeps. When tapping the upper fibres, a reflex was always evoked in both the ipsilateral and contralateral upper fibres (100%, n=9) but not in the ipsilateral and contralateral lower fibres of the muscles (78% and 67% respectively, n=9). When tapping the lower fibres of trapezius, a reflex was always evoked in both the ipsilateral and contralateral lower fibres (100%, n=16) but not in the ipsilateral and contralateral upper trapezius fibres (88% and 63% respectively, n=8). These results are summarised in table 1. The amplitude of the crossed upper trapezius reflex averaged 55% of the amplitude of the ipsilateral upper trapezius reflex. The amplitude of the crossed lower trapezius reflex averaged 22% of the ipsilateral lower trapezius reflex.

		Ipsilateral upper fibres	*Contralateral upper fibres*	*Ipsilateral lower fibres*	*Contralateral lower fibres*
Tap upper fibres	latency (ms) mean ± S.D.	12.2 ± 1.1	13.5 ± 1.3	15.7 ± 1.2	16.7 ± 1.8
	Occurrence	9/9 (100%)	9/9 (100%)	7/9 (78%)	6/9 (67%)
Tap lower fibres	latency (ms) mean ± S.D.	13.1 ± 2.1	14.6 ± 2.0	11.9 ± 1.4	14.3 ± 1.7
	Occurrence	7/8 (88%)	5/8 (63%)	16/16 (100%)	16/16 (100%)

Table 1. The latency and occurrence of reflexes observed in upper and lower trapezius evoked by a mechanical tap to the upper and the lower trapezius muscle. (Standard deviation is abbreviated to S.D.)

In addition, the reflexes of both the ipsilateral and contralateral lower trapezius responded in a similar way to voluntary contraction. Voluntary contraction of the ipsilateral trapezius muscle also increased the mean background activity of the contralateral trapezius muscle 2.9 fold. Thus, unsurprisingly, the amplitude of both the ipsilateral and crossed reflexes were significantly increased (both $p>0.001$) with a combined retraction and depression of the shoulder girdle of the ipsilateral arm (n=19, see figure 15). Using a paired Student's t test, the percentage increase in the ipsilateral reflex was not significantly different from the percentage increase in the crossed trapezius increase (p=0.61).

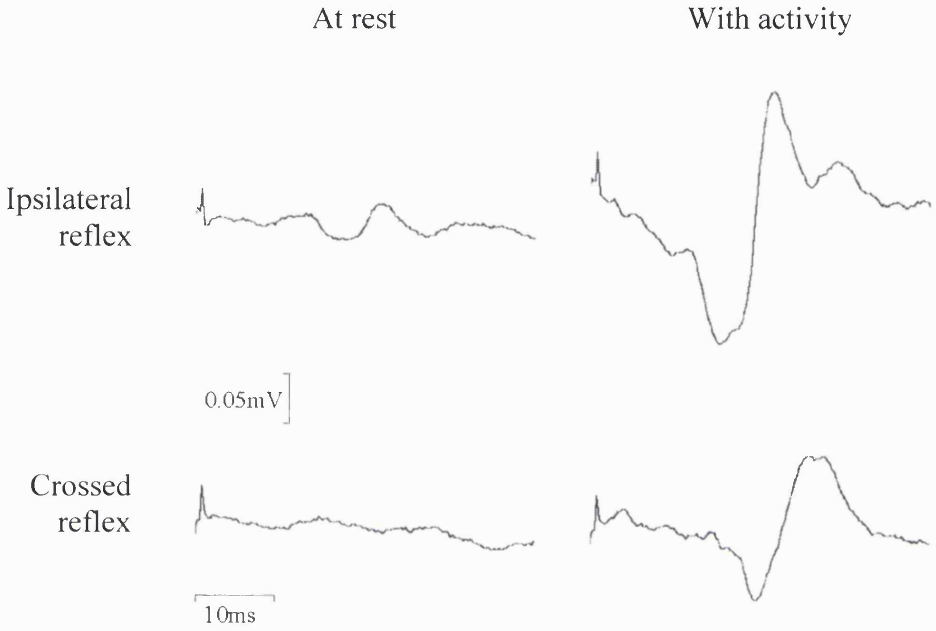


Figure 15. The effect of voluntary activity on trapezius reflex amplitude. Average ipsilateral and crossed lower trapezius reflex evoked by single taps of the ipsilateral muscle. The average reflexes were constructed from the result of 30 taps, whilst trapezius is at rest and with an ipsilateral trapezius contraction. The stimulus occurred at the onset of each trace.

2.3.1.1 Possible effect of transmission of the vibration from the tap across the body.

It is conceivable that the crossed trapezius reflex may have been a local reflex evoked from contralateral Ia activity evoked by mechanical transmission of the tap to the contralateral side. Thus, the mechanical tap may have been strong enough to cause a stretch contralaterally and therefore evoke a reflex locally on that side (Lance, 1965). This possibility was investigated in three subjects by using an accelerometer positioned upon the superior aspect of the acromion. The accelerometer recorded movement of the ipsilateral acromion during the tap of the ipsilateral trapezius. Movement of the contralateral acromion was then recorded during the tap of the ipsilateral trapezius. The mean decrease in movement of the acromion measured contralaterally was 83 ± 18% of that measured ipsilaterally (see figure 16). The reduction in movement across the trunk as measured by the accelerometer is summarised in table 2.

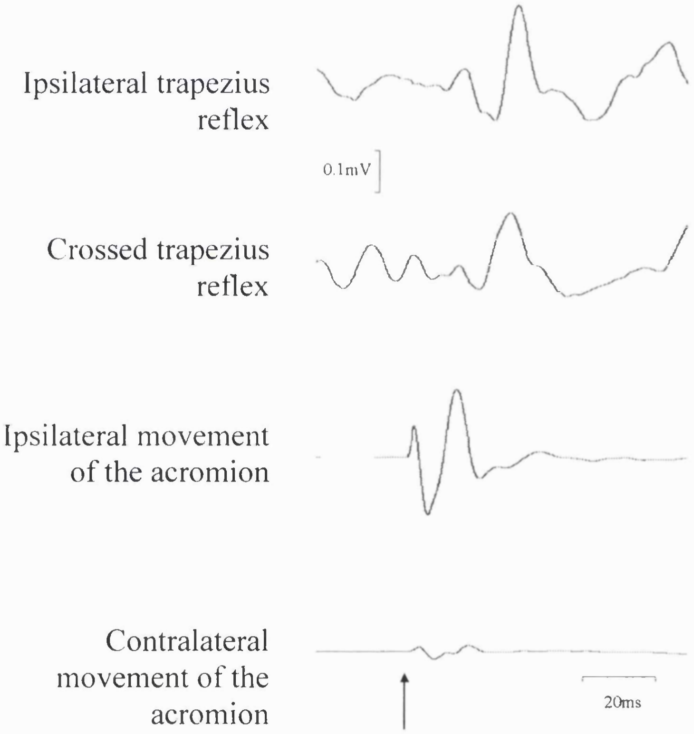


Figure 16. The degree of movement of the acromion during first an ipsilateral and then a contralateral trapezius tap. A mechanical tap to the ipsilateral trapezius evoked the average ipsilateral and crossed lower trapezius reflexes. Each average was constructed from the result of 10 stimuli. The movement of the scapula was recorded bilaterally using an accelerometer. The arrow marks the stimulus onset.

Ipsilateral movement	*Contralateral movement*	**% drop in movement**
0.4	0.02	94
0.86	0.33	62
1.68	0.13	92
	Mean	83 ± 18

Table 2. Movement of the acromion during first an ipsilateral and then a contralateral trapezius tap. The movement of the acromion was recorded using an accelerometer positioned upon the acromion process of first the ipsilateral and then the contralateral side. The movement was in response to a tap of the insertion of the lower fibres of trapezius on the ipsilateral side.

Although this movement is only a record of superior/inferior movement of the scapula and not an accurate measure of the vibration transmitted to the contralateral trapezius, it does reflect movement of a bony tissue, which will be particularly vulnerable to the passage of vibration. In conclusion, the vibration recorded here across the body in response to an ipsilateral tap of trapezius is unlikely to be sufficient to evoke this crossed reflex. Indeed, as can be seen in the next section, a similar crossed reflex is evoked with an electrical stimulus of the ipsilateral side thus these crossed reflexes are not subject to this methodological caveat.

2.3.2 *Reflexes evoked by electrical stimulation of the afferent nerve to trapezius.*

2.3.2.1 The ipsilateral H reflex in trapezius.

A short latency reflex in the ipsilateral lower trapezius muscle was evoked using electrical stimulation of the cervical nerve of C3/4 i.e. an H reflex (see figure 17). The mean latency of the reflex to the lower fibres was 10.9 ± 1.4ms (n=15). Although the average reflex was used to measure the latency, figure 18 illustrates that the ipsilateral lower trapezius reflex could be visualised with every stimulus. A similar response from the upper fibres of trapezius was impossible to analyse as the stimulation site was adjacent to the recording electrodes and this led to a large, long lasting stimulus artifact. Thus, analysis of the electrically evoked reflex was confined to recordings from the lower fibres.

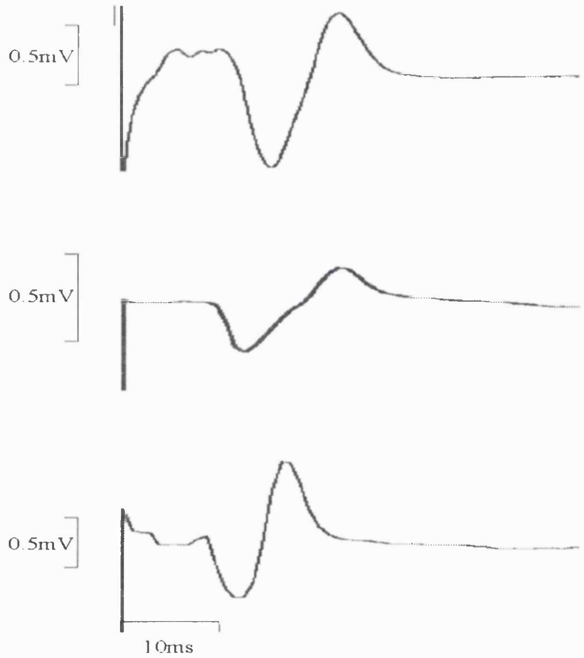


Figure 17. Ipsilateral lower trapezius H reflexes recorded from three subjects. These reflexes are the average of 30 sweeps. The artifact at the start of the trace marks the stimulus onset.

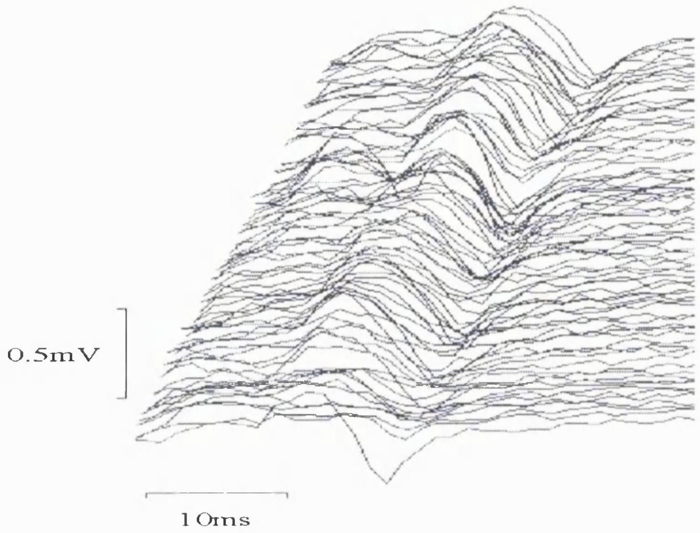


Figure 18. Single sweep recordings of lower trapezius H reflexes. This reflex can be seen with every stimulus. The stimulus occurred at the onset of the trace.

2.3.2.2 The electrically evoked motor (M) response evoked with the H reflex.

Since the contribution of an efferent supply from the cervical nerve of C3/4 is variable, an M response was not expected with electrical stimulation of this nerve in every subject. However, on some occasions an M response was evoked along with the H reflex (see figure 19). Whilst it was always clear that the H reflex was present, the precise onset of the M response and the H reflex was not always clear. Therefore, only the latencies of those H reflexes with a clear onset that could be differentiated from the M response were used. Not withstanding the difficulties of onset, figure 19 illustrates examples of both the M response and H reflex.

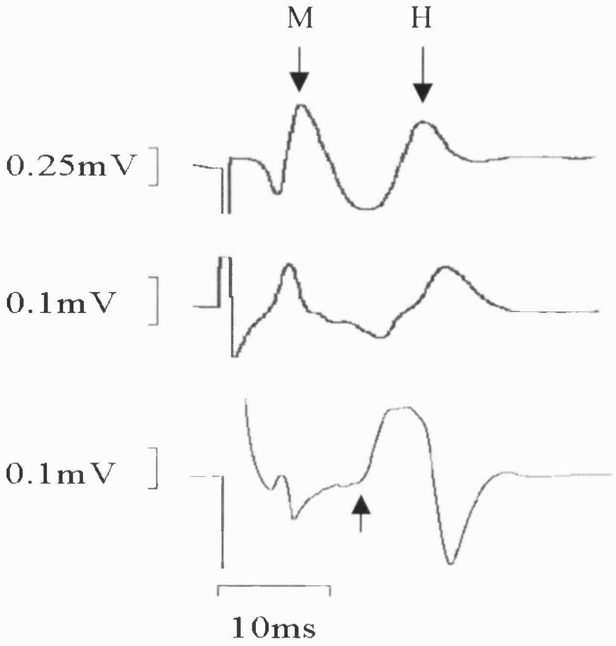


Figure 19. Three examples of trapezius M responses and H reflexes from three subjects. These averages are constructed from the result of 30 stimuli. The downward arrows identify the M response and the H reflex. The stimulus artifact marks the stimulus onset. The latency of the H reflex could not always be determined due to the persistent nature of the M response. The upward arrow marks the onset of an H reflex and is an example in which the latency was measurable.

2.3.2.3 The crossed trapezius reflex.

A crossed H reflex was evoked electrically and recorded in the lower fibres of trapezius, the mean latency being 11.9 ± 1.5ms, 1.0 ± 0.7ms later than the ipsilateral reflex ($p=0.003$) (see figure 20).

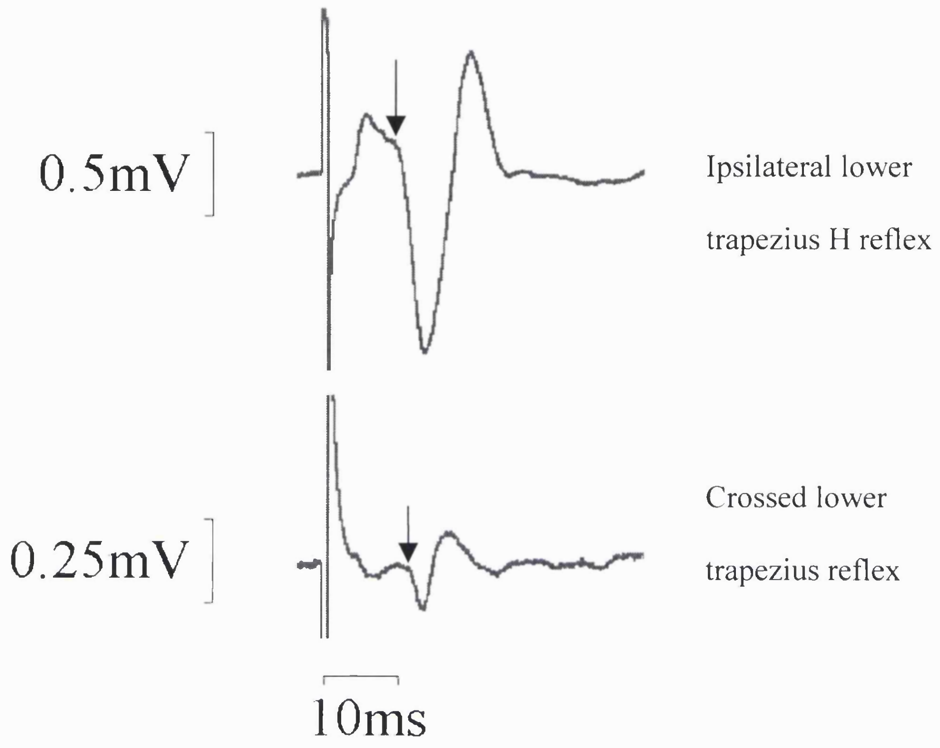


Figure 20. The average ipsilateral and crossed lower trapezius reflex. Each average is constructed from the result of 30 stimuli. The artifact marks the stimulus onset. The arrows mark the reflex onset.

The amplitude of the crossed reflex averaged 23.6 ± 13.1% of the amplitude of the ipsilateral trapezius reflex. This is similar to the difference in size between the two reflexes evoked in the lower fibres by a mechanical tap (22%). The electrically evoked crossed reflex was always large enough to be seen easily with single stimuli i.e. without averaging. A typical example is shown in figure 21.

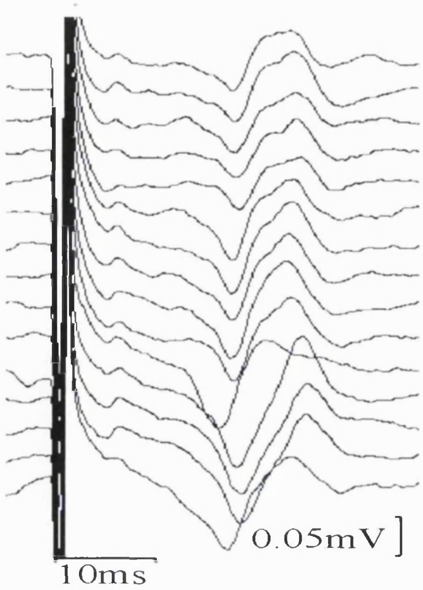


Figure 21. Single sweep recordings of the crossed lower trapezius H reflexes. The reflex can be seen with every stimulus. The stimulus artifact marks the stimulus onset.

2.3.2.4 The effect of voluntary activity on reflex amplitude.

With retraction and depression of the ipsilateral trapezius, there was an increase in both the ipsilateral and contralateral mean trapezius background activity. Like the mechanically evoked reflexes, both the ipsilateral and contralateral lower trapezius reflexes significantly increased in amplitude ($n=10$, $p<0.02$ & 0.03 respectively). Using a paired Student's t test, the percentage increase in the ipsilateral trapezius H reflex was not significantly different from the percentage increase of the contralateral reflex ($p = 0.32$). Examples of the increase in amplitude of the ipsilateral trapezius H reflex with voluntary activity can be seen in figure 22. Examples of the increase in amplitude of the crossed trapezius reflex can be seen in figure 23.

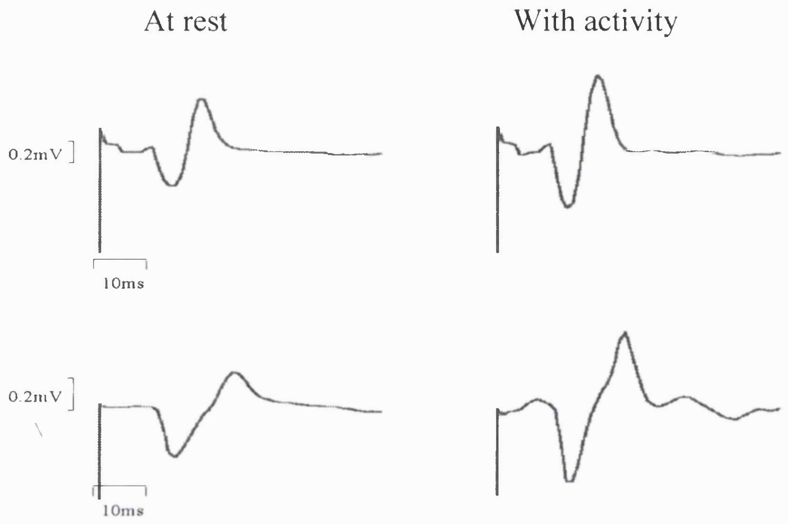


Figure 22. The effect of voluntary activity on the ipsilateral trapezius H reflex amplitude. Surface EMG recordings of the average lower trapezius H reflex evoked from 30 stimuli (left). The H reflex increased in amplitude with activity of the lower fibres of trapezius (right). The stimulus artifact marks the stimulus onset.

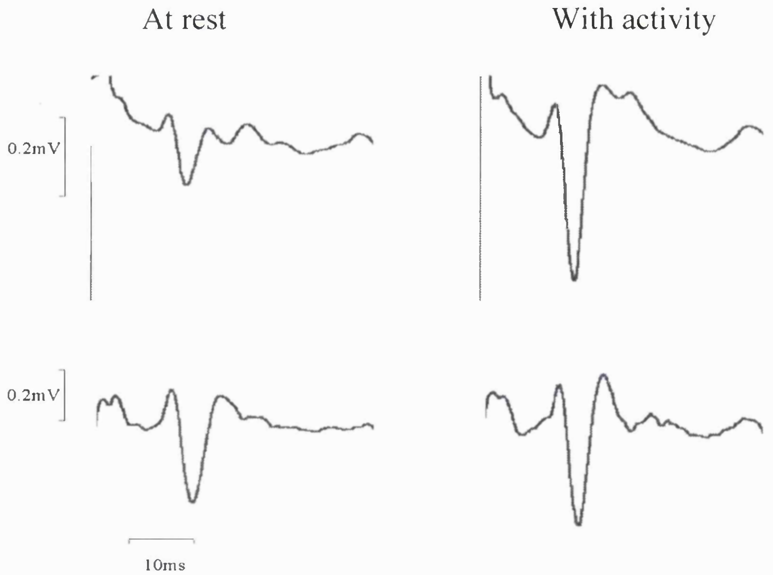


Figure 23. The effect of voluntary activity on the crossed trapezius reflex amplitude. The average crossed lower trapezius reflex evoked from 30 stimuli (left). The crossed reflex also increased in amplitude with activity of the ipsilateral lower trapezius muscle (right). The stimulus occurred at the onset of each trace.

2.3.2.5 Recruitment curve of the trapezius H reflex.

With the soleus H reflex, the relationship between amplitude of the reflex and stimulus strength typically exhibits a bell shaped curve. The ascending limb of the curve is thought to reflect the fact that increasing the number of afferents activated leads to a larger reflex. The descending limb reflects the fact that at larger stimulus strengths more and more motor axons are activated and the antidromically produced action potentials in these axons collide with orthodromic ones, which would otherwise participate in the reflex (see Discussion section 2.4.1.1 for further detail). Given that there are few motor axons in the cervical nerve of C3/4, it is to be expected that any descending limb of the trapezius H reflex recruitment curve would be either absent or much reduced. Indeed, figure 24 shows a typical result in which increasing the stimulus strength produced a smooth increase in H reflex amplitude, without any decrement in amplitude at higher stimulus strengths. Such a result was observed in seven of ten subjects.

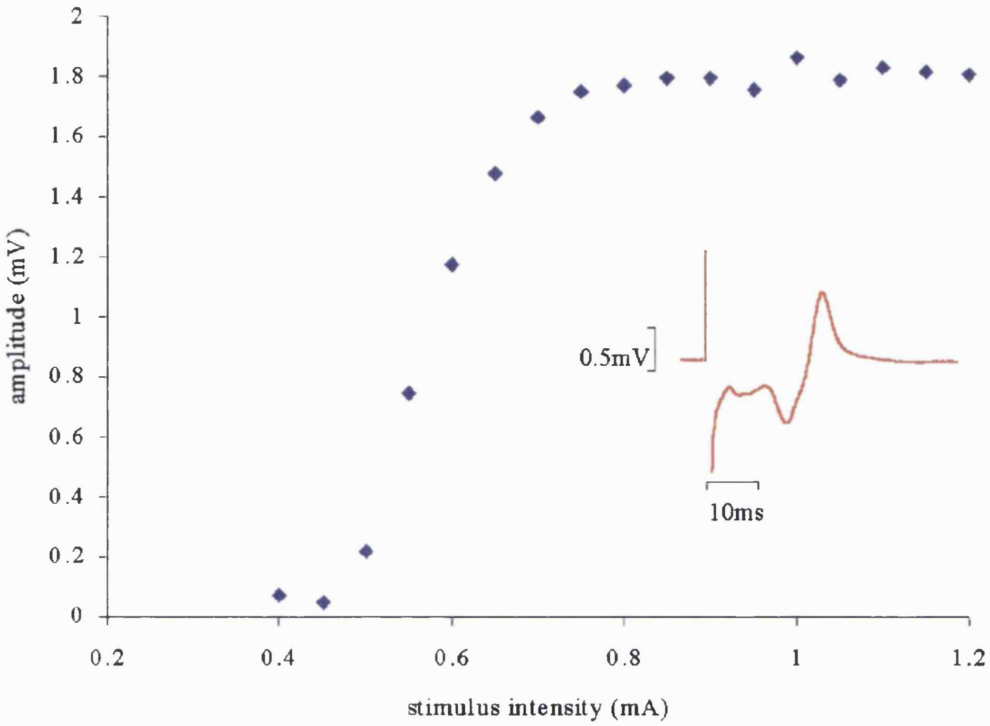


Figure 24. A typical recruitment curve of the ipsilateral trapezius H reflex. The recruitment curve illustrates that the amplitude of the ipsilateral lower trapezius H reflex increases with increasing stimulus intensity until further increases in stimulation no longer increase amplitude. The average lower trapezius H reflex is inserted. The stimulus artifact marks the stimulus onset. In this subject there was no discernible M response.

This result confirms that in many subjects the cervical nerve is mainly afferent. On the other hand, a motor response was evoked in four of the ten subjects. Typically, in these subjects, the reflex increased to a maximum and then declined to a new level (see figure 25). These results imply that in these subjects, the cervical nerve carries a significant number of motor axons to trapezius.

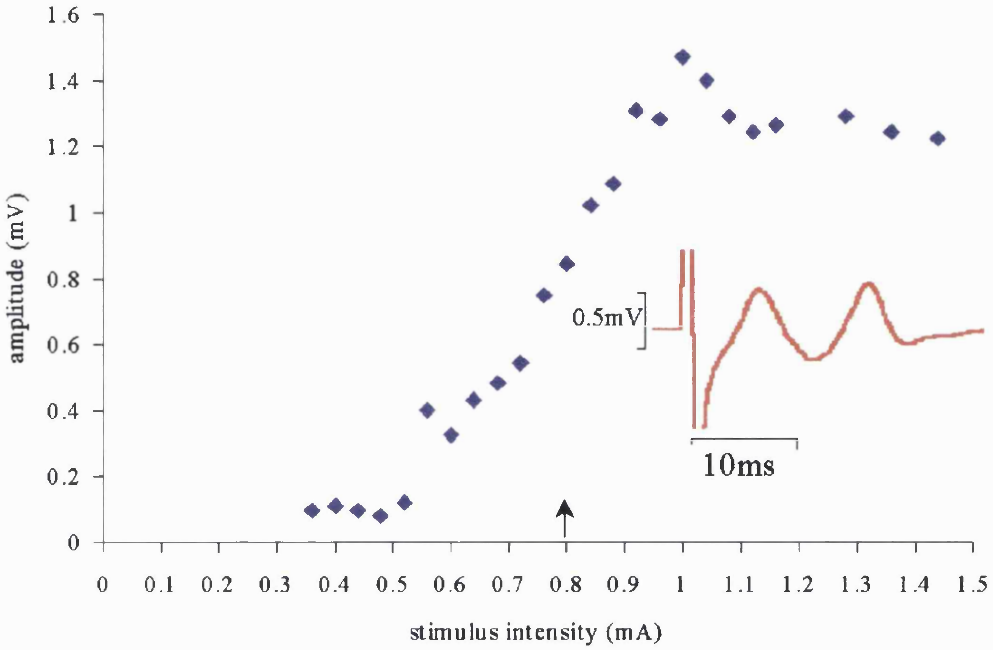


Figure 25. A recruitment curve of the trapezius H reflex when evoked with an M response. The relationship between amplitude of the ipsilateral lower trapezius H reflex and increasing stimulus intensity varies. Here, the amplitude increases until it reached a peak, after which it declines slightly to a plateau just below its peak. The average lower trapezius reflex is inserted. The stimulus artifact marks the stimulus onset. Arrow marks the onset of the motor response. The amplitude of the M response could not be reliably measured, so the recruitment curve for the M response has not been plotted.

In contrast to the ipsilateral reflex, the crossed lower trapezius reflex always increased with increasing stimulus strength. The amplitude reached a plateau at its maximum (see figure 26). This is to be expected as no M response is evoked with the crossed reflex.

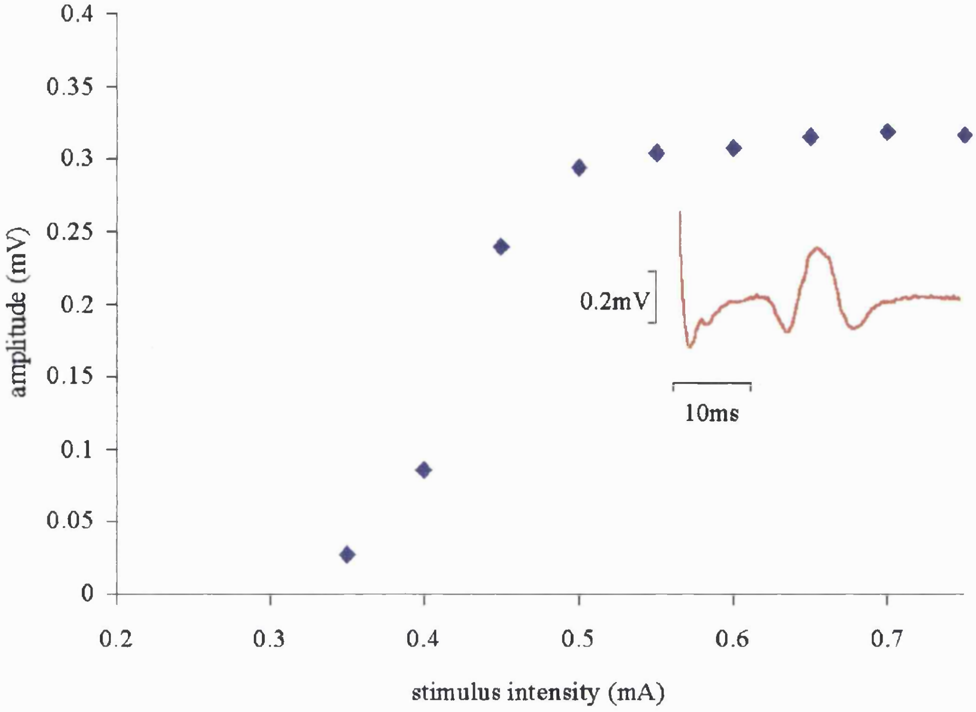


Figure 26. The recruitment curve of the crossed trapezius H reflex. The relationship between amplitude of the crossed lower trapezius reflex and stimulus intensity. The reflex amplitude increases to a maximum and plateaus with increasing stimulus intensity. The average crossed lower trapezius reflex is inserted. The stimulus artifact marks the stimulus onset.

2.3.3 The central connection of the crossed trapezius.

Thus far the crossed trapezius reflex has been seen to be of large amplitude and is seen on single sweeps. In addition, the recruitment curve of the crossed reflex is as expected for a reflex evoked by the same afferent origin. Thus the behaviour of the crossed reflex is that of a close synergist to the ipsilateral trapezius. Indeed, one might expect a close ipsilateral synergist to behave in such a manner. This idea was explored further to investigate the crossed afferent origin and connectivity with the ipsilateral trapezius. Several approaches were employed to explore this further.

2.3.3.1 Variation of reflex latency with reflex amplitude.

While the amplitude of the reflex varied, it became clear that the latency of the reflex also varied with amplitude (see figure 27). This is relevant here since while the latency of the crossed reflex is longer that the ipsilateral reflex, the crossed reflex is also smaller. Thus, any amplitude/latency relationship may be sufficient to explain the latency difference. To this end, the average peak to peak amplitude and the latency of the ipsilateral lower trapezius H reflex recorded from one subject over 30 recording periods (the author) were plotted on a scatter diagram. When the amplitude (ordinate) and latency (abscissa) of the lower trapezius H reflex were plotted on a scatter diagram, the relationship was not linear. The values were therefore plotted on a log-log plot to achieve a linear relationship. The correlation co-efficient $r = 0.67$ suggests that a correlation exists between amplitude and latency. To enable a prediction of latency for particular reflex amplitudes to be calculated, the regression line was plotted.

A regression line is usually calculated with the presumption that there is both a dependent and an independent variable. Classically, the dependent variable is plotted on the y axis and the independent variable on the x axis. In the present case, where there is a wide degree of error, both latency and amplitude can be seen as independent. Thus, as with any data, two regression lines can be plotted. Neither of these reflects the true relationship of amplitude and latency. So, a fair reflection of this relationship is an intermediate line between these two lines of regression, which was plotted.

With this combined regression line, the relationship between latency and amplitude became clear. The crossed reflex is, on average, 23% of the ipsilateral reflex. Accordingly, as can be seen in figure 27, an electrically evoked ipsilateral lower trapezius reflex of 23% of maximal has an onset latency of 1.2ms longer. Therefore, if the latency of the crossed reflex is corrected for amplitude, the latency difference between the electrically evoked reflexes of ipsilateral and contralateral trapezii is reduced by 1.2ms. While the precise mathematical relationship in figure 27 might not be exactly followed in the contralateral muscle, the point is made that larger amplitude reflexes will occur at shorter latencies. This results in the adjusted crossed reflex being 0.2ms shorter than that of the ipsilateral reflex, which is not considered to be a significant difference. Thus, to all intents and purposes the electrically evoked ipsilateral H reflex and the crossed reflex have the same latency.

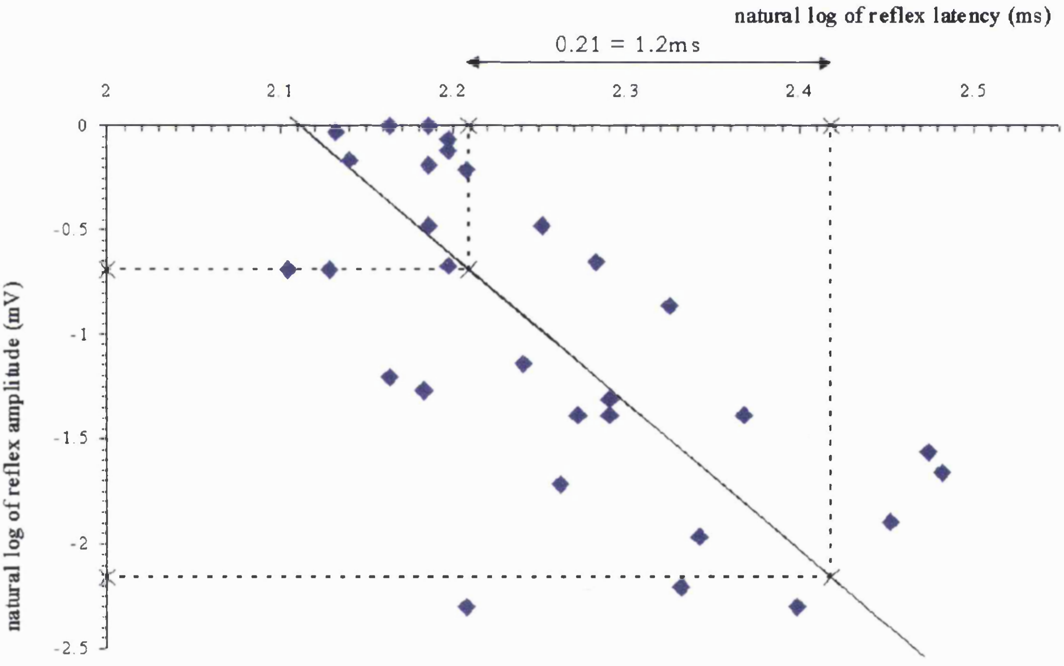


Figure 27. The relationship between amplitude of the electrically evoked ipsilateral lower trapezius reflex and its latency. The two points selected on the ordinate reveal the increase in latency expected by a reflex of 23% of the ipsilateral reflex.

2.3.3.2 The effect of muscle vibration on reflex amplitude.

Vibration facilitates Ia activation and so one might expect that this facilitation of Ia afferents would also increase the amplitude of monosynaptic reflexes, however the opposite occurs. Vibration induces classical presynaptic inhibition of the Ia fibres, with accompanying PAD (Gillies *et al.*, 1969). Thus, the amplitude of an H reflex and tendon jerk of muscles such as soleus is reduced (Van Boxtel, 1986). Indeed, as vibration facilitates polysynaptic reflexes (see Discussion, section 2.4.2.1), the effect of vibration upon reflex amplitude has been used to differentiate between reflexes that are monosynaptically and polysynaptically mediated (Dimitrijevic *et al.*, 1980). Thus, one might expect the ipsilateral trapezius reflex to behave as other H reflexes and tendon jerks by reducing in amplitude. If the crossed trapezius reflex is monosynaptically mediated by the ipsilateral Ia afferents crossing the mid-line, one might also expect the crossed trapezius reflexes to behave in the same way as the ipsilateral reflex. As can be seen in figure 28, the amplitude of both the average ipsilateral and crossed reflexes evoked by a mechanical tap were significantly decreased by vibration of the ipsilateral trapezius (both $p<0.02$, $n=17$).

Both the ipsilateral and the crossed reflexes evoked by electrical stimulation were also significantly decreased in amplitude with vibration of the ipsilateral muscle ($n=7$, $p<0.03$ & 0.04 respectively). This is illustrated in figure 29. Indeed, using paired Student's t-tests, the percentage decrease in the ipsilateral trapezius reflex was not significantly different from the percentage decrease of the crossed trapezius reflex whether the reflexes were evoked mechanically or electrically ($p = 0.90$, 0.27 respectively).

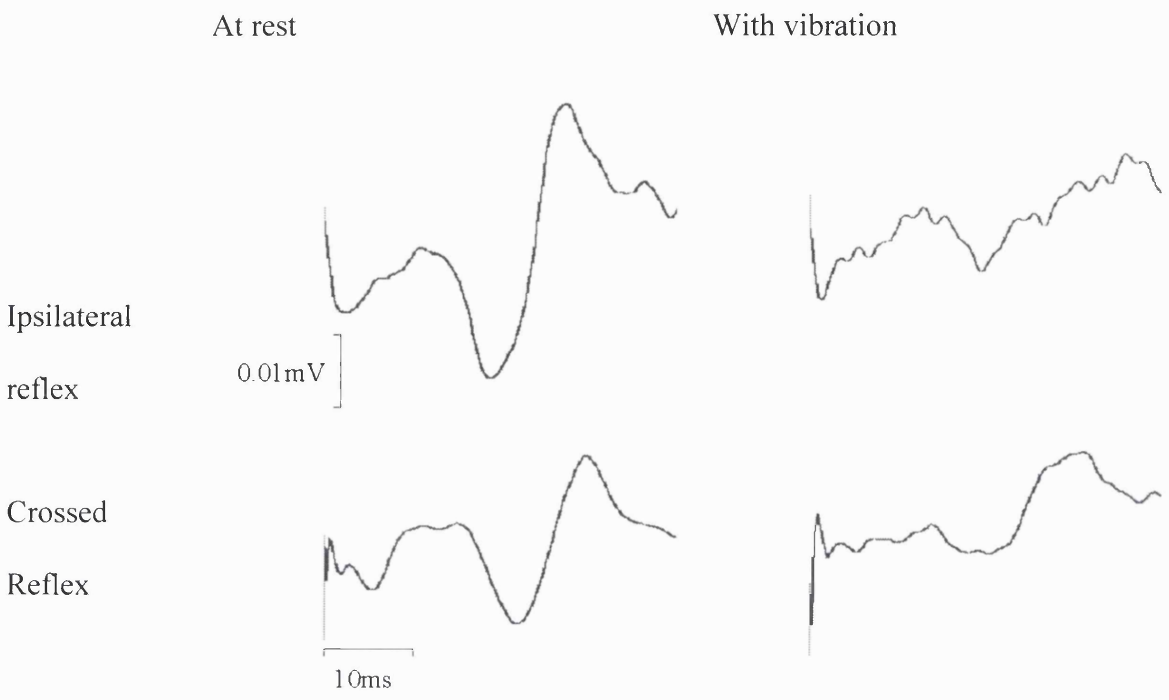


Figure 28. The effect of muscle vibration on the tap evoked reflex amplitude. Average ipsilateral and crossed trapezius reflexes evoked by a mechanical tap to the insertion of the lower fibres of trapezius. The average reflexes were evoked before and during vibration of the ipsilateral trapezius muscle. Each reflex is the average of 30 sweeps. The stimulus occurred at the onset of each trace.

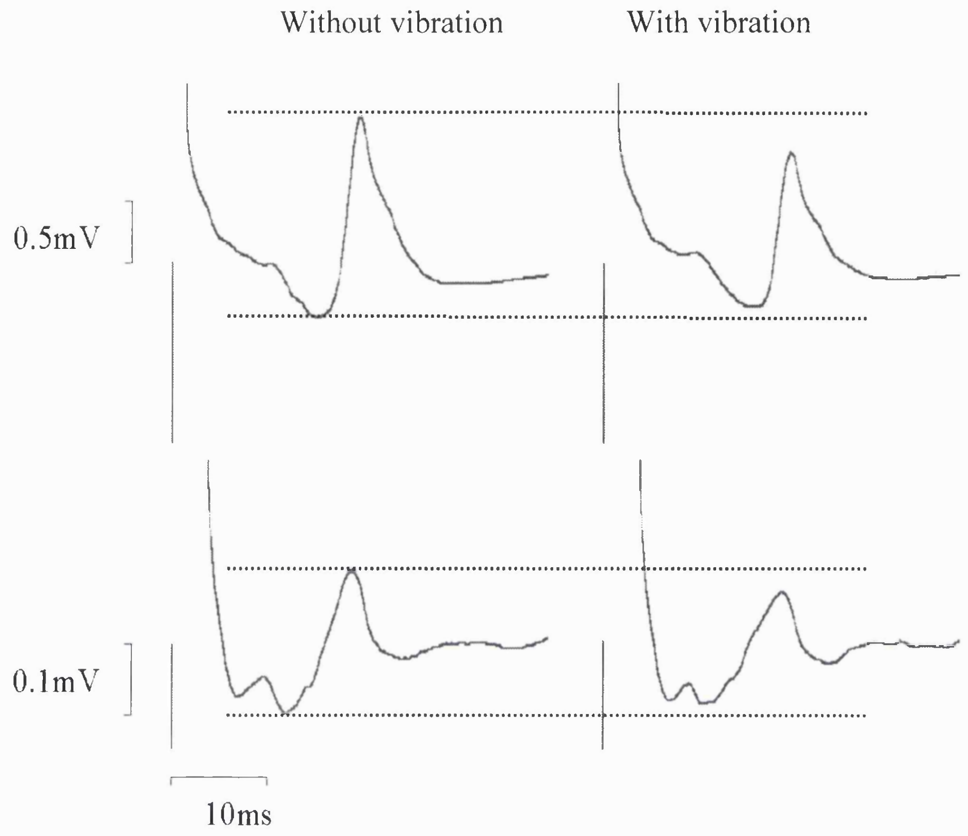


Figure 29. The effect of muscle vibration on H reflex amplitude. The average ipsilateral (top) and crossed (bottom) lower trapezius reflex with and without vibration of the ipsilateral trapezius muscle at 50Hz. The stimulus artifact marks the stimulus onset. Each average reflex is constructed from the result of 10 stimuli.

The effect of vibration upon both the ipsilateral and crossed trapezius reflexes was further explored by plotting a recruitment curve twice, the second time whilst vibrating the ipsilateral trapezius muscle belly. During vibration, the amplitude of the reflex failed to reach the pre-vibration maximum (see figure 30). The crossed lower trapezius reflex responded to vibration in the same way as the ipsilateral reflex (see figure 31).

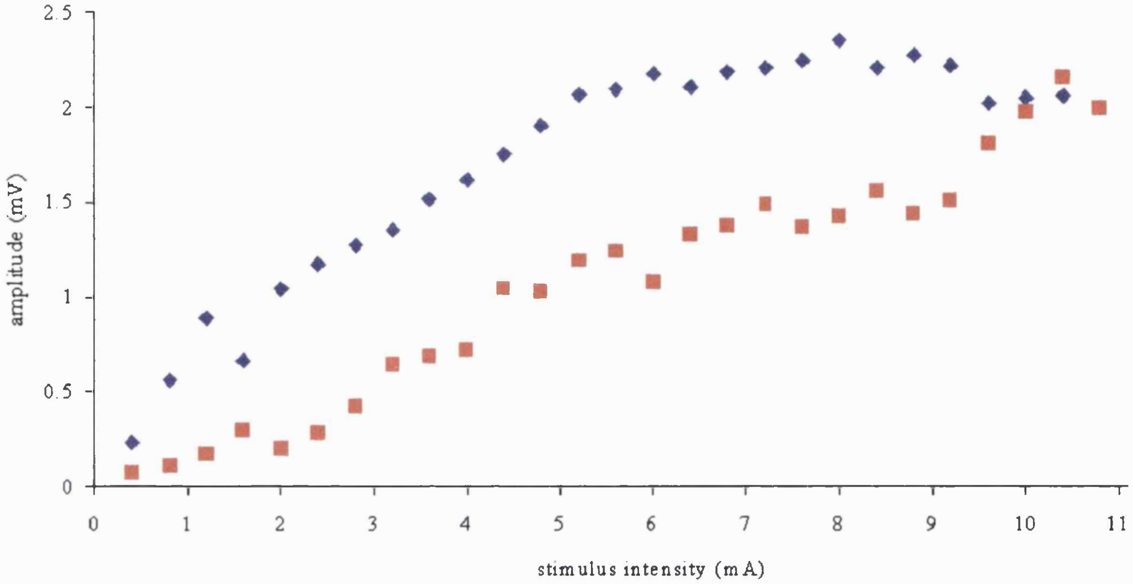


Figure 30. The effect of muscle vibration on the recruitment curve of the ipsilateral H reflex. A recruitment curve of the ipsilateral lower trapezius H reflex with (red) and without (blue) vibration of the ipsilateral trapezius muscle belly.

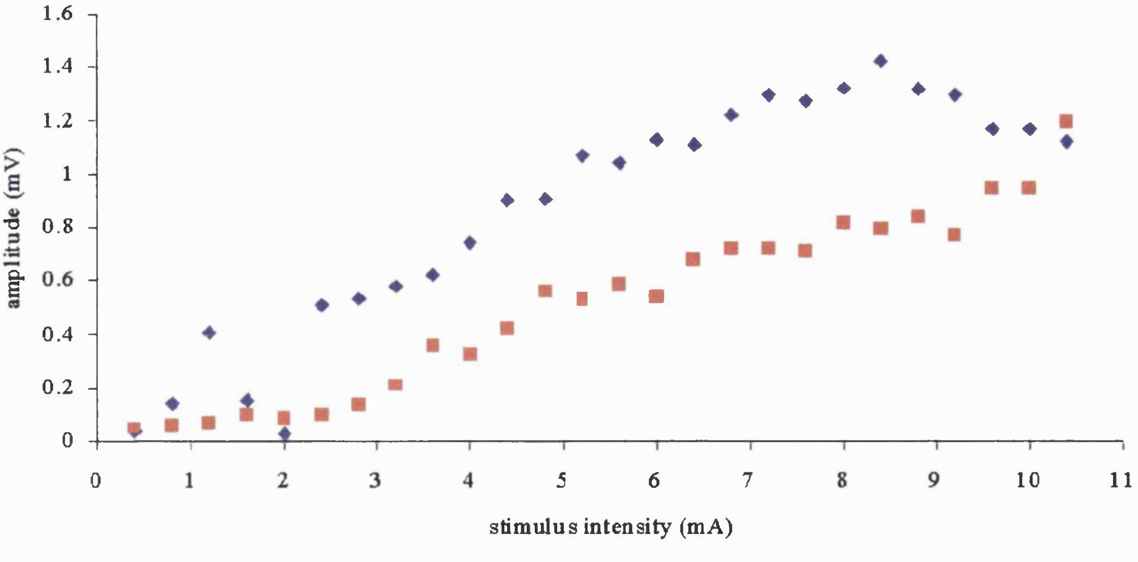


Figure 31. The effect of muscle vibration on the recruitment curve of the crossed reflex. The recruitment curve of the crossed lower trapezius reflex with (red) and without (blue) vibration of the ipsilateral trapezius muscle belly.

2.3.3.3 Cross correlation of trapezius activity.

An interpretation of the previous results could be that trapezius Ia afferents cross the mid-line to monosynaptically activate the trapezius motoneurone pool contralaterally. In other words, these muscles share last order common presynaptic input. If this occurs then bilateral activity of this muscle pair should result in a central peak in a cross correlogram. Cross correlograms were constructed between multiunit spike trains of the left and right upper fibres of trapezius (eleven subjects), left and right lower fibres of trapezius (seven subjects) and the upper and lower fibres of trapezius on the same side (fifteen subjects). Examples of these are shown in figure 32.

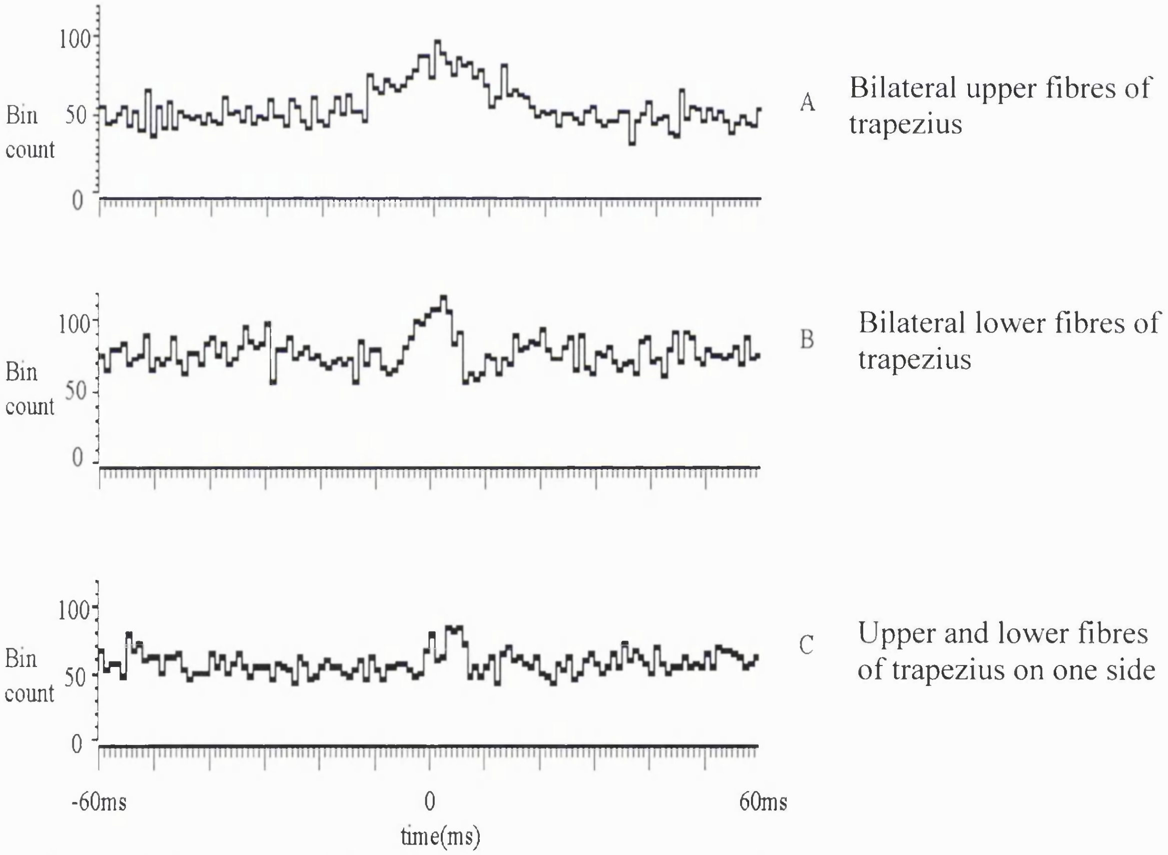


Figure 32. Cross correlation of the trapezius muscles. The cross correlograms were constructed from a subject during abduction of the arms between multiunit spike trains generated from A) the bilateral upper fibres of trapezius, B) the bilateral lower fibres of trapezius and C) the ipsilateral upper and lower fibres of trapezius from one side.

Significant short duration peaks were seen in 85% of the correlograms. The strength (κ (peak/mean) & E/M (extra spikes/mean)) and duration of the peak has been summarised for each muscle pair in Table 3.

Trapezius fibres	*Number of subjects*	*Synchrony present*	*κ*	*E/M*	*Duration (ms)*
Upper / upper	11	9/11	1.7 ± 0.5	3.8 ± 3.0	12.7 ± 9.5
Lower / lower	7	7/7	1.8 ± 0.3	2.7 ± 0.9	5.6 ± 1.6
Upper / lower	15	12/15	1.5 ± 0.2	1.8 ± 1.1	8.2 ± 7.9

Table 3. Characteristics of cross correlograms from trapezius muscle pairs. Values for κ, E/M and duration are given as mean ± S.D.

In the cross correlograms constructed between both the ipsilateral and contralateral upper parts of trapezius and the ipsilateral and contralateral lower parts of trapezius, the peak was centred around time zero. However, in the cross correlograms constructed between the ipsilateral upper and lower parts of trapezius the peak was offset by a mean of 3.8 ± 3.5ms (see figure 32). This is most easily explicable on the basis of the difference in conduction distance between the upper and lower parts of trapezius.

In five subjects, complete results were obtained for all three muscle pairs. In these subjects there were significant differences between the various muscle pairs. The E/M and duration of peak for the left and right upper fibres of trapezius muscle was greater than the left and right lower fibres of trapezius muscle, which was greater than the upper and lower fibres of trapezius on one side ($p<0.02$ and 0.02 respectively). There was no significant difference of the value for κ between the groups (p=0.42). These results suggest that the left and right trapezius muscles receive common presynaptic input, as would be expected if the same Ia afferents projected to motoneurones of both the left and right trapezius.

2.3.3.4 Magnetic stimulation of the trapezius motor cortex.

While it is to be expected that the Ia input will contribute to the common presynaptic input determined above, this does not preclude the possibility that other inputs might contribute substantially. One such common input might originate from the corticospinal tract which is known to give bilateral supply to some axial muscles (Carr *et al.*, 1994). To investigate this possibility, the corticospinal trapezius connection was investigated in five normal subjects by using magnetic stimulation to the trapezius motor cortex. Figure 33 shows an example of the contralateral effects of stimulation to the motor cortex of trapezius. As can be seen, such stimulation produced an early response (at 10.1 ± 1.4ms) and a late response (at 38.3 ± 4.6ms) in the contralateral upper trapezius. The contralateral lower trapezius also shows an early response (at 11.2ms) and a late response (at 28.9 ± 9.0ms). On occasion, the individual stimuli evoked the late contralateral response independently of any early contralateral response (see figure 34). Responses to stimulation of the trapezius cortex were also recorded ipsilaterally. No early responses were seen ipsilaterally (see figure 35). However, late responses were seen in both the upper and lower trapezius (30.4 ± 1.5ms and 46.9 ± 6.2ms respectively). The ipsilateral results from one subject were discarded since it was not clear that the stimulus was confined to one side. A summary of these results including the frequency with which they were evoked are presented in table 4.

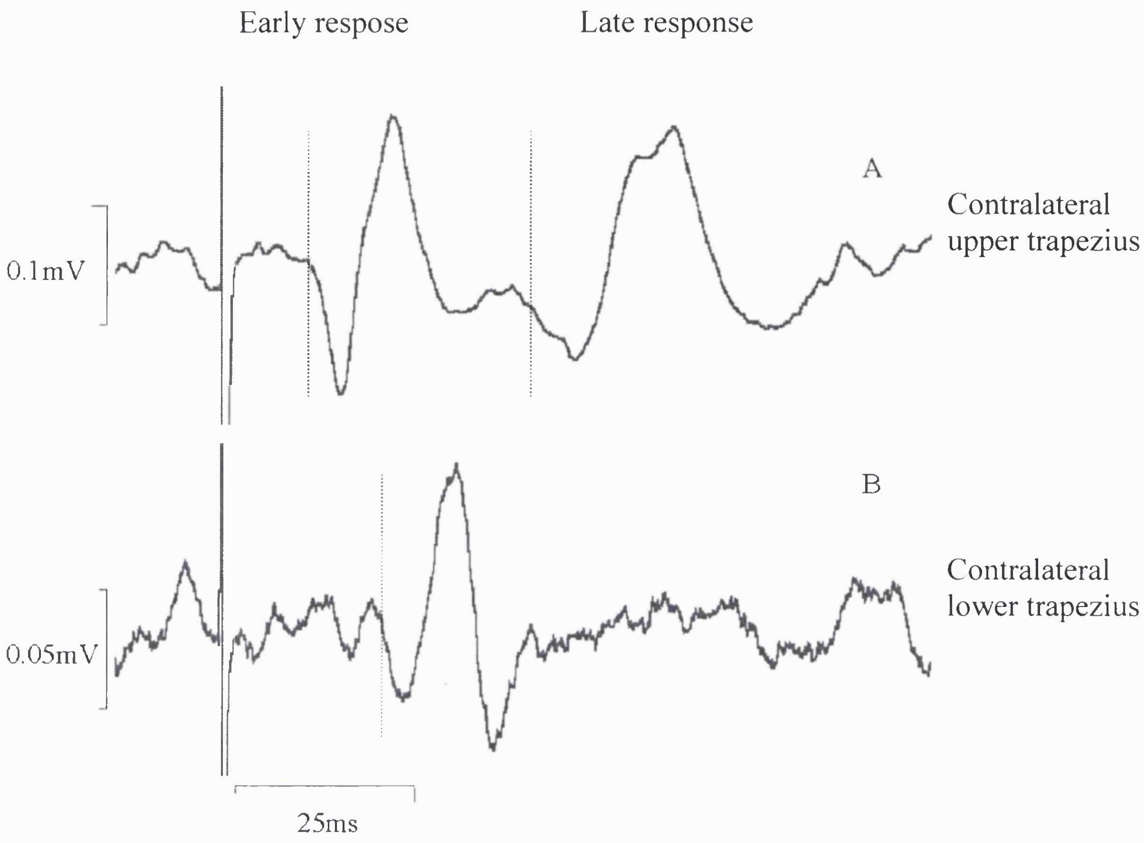


Figure 33. The contralateral trapezius response evoked by magnetic stimulation of the contralateral cortex. A. Average contralateral upper trapezius responses evoked by magnetic stimulation of the contralateral cortex. B. The average contralateral lower trapezius response evoked by magnetic stimulation of the contralateral cortex. Each response is the average of 25 sweeps. The stimulus artifact marks the stimulus onset. The vertical cursors mark the onset of the responses.

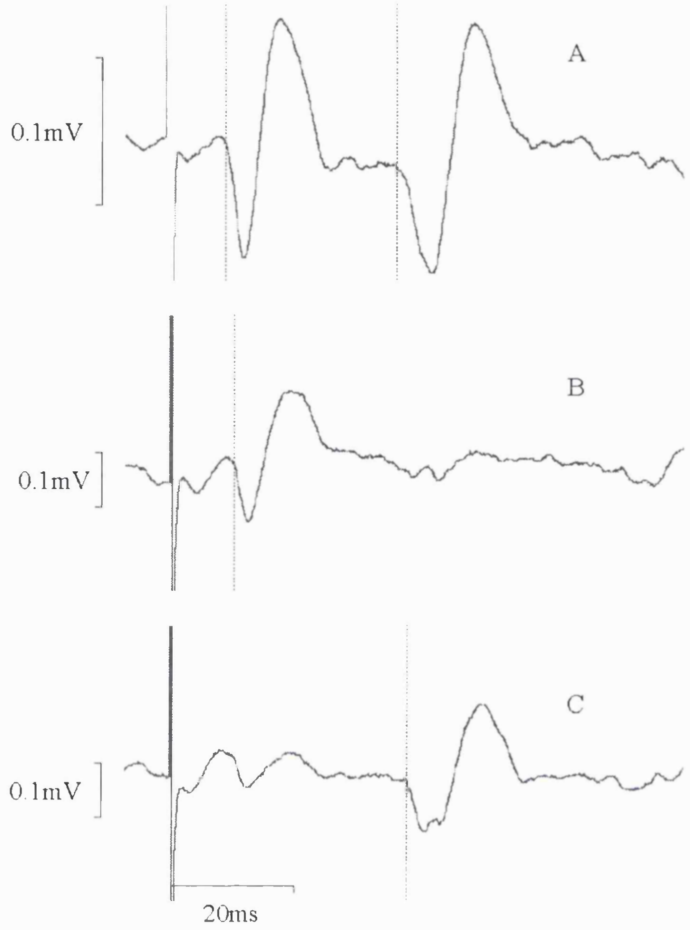


Figure 34. The early and late contralateral upper trapezius responses to magnetic stimulation of the trapezius motor cortex. A. The contralateral upper trapezius response is an average of 25 sweeps and shows the early and late response evoked by magnetic stimulation of the contralateral motor cortex. The results of a single stimulus reveal that the late response (C) may be independent of the early response (B). The cursors mark the onset of the responses. The stimulus artifact marks the stimulus onset.

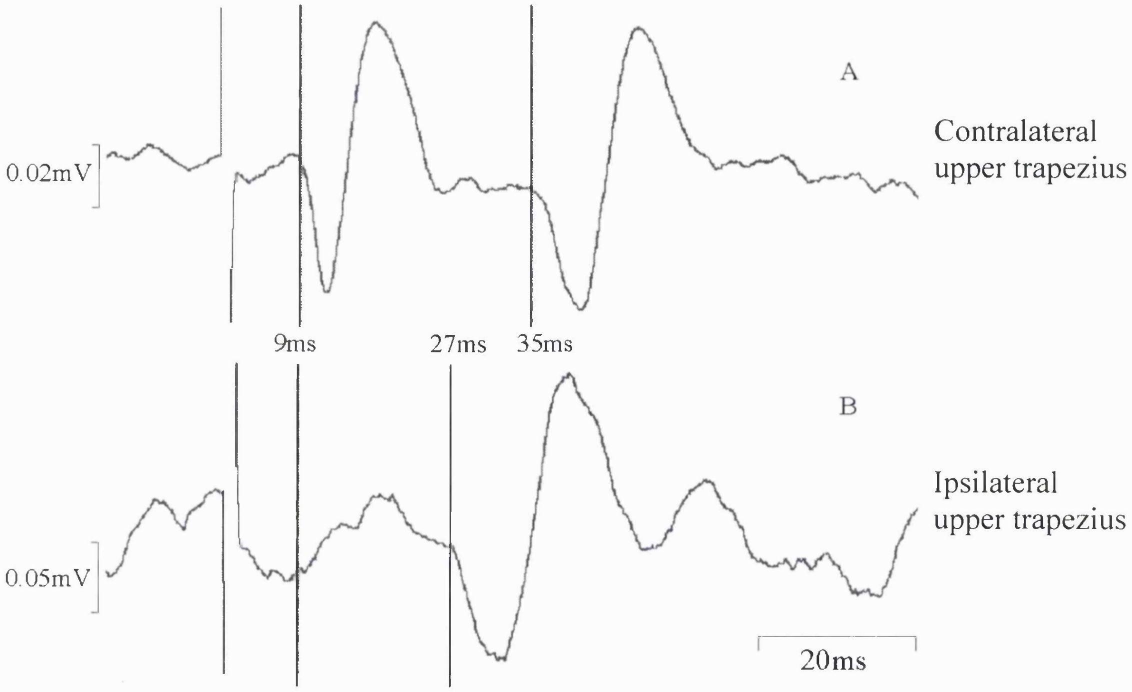


Figure 35. The contralateral and ipsilateral upper trapezius response to magnetic stimulation of the trapezius motor cortex. A. The average contralateral upper trapezius response to magnetic stimulation of the ipsilateral cortex. B. The average ipsilateral upper trapezius response recorded simultaneously. The response is the average of 25 sweeps. The stimulus artifact marks the stimulus onset. The vertical cursor at 9ms marks the onset of the contralateral early response. The vertical cursor at 35ms marks the onset of the contralateral late response.

			Early response	*Late response*
Contralateral trapezius	Upper fibres	Latency (ms)	10.1 ± 1.4	38.3 ± 4.6
		Occurrence	39/39 (5/5 subjects)	13/39 (3/5 subjects)
	Lower fibres	Latency (ms)	11.2	28.9 ± 9.0
		Occurrence	8/39 (1/5 subjects)	11/39 (2/5 subjects)
Ipsilateral trapezius	Upper fibres	Latency (ms)	-	30.4 ± 1.5
		Occurrence	0/32 (0/4 subjects)	16/32 (3/4 subjects)
	Lower fibres	Latency (ms)	-	46.9 ± 6.2
		Occurrence	0/32 (0/4 subjects)	13/32 (2/4 subjects)

Table 4. The latency (mean ± S.D.) of the trapezius responses from magnetic stimulation of the trapezius motor cortex. The mean ± S.D. was calculated from the mean response of each subject. The occurrence of these responses is displayed as the frequency of responses/total number of responses evoked (responses evoked per subject).

These results do not suggest a strong support for bilateral monosynaptic projection to the trapezius motoneurone pools. Therefore, this speaks against corticospinal projections providing significant contribution to the common pre-synaptic input recorded in section 2.3.3.3. This strengthens the view that the monosynaptic Ia input is a significant factor in the origin of this common presynaptic input.

2.4 Discussion

A novel result of this study was that a short latency, ipsilateral reflex in trapezius can be evoked by electrically stimulating the cervical nerve of C3/4 and by tapping the muscle as it inserts into the medial edge of the spine of the scapula. More surprising was that, a) a reflex in the contralateral trapezius was evoked when these stimuli were applied ipsilaterally; and b) cross correlation of motor unit activity between the two trapezii was equal or stronger than that between the upper and lower motor units within one muscle.

2.4.1 Ipsilateral reflexes.

With a mean latency of the electrically evoked reflex at 10.9ms, we might consider that at least the earliest part of this reflex is monosynaptic. A preliminary examination of this issue can be addressed by considering the length of the conduction pathway together with an estimate of the conduction velocity. This calculation is complicated by the unusual and varying nerve supply to trapezius. Unlike other peripheral nerves the afferent and efferent pathways are, in the main, separate. The efferent pathway is *mainly* via the spinal accessory nerve with the afferent supply via the cervical nerves of C3/4 (Soo *et al.*, 1993; Stacey *et al.*, 1996). Therefore, the reflex latency can be estimated by the addition of the afferent conduction time, the efferent conduction time and time for the synaptic delays. Taking measurements from four cadavers, the afferent pathway from the site of stimulation was found to be 7cm, the efferent pathway was found to be 39cm. Maximum afferent Ia conduction velocity has been estimated in man to be 65m/s (Burke *et al.*, 1983) and the efferent conduction velocity of the spinal accessory nerve has been measured in man to be 54m/s (Priori *et al.*, 1991). If 1ms is added for each synaptic delay, then the earliest time for a monosynaptic reflex can be estimated to be 10.3ms. This is remarkably similar to the actual mean latency of 10.9ms and therefore suggests that the latency of the earliest part of the electrically evoked response is consistent with a monosynaptic reflex.

It is interesting to note that the latency of the mechanically evoked lower trapezius reflex, at 11.9ms, is 1ms slower than the lower trapezius H reflex. This latency difference might be due to the difference in reflex amplitude, the mechanically evoked reflex being smaller than the electrically evoked reflex. The difference in latency may also be due to the asynchronous afferent volley generated by the tap as compared to the synchronous afferent volley generated by electrical stimulation. The motoneurone pool would take longer to reach firing threshold with asynchronous input such as that generated by a mechanical tap. Indeed, comparisons of the rise time of the mechanically evoked EPSP with that of the electrically evoked EPSP in human soleus motoneurones shows this to be the case. The soleus compound EPSP rise time is 1-2ms for the soleus H reflex, where as the compound EPSP rise time evoked by an Achilles tendon jerk is greater than 10ms (Uysal *et al.*, 1999). The shortest difference recorded between the latencies of the soleus tendon jerk and H reflex is 7.5ms (Uysal *et al.*, 1999), whereas the difference between the trapezius tendon jerk and H reflex is less, at 1ms. This shorter difference between the electrically and mechanically evoked trapezius reflexes may be due to the shorter conduction distance of the trapezius reflex by comparison to the soleus reflex. This shorter distance would create less asynchrony along the conduction pathway (Jack *et al.*, 1985; Burke & Gandevia, 1999). Thus, it is unsurprising that the latency of the trapezius tendon jerk is longer than that evoked by electrical stimulation.

2.4.1.1 The trapezius M response.

The ipsilateral trapezius reflex was sometimes present with and sometimes without an M response. This may be due to the variation in the nerve supply to trapezius. In a proportion of the population, the cervical nerve of C3/4 carries afferent and a varying proportion of efferent axons, in others it is a purely afferent nerve (Soo *et al.*, 1993; Krause *et al.*, 1993). Thus, stimulation of the cervical nerve evokes, in some individuals, both an M response and an H reflex and in others just an H reflex.

This variation in nerve supply was also evidenced by the relationship between the amplitude of the trapezius H reflex and stimulation intensity. If the nerve supply to trapezius were purely afferent, one might expect that with increasing stimulation intensity there would be a systematic monotonic increase in the amplitude of the trapezius reflex. Once all afferent axons have been recruited any further increase in stimulation intensity could not further increase the peak amplitude therefore a plateau would be reached. Indeed, this was often the case. Seven of the ten recruitment curves demonstrated an increase in amplitude with increasing stimulation intensity until the amplitude reached a plateau at its maximum. Since, by analogy with the soleus H reflex one might expect collision of antidromic potentials in motor axons to collide with orthodromic evoked potentials (see later) then, with a small motor supply from the cervical nerve one might expect a corresponding reduction in the peak amplitude with further increases in stimulation intensity. Indeed, three of ten results demonstrated an increase in amplitude with increasing stimulation intensity until a maximum, when further increases in stimulus strength produced a decrease in the amplitude before reaching a plateau. This decrease from maximum amplitude is less than that seen for the soleus H reflex. With stimulation of the mixed nerve to soleus, the H reflex is reduced dramatically with an increasing M response. The mechanism by which this reduction in amplitude of the H reflex occurs centres around 3 hypotheses. First, the antidromic motor activity collides with the orthodromic activity within the motor axons generated by the stimulation of Ia fibres. Second, the α motoneurone pool is rendered refractory by the initial arrival of the antidromic motor impulse. Third, the action of motor fibres evokes recurrent inhibition of the those motoneurones (Desmedt & Godaux, 1978; Dindar & Verrier, 1975; Gottlieb & Agarwal, 1976; Rothwell, 1994). Although Desmedt & Godaux (1978), Dindar & Verrier (1975) and Gottlieb & Agarwal (1976) argue that refractoriness of the motoneurone pool is most likely to generate the majority of the effect, this contrasts with the summary of Rothwell (1994) who suggests that antidromic block of the motor fibres is the most likely cause. Nevertheless, regardless of mechanism, a slight reduction in maximum amplitude of the trapezius H reflex with increasing stimulus intensity is as expected on the basis that a proportion of motor fibres supplying the lower fibres of trapezius lie within the cervical nerve of these subjects. Therefore, one might expect that in these cases the H reflexes are accompanied by an M response. Indeed, this was typically the case. Whilst this adequately explains the reduction in maximum amplitude in the recruitment curve, there may be other issues that contribute to the shape of the curve. In particular, the relative diameters of the afferent and efferent axons are a key factor in determining whether or not an H reflex occurs. Selective activation of large diameter Ia afferents by the electrical stimulus is essential in order to observe an H reflex at all. On the other hand, comparable diameters of afferent and efferent axons would lead to automatic collision of antidromic action potentials with reflexly evoked orthodromic action potentials in the motor axons. Thus, the occurrence of an H reflex at all in trapezius, implies that there is a difference in the afferent and efferent axon size. Indeed, in accordance with this it is notable that the trapezius efferent axons have a conduction velocity of 54m/s (Priori *et al.*, 1991), rather slower than that measured from human soleus afferents, and presumably also slower than the human trapezius afferents.

2.4.2 Crossed reflexes.

The mean latency of the mechanically evoked crossed reflex in the lower fibres of trapezius was 14.3ms, i.e. 2.4ms longer than the ipsilateral reflex. By comparison, the difference in latency in the lower fibres of trapezius using the more synchronous afferent barrage of electrical stimulation was less, the crossed H reflex being evoked on average 1.0ms later than the ipsilateral H reflex. Bearing in mind that large H reflexes were generally of shorter latency (see figure 27) and that crossed H reflexes averaged only 23% of the ipsilateral reflex, then it is to be expected that the reflex latencies would be more comparable when corrected for amplitude. Indeed, from figure 27, decreasing the amplitude of an ipsilateral reflex by 77% reduced the latency by 1.2ms, therefore obliterating any significant difference in latency between the two reflexes. Thus, the latency of the reflexes in the contralateral muscle is sufficiently short to suggest that that these crossed reflexes are monosynaptically mediated.

That a reflex of smaller amplitude also has a longer latency is seen when comparing the amplitude and latency of both the electrically and mechanically evoked lower trapezius reflexes. For example, the average amplitudes of the mechanically evoked lower trapezius reflexes (ipsilateral 0.8mV ± 0.8, crossed 0.2mV ± 0.2) were less than the amplitudes of their counter-parts evoked by electrical stimulation (ipsilateral 2.8mV ± 1.5, crossed 0.8mV ± 0.8). Indeed, the amplitude of the ipsilateral reflex evoked from a tap was the same as the amplitude of the crossed reflex evoked by electrical stimulation. So, being of the same amplitude, one might expect that the reflexes also have the same latency. Indeed, this was the case with the crossed H reflex having a mean latency of 11.9 ± 1.4ms and the mechanically evoked ipsilateral trapezius reflex having a mean latency of 11.9 ± 1.5ms. This phenomenon of a reduction in reflex latency with increasing amplitude is supported in the literature. For example, Ratto *et al.* (1986) demonstrated a reduction in soleus H and tendon jerk reflex central delay with increasing stimulus intensity. These results were further explored by Abbruzzese *et al.* (1998) who demonstrated a reduction in central delay with voluntary contraction.

2.4.2.1 The monosynaptic nature of the trapezius crossed reflex.

The latency of the reflexes to the contralateral muscle are sufficiently short to suggest that that these crossed reflexes, as well as the ipsilateral reflex, are also monosynaptically mediated. This is particularly evident with the crossed H reflex, which is only 1ms longer than the ipsilateral H reflex. Taken together with the consideration of the amplitude and latency, which suggests no significant delay between the two sides, if one accepts that the ipsilateral H reflex is monosynaptic then one might expect the crossed trapezius reflex to also be monosynaptic. Other considerations also indicate that this is not an oligosynaptic connection. With an oligosynaptic connection, one might expect a much greater attenuation of the size of the crossed reflex such that a large number of sweeps needs to be averaged. Indeed, in other experimental situations it is usually necessary to condition the H reflex with appropriately timed conditioning stimuli to reveal the presence of most non-monosynaptic reflex connections (Cavallari *et al.*, 1992). In contrast to this, the contralateral trapezius reflex was visible on single sweeps and the tap evoked reflex needed only 10 sweeps before a discernible reflex was evident.

In addition, one might also expect oligosynaptic reflexes to behave differently from monosynaptic reflexes when tested under the same conditions. In fact, both the crossed and the ipsilateral reflexes behave similarly with varying activity and with vibration of the ipsilateral muscle, both of which are conditions known to alter the amplitude of monosynaptic reflexes (Desmedt & Godaux, 1978; Dindar & Verrier, 1975; Gottlieb & Agarwal, 1973a; Gottlieb & Agarwal, 1973b).

The background EMG of the both the ipsilateral and contralateral trapezii increased with just ipsilateral trapezius action. That the reflexes also increased in amplitude with voluntary activity is most likely due to the fact that voluntary activity may increase the amplitude of the reflexes by increasing the descending drive to both the ipsilateral and contralateral motoneurone pools. This takes the motoneurones closer to firing threshold facilitating the action of an incoming afferent volley (Abbruzzese *et al.*, 1998; Burke *et al.*, 1989; Burke & Gandevia, 1999; Desmedt & Godaux, 1978; Dindar & Verrier, 1975; Gottlieb & Agarwal, 1973b; Harrison & Taylor 1981). To increase the amplitude of both the ipsilateral and crossed trapezius reflexes seen here, suggests the presence of bilateral descending input upon both motoneurone pools. Indeed, long latency bilateral responses were revealed with magnetic stimulation of the ipsilateral trapezius motor cortex. This suggests that bilateral descending pathways could increase the drive to the ipsilateral and contralateral motoneurone pools.

The response of the ipsilateral and crossed trapezius reflex amplitude to vibration was equally reduced. Vibration inhibits monosynaptic reflexes but facilitates polysynaptic reflexes. This 'paradox' has been used by others to differentiate between reflex pathways. Both Dimitrijevic *et al.* (1977) and Myriknas *et al.* (2000) evoked short and long latency reflexes by tapping trunk muscles. They demonstrated a decrease in the amplitude of the monosynaptic short latency reflex and an increase in amplitude of the long latency, polysynaptic reflexes. The differential effect upon monosynaptic and polysynaptic reflexes has been termed the 'vibration paradox' and the reasons for these different effects have been reviewed by Desmedt (1983). Muscle spindle afferents are sensitive to vibration. So, vibrating a muscle excites Ia action that facilitates the motoneurone pool and evokes a tonic vibration reflex (TVR). This TVR results in a slow increase in EMG, the frequency of which mirrors the frequency of the vibration. So, the TVR is thought to be due to the Ia facilitation of polysynaptic pathways acting upon the motoneurone pool. Dimitrijevic *et al.* (1980) and Myriknas *et al.* (2000) demonstrated this facilitation upon other polysynaptic pathways such as the long latency stretch reflex. If the amplitude of the crossed trapezius reflex had increased, this would have suggested the presence of interposed interneurones. This did not occur.

Given that, vibration facilitates Ia activation, one might expect that this facilitation of Ia afferents would also increase the amplitude of monosynaptic reflexes. In fact, the opposite occurs. Vibration induces classical presynaptic inhibition of the Ia fibres, with accompanying primary afferent depolarization (Gillies *et al.*, 1969). This presynaptic action inhibits motoneurones reducing the amplitude of both the stretch reflex and the H reflex. The mechanism by which this reduction in amplitude of monosynaptic reflexes occurs is supported by the evidence of Desmedt (1983). They demonstrated that the stretch reflex of masseter (a jaw closing muscle), which is known to lack presynaptic inhibition, is facilitated by vibration as the unchecked action of the Ia afferents facilitates the motoneurone pool (Desmedt, 1983). Thus, the Ia facilitation upon polysynaptic pathways is reduced by this presynaptic mechanism and the H reflex and stretch reflex are inhibited (Deschuytere *et al.*, 1976; Van Boxtel, 1986). To summarise, vibration activates Ia fibres; this action facilitates polysynaptic pathways. Vibration also presynaptically inhibits Ia fibres so decreasing the amplitude of monosynaptic reflexes. The vibration of the ipsilateral side equally inhibited both the ipsilateral and the crossed trapezius reflexes.

Additional evidence that the crossed reflexes were of monosynaptic Ia origin was sought using cross correlation techniques. If the crossed reflex is mediated, at least in part, monosynaptically, one might expect that cross correlation of activity between the trapezius muscle pairs would reveal a short duration peak suggestive of common, last order presynaptic input (Sears & Stagg, 1976). Indeed, this was the case. However, while these results could add to the evidence for a monosynaptic crossed reflex, they might also be explicable on the basis that descending pathways provide common bilateral inputs upon the two motoneurone pools. Bilateral connections from the ventral, corticospinal tract might provide a pathway for this bilateral input, which has been described for other axial muscle pairs (Carr *et al.*, 1994). However, while Berardelli *et al.* (1991) generated motor evoked potentials in the contralateral trapezius using transcranial magnetic stimulation over the ipsilateral motor cortex, they were unable to generate any response in the ipsilateral trapezius suggesting that bilateral corticospinal innervation to trapezius does not exist. It follows that there is no evidence for descending bilateral monosynaptic connections to trapezius such as would generate the correlograms described. The investigation of descending bilateral innervation of trapezius was extended here. In accordance with the results of Berardelli *et al.* (1991), there was no ipsilateral short latency response evoked in these experiments. However, bilateral long latency responses were evoked in both the upper and lower trapezii (contralaterally:38.3ms ± 4.6 and 38.9ms ± 5.2 respectively; ipsilaterally: upper fibres 30.4ms ± 1.5; lower fibres 51.3ms ± 36.9). So, while there is evidence of a bilateral descending connection, the latencies of the responses are inconsistent with a common, last order input and so could not generate the correlograms described here. Thus, although this common presynaptic input may be due to common descending input other than that from the corticospinal tract or from common interneurones, it is also consistent with common Ia input, that is, a crossed monosynaptic Ia pathway.

The control of bilateral muscle pairs has been previously reported. Control mechanisms between the erector spinae (Dimitrijevic *et al.*, 1980; Zedka *et al.*, 1998) and the intercostal muscles Sears & Stagg (1976) suggest a dual motor function. Crossed monosynaptic reflexes have also been reported in both animals and humans. For example, in the cat, crossed, monosynaptic pathways have been demonstrated from group I muscle afferents to motoneurones controlling the contralateral tail musculature (Curtis *et al.*, 1958; Wada & Kanda, 2001). In man, crossed monosynaptic pathways have been proposed to exist in another axial muscle group, rectus adominis (Myriknas *et al.*, 2000). In terms of mechanisms, crossed monosynaptic reflexes may be a consequence of any one of three possible mechanisms. 1. The primary afferents may cross the midline to synapse with the contralateral motoneurone pool (Matsushita & Tanami, 1983; Morgan *et al.*, 1981; Ritz *et al.*, 1991). 2. Dendrites of motoneurones may cross the midline and synapse with afferents on the other side (Ritz *et al.*, 1991; Rose & Richmond, 1981). 3. Motoneurones exiting the spinal cord ipsilaterally may be located contralaterally (Abrahams & Keane, 1984).

It is clear therefore that the suggestion here that Ia afferents monosynaptically activate motoneurones projecting to contralateral muscles is not without experimental support in other muscle groups. In relation to the trapezius muscle, while there is some information available in relation to afferent organisation and motoneurone location, it is clear that some of these possibilities have yet to be explored before the anatomical basis of our observations can be elucidated. In terms of afferent organisation it appears that, at least in the rat, that trapezius afferents only project ipsilaterally (Ishii, 1989). In terms of motoneurone organisation however, certain intriguing possibilities remain to be clarified. The trapezius has two motoneurone pools; those motoneurones that course in the spinal accessory nerve and those that course in the cervical spinal nerve. The motoneurone pool of the spinal accessory nerve is ipsilaterally placed in rats, cats and sheep (Clavenzani *et al.*, 1994; Kitamura & Sakai, 1982; Liinamaa *et al.*, 1997) and its dendrites do not appear to cross the mid-line (Rose & Richmond, 1981). On the other hand, Vanner & Rose (1984) stained the dendrites of the cat trapezius motoneurones and found that the dendritic tree of the upper motoneurones spread as far medially as the mid-line. Here, the two sides could interact. Another point of communication may be from the cervical spinal nerve. This motoneurone pool is medial to that of the spinal accessory nerve and the extent of these dendrites has not been explored. The possibility that the dendrites of these medially placed motoneurones might also be the area of interaction with afferents from the other side gains support from the observations of Peterson (1989). In a review of the organisation of the motoneurone pools to vertebrate axial muscles he notes that axial motoneurones often have markedly asymmetrical dendritic fields that are orientated preferentially towards the contralateral spinal cord. Peterson (1989) elaborates to suggest that when a muscle has both medial and lateral motoneurone pools, a functional subdivision exists, such that the laterally placed motoneurones have a unilateral function and the medially placed motoneurones help to co-ordinate crossed activity. The crossed monosynaptic connections between the trapezii reported here could well be a common feature of the axial muscles with medially positioned motoneurone pools.

To summarise, in humans it is not possible to give a definitive statement that Ia afferents synapse monosynaptically with the contralateral trapezius motoneurone pool. However, the author has remained open to the possibility that this is so. Functionally, it is clear that the trapezii work closely together. So, although it would be detrimental to movement to have equal bilateral input to the muscle pair, functional expectations are such that close connections must exist to co-ordinate these synergistic muscles. With ipsilateral stimulation the reflexes described here are large enough to be recorded contralaterally without the necessity of the usual conditioning stimuli. In fact, they can often be seen as a result of a single stimulus. They respond equally to vibration and voluntary contraction. The motoneurones share common presynaptic input and, most compellingly, the reflex pathway is sufficiently short enough to be mediated monosynaptically. Individually, the evidence is not conclusive but taken together the most economical interpretation of the evidence is that a crossed monosynaptic connection exists between this muscle pair.

3 REFLEXES IN SERRATUS ANTERIOR

3.1 Introduction

As reported in the introduction to this thesis, one of the prime functions of the serratus anterior muscle is to stabilise the scapula to the chest wall during movements of the arm. Indeed, if the muscle is paralysed, the scapula will wing away from the thorax whilst the arm is at rest but especially during pushing movements (Watson & Schenkmann, 1995). Weakness as well as paralysis of this muscle can also lead to winging of the scapula away from the chest wall. This can cause a non-specific ache in the upper back (Warner *et al.*, 1992; Belling Sorensen & Jorgensen, 2000; Ludewig & Cook, 2000). Weakness of serratus anterior is also associated with other dysfunctions of the shoulder complex. It alters the co-ordinated movement of the scapula and humerus such that the scapula is no longer able to move away from the rotator cuff when the hand is above the head (Arroyo *et al.*, 1997). This causes secondary impingement syndromes which can be painful and disabling (Belling Sorensen & Jorgensen, 2000; Ludewig & Cook, 2000; Wadsworth & Bullock-Saxton, 1997; Warner *et al.*, 1992). Serratus anterior weakness is also implicated in those glenohumeral instability syndromes promoted by throwing actions (Glousman *et al.*, 1988). Thus, during the transition phase between the late cocking stage of throwing and the follow through, the humeral head is forced anteriorly in lateral rotation and horizontal extension. This anterior sheer generates instability of the shoulder complex.

Unlike trapezius, the two serratus anterior muscles tend to work independently. This is illustrated by the lack of activity of the contralateral muscle during abduction of the ipsilateral arm (see figure 36). However, some argue that these muscles work bilaterally when functioning as an accessory muscle to respiration. Williams *et al.* (1989) point out that a person struggling for breath will tend to grip a table or grip their hands on to their knees in order to stabilise the chest. In this case, the serratus anterior muscles may work together as accessory muscles to respiration. That the activity of one side affects the output of the other is hinted at from the results of the investigations of Wadsworth & Bullock-Saxton (1997). They demonstrated an increased variability of the timing of onset of serratus anterior with bilateral abduction, in a group with ipsilateral shoulder pathology when compared to an uninjured control group. However, they also demonstrated a delayed onset of serratus anterior activity on the uninjured side. So, although crossed activity does not seem to be strongly locked to the ipsilateral side, a contralateral connection may exist.

While the normal function of serratus anterior is integral to scapula stability and movement, the reflex control of this muscle has not been previously explored. Thus, the aim of this investigation was to explore both the ipsilateral and contralateral reflex control of this muscle. As the serratus anterior muscle pair tends to act independently, the aim was to compare the reflex control of serratus anterior to that of the inter-dependent trapezius muscle pair.

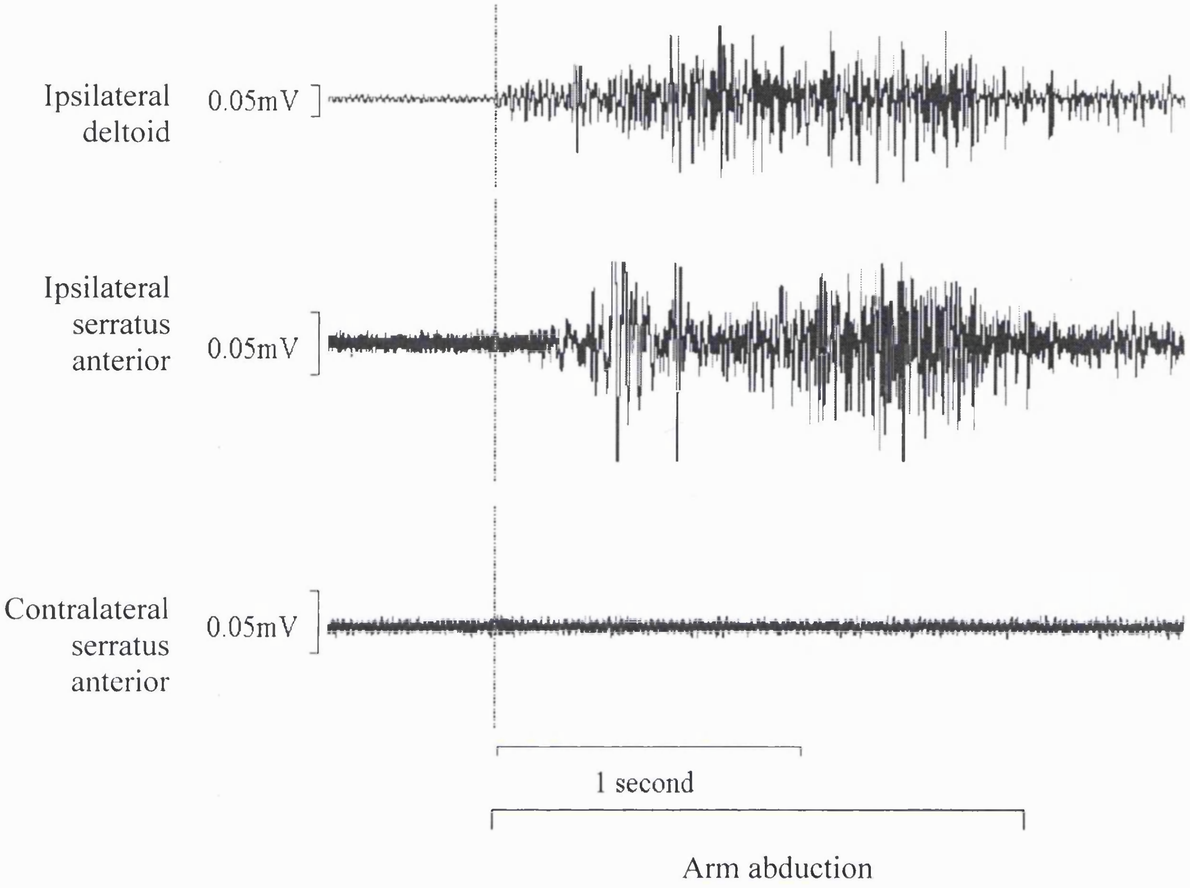


Figure 36. EMG recordings of deltoid and serratus anterior muscles during abduction of the arm. Surface EMG of the ipsilateral deltoid (top), the ipsilateral serratus anterior (middle) and the contralateral serratus anterior (bottom). The EMG is recorded before, during and after abduction of the ipsilateral arm. The lack of EMG activity of the contralateral serratus anterior illustrates that this muscle is inactive during ipsilateral abduction. The dotted line marks the onset of the movement.

3.2 Methods

Recordings were made, with local ethical approval and informed consent from nineteen healthy subjects aged between 21 and 51years.

3.2.1 Reflex activity evoked by a mechanical tap to the serratus anterior muscle.

Surface EMG was recorded using adhesive electrodes placed edge to edge with the recording area 3cm apart. The electrodes were positioned longitudinally over the 6th digitation of the ipsilateral (nineteen subjects, n=39) and contralateral (eighteen subjects, n=36) serratus anterior muscles (see figure 37; Lo Monaco *et al.*, 1983).

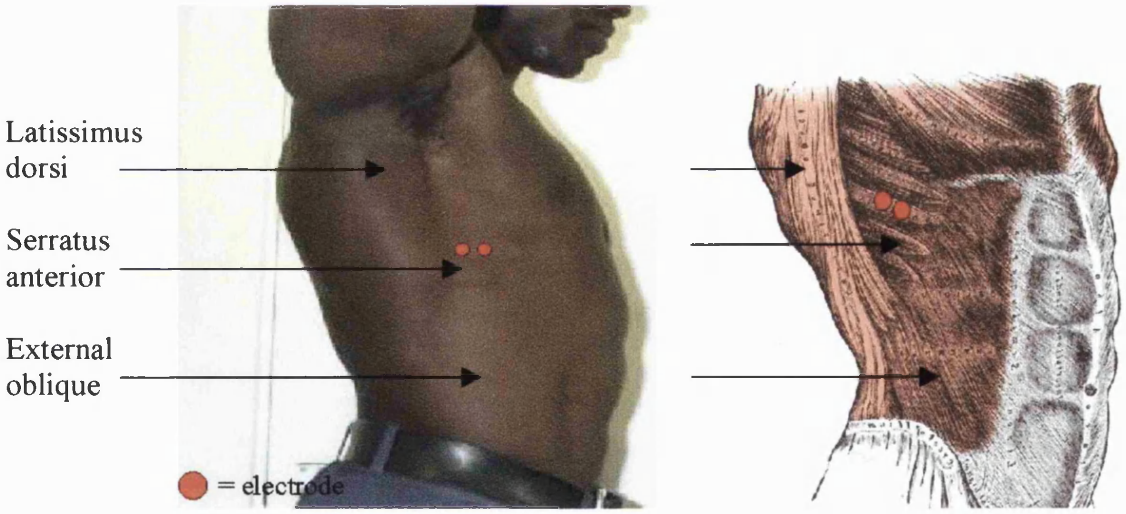


Figure 37. The location of electrodes used to record serratus anterior EMG. A lateral view of the trunk along with a diagrammatic representation to illustrate the position of electrodes over a digitation of serratus anterior. The diagram is adapted from Williams *et al.* (1989).

Care was taken to avoid recording from the external abdominal oblique and latissimus dorsi muscles that lie adjacent to serratus anterior. The tapping device, triggered by a digital pulse from a CED 1401, delivered single taps at constant amplitude and at a rate of 0.33Hz. Usually data sequences consisted of 30 consecutive taps in order to average reflex responses. The reflexes were evoked by tapping the belly of the 5th digitation of serratus anterior.

The data was converted from an analogue to a digital signal at a sampling frequency of 4KHz, (CED 1401) and stored for later analysis by CED Signal software. The waveforms were rectified and averaged. The latency of any evoked reflex was recorded from where it clearly deflected from the baseline. If a clear deflection could not be visualised, the latency was taken from the point where the reflex deflected above the pre-stimulus mean ± 95% confidence interval (Wohlert, 1996). As the procedure was repeated with some subjects, each subject's mean latency was used to construct the final results. The latency of the late ipsilateral reflex was compared to the latency of the crossed reflex using a Student's unpaired t-test assuming equal variance. The amplitudes of the rectified reflexes were recorded using the maximum amplitude to calculate the percentage increase above the pre-stimulus mean activity.

3.2.2 Magnetic stimulation of the serratus anterior motor cortex.

Preliminary investigations were made of the corticospinal input upon the serratus anterior motoneurone pool. EMG recordings were made during magnetic stimulation of an area of the motor cortex found to activate serratus anterior (henceforth referred to as the serratus anterior motor cortex). This was found adjacent to the trapezius motor cortex (see section

2.2.3.3). EMG was recorded bilaterally from three subjects using surface electrodes as previously described. A 70mm double coil from the magnetic stimulator was centred over the motor area and the coil was held in place. A maximum of 40 stimuli was delivered in a posterior anterior direction and this was repeated at different stimulus intensities using an external triggering mechanism. The stimulus intensities used generally ranged from 50% to 75% of the stimulator's output. The waveforms were rectified, averaged and the latency of the evoked reflexes were recorded. As the procedure was repeated with each subject, each subject's mean latency was used to construct the final results.

3.3 Results

3.3.1 Reflex activity evoked by a mechanical tap to the serratus anterior muscle.

A brief tap to the serratus anterior muscle evoked homonymous short and long latency reflexes. In contrast to the short latency crossed trapezius reflex, the tap did not evoke a short latency crossed serratus anterior reflex. However, the tap did evoke a long latency facilitatory reflex in the contralateral serratus anterior muscle.

The mean latency of the early ipsilateral facilitation was 18.4ms. However, the latencies varied widely, ranging from 9ms (see figure 38) to 26ms.

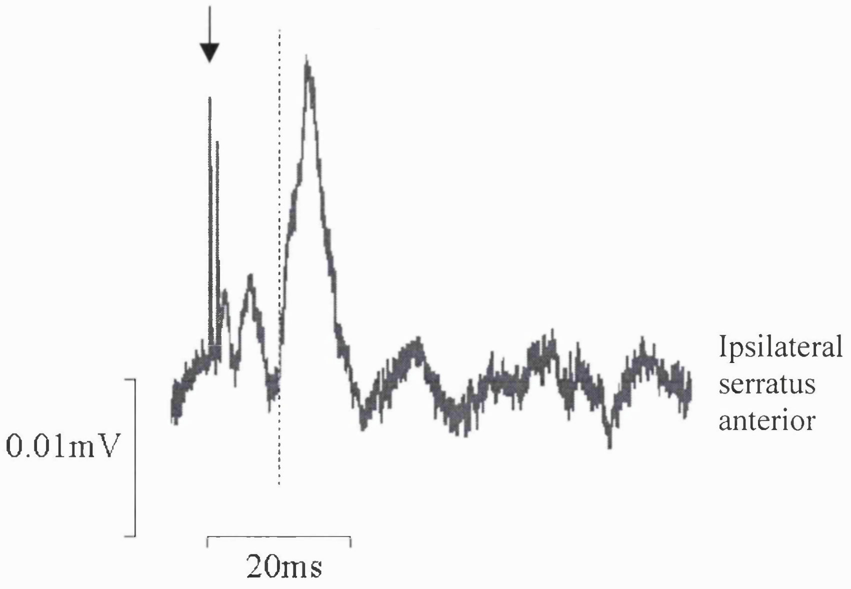


Figure 38. The ipsilateral serratus anterior reflex evoked by a mechanical tap to the 5th digitation of the muscle. The early reflex is evoked at 9ms, which is indicated by the vertical cursor. The trace is the result of rectifying and averaging 30 sweeps. The arrow marks the stimulus onset.

A crossed serratus anterior reflex was evoked on 42% (15/36) of occasions. The latencies of the reflex evoked contralaterally were compared to the latencies of the late reflex evoked ipsilaterally. As table 5 demonstrates and figure 39 exemplifies, these reflex latencies were not significantly different from each other (p=0.79). The latency, amplitude and frequency of occurrence of all these reflexes are summarised in table 5.

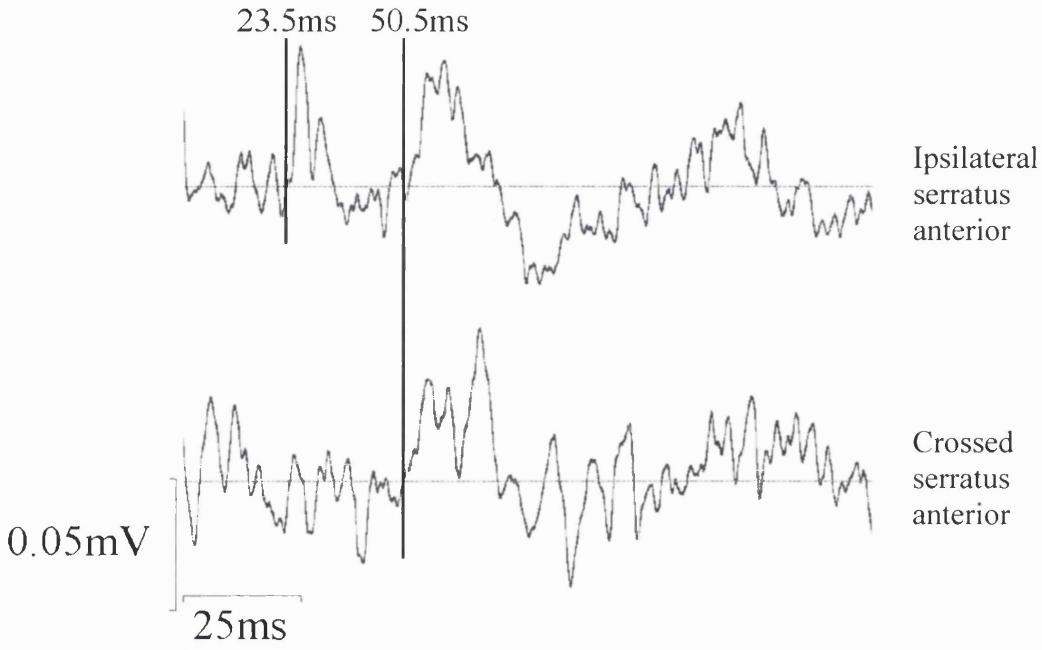


Figure 39. The ipsilateral and crossed serratus anterior reflexes. The average rectified ipsilateral serratus anterior short and long latency reflex evoked by a mechanical tap to the ipsilateral muscle (top). The average rectified reflex in the contralateral serratus anterior (bottom). The traces are the result of rectifying and averaging 30 sweeps. The stimulus occurred at the onset of each trace. The horizontal cursor lies upon the mean + 95% confidence interval. The first vertical cursor marks the early reflex latency. The second vertical cursor marks the latency of the contralateral reflex and shows that the ipsilateral and contralateral long latency reflexes were evoked at very similar latencies.

	Ipsilateral serratus anterior reflex		*Crossed serratus anterior reflex*	
	early facilitation	late facilitation	early facilitation	late facilitation
Latency (ms) mean ± S.D.	18.4 ± 5.7	50.4 ± 11.1	-	50.8 ± 16.9
Amplitude	57%	70%	-	52%
Occurrence	72% (28/39)	62% (24/39)	0% (0/36)	42% (15/36)

Table 5. Summary of reflex responses recorded in serratus anterior. The latency, amplitude and occurrence of the ipsilateral and crossed serratus anterior reflex evoked by a mechanical tap to the ipsilateral serratus anterior muscle. The amplitude is recorded as the percentage increase above the mean EMG activity. The occurrence is reported as a percentage and the number of responses evoked over the total number of experiments.

3.3.2 Magnetic stimulation of the serratus anterior motor cortex.

The ipsilateral long latency stretch reflex may be of transcortical origin. The crossed reflex, being of the same latency, may also employ a transcortical route. In order to investigate this possibility, we recorded the response of both ipsilateral and contralateral muscles to magnetic stimulation of the serratus anterior motor cortex.

The responses were more easily visualised once rectified. An example of these bilateral responses is given in figure 40. The latency of the responses and their occurrence are presented in table 6.

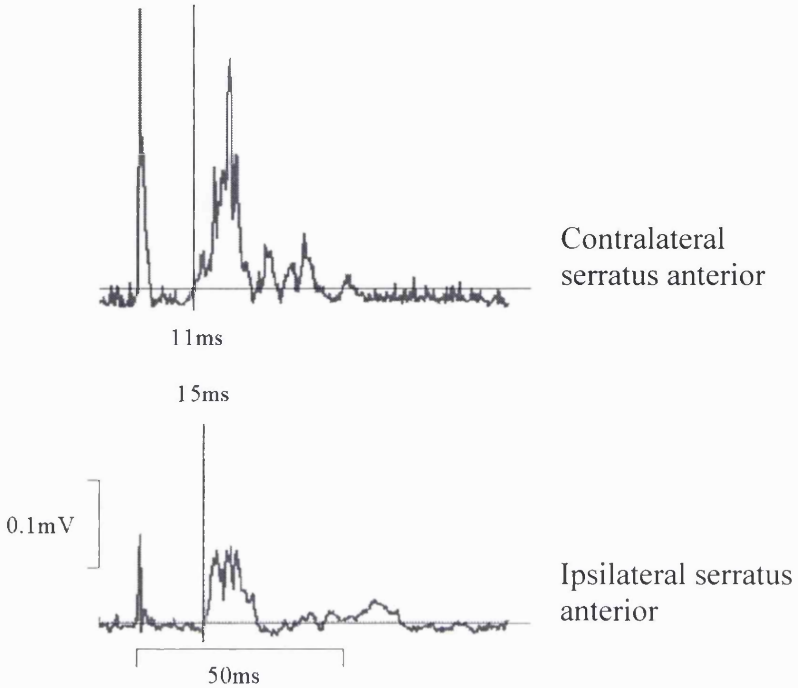


Figure 40. The average rectified contralateral (top) and ipsilateral (bottom) serratus anterior responses evoked by magnetic stimulation of the ipsilateral motor cortex. Each average was constructed from the result of 10 stimuli. The artifact marks the stimulus onset. The horizontal cursor lies upon the mean + 95% confidence interval. The vertical cursors mark the onset of the responses.

	Contralateral serratus anterior	*Ipsilateral serratus anterior*
Latency (ms), mean ± S.D.	17.8 ± 5.5	19.6 ± 4.8
Occurrence	100% (5/5)	60% (3/5)

Table 6. The latency and occurrence of the contralateral and ipsilateral serratus anterior responses to magnetic stimulation of the ipsilateral serratus anterior motor cortex. The occurrence of the responses is displayed as the number of responses evoked over the total number of experiments.

3.4 Discussion

3.4.1 Short latency reflexes.

Short latency stretch reflexes were evoked in serratus anterior by a brief tap to the muscle. The mean latency of this reflex was 18.4 ± 5.7ms ($n = 39$), although the fastest reflex was evoked at 9ms. Like the trapezius reflex, one might expect this short latency reflex to be evoked monosynaptically. A monosynaptic serratus anterior reflex latency can be estimated by the addition of the afferent conduction time, the efferent conduction time and time for the synaptic delays. The conduction times can be estimated if the length of the conduction pathway is known together with an estimate of the conduction velocity. Taking measurements from twelve skeletons, the distance from the 5th rib to the lower cervical spine following the path of the nerve supply, the long thoracic nerve, a mean distance of 0.25m was established. With an afferent conduction velocity of the fastest afferents estimated at 65m/s taken from soleus afferents (Burke *et al.*, 1983), (as no data is available relating to the conduction velocity of serratus anterior afferents) the afferent conduction time can be estimated at 4ms. The efferent conduction velocity of the long thoracic nerve has been recorded at a range of velocities from 50 to 67m/s (Alfonsi *et al.*, 1986; Lo Monaco *et al.*, 1983; Petrera & Trojaborg, 1984). Thus, taking the fastest conduction velocity of 67m/s, the fastest efferent conduction time can also be estimated at 4ms. With a 1ms central delay and a 1ms delay at the neuromuscular junction, the fastest time to evoke a monosynaptic reflex is 10ms. Therefore, this is comparable to the fastest latency of the reflex evoked here. Thus, it is reasonable to presume that, at least the earliest component of the short latency serratus anterior reflex is monosynaptically mediated. On the other hand, this reflex had a wide range of latencies, which imply that other reflex pathways may contribute to this response. Alternatively, this wide range of latencies may well be explained by the low efficacy of the mechanical stimulus applied to the serratus anterior muscle. These factors are considered below.

3.4.1.1 Afferent origin of the serratus anterior reflex.

As stated above, the earliest component of the short latency reflex in serratus anterior is entirely compatible with a Ia mediated monosynaptic reflex. The later components could however, be mediated by other reflex pathways. One such possibility is that they may be mediated by cutaneous afferents that are activated by the tap (Burke *et al.*, 1983). That the cutaneous afferent input contributes to the short latency reflex is especially plausible as the fastest cutaneous afferents (evoked by electrical stimulation) conduct at similar velocities to group I afferents (Macefield *et al.*, 1989). Another possibility is to consider that group II afferents are involved. The conduction velocity of group II afferents recorded from investigations of human leg stretch reflexes is 21.4m/s (Nardone & Schieppati, 1998). Thus, if the earliest part of this serratus anterior reflex were mediated by group II muscle spindle afferents, the afferent conduction time would increase from 4ms to 11.7ms. So, if this short latency reflex was an oligosynaptically mediated group II reflex, the onset would be delayed by 7.7ms as well as any extra central synaptic delay taking the reflex onset to or after approximately 18ms. Therefore, it is possible that group II input may contribute to the later part of the response. On the other hand, group II afferents are not easily evoked by mechanical tap to a muscle (Burke *et al.*, 1983) and so it is unlikely that there is a large group II contribution to this reflex.

3.4.1.2 Methodological issues.

Although a tap to the digitation of the serratus anterior muscle evoked a reflex, these reflexes were small by comparison to the reflexes observed in trapezius. Indeed, the signal to noise ratio was smaller and the reflex was harder to evoke when compared to trapezius. On the other hand, serratus anterior does not have an obvious tendinous attachment and tapping the muscle belly is not an effective way of stretching the muscle. Indeed, as a simple demonstration of this phenomenon, the quadriceps reflex was evoked from one subject on three occasions by a) tapping the quadriceps tendon and b) tapping the quadriceps muscle belly (see figure 41). When a quadriceps reflex was evoked by a tap to the muscle belly, both the latency and amplitude were much reduced. Indeed, the amplitude of the quadriceps reflex evoked by tapping the patella tendon was, on average 3.6 ± 0.3 times greater than the amplitude of the reflex evoked by tapping the muscle belly (see figure 41). Thus, if the serratus anterior reflex could be evoked by a more effective muscle stretch, it may have resulted in a reflex of greater amplitude and thus shorter latency.

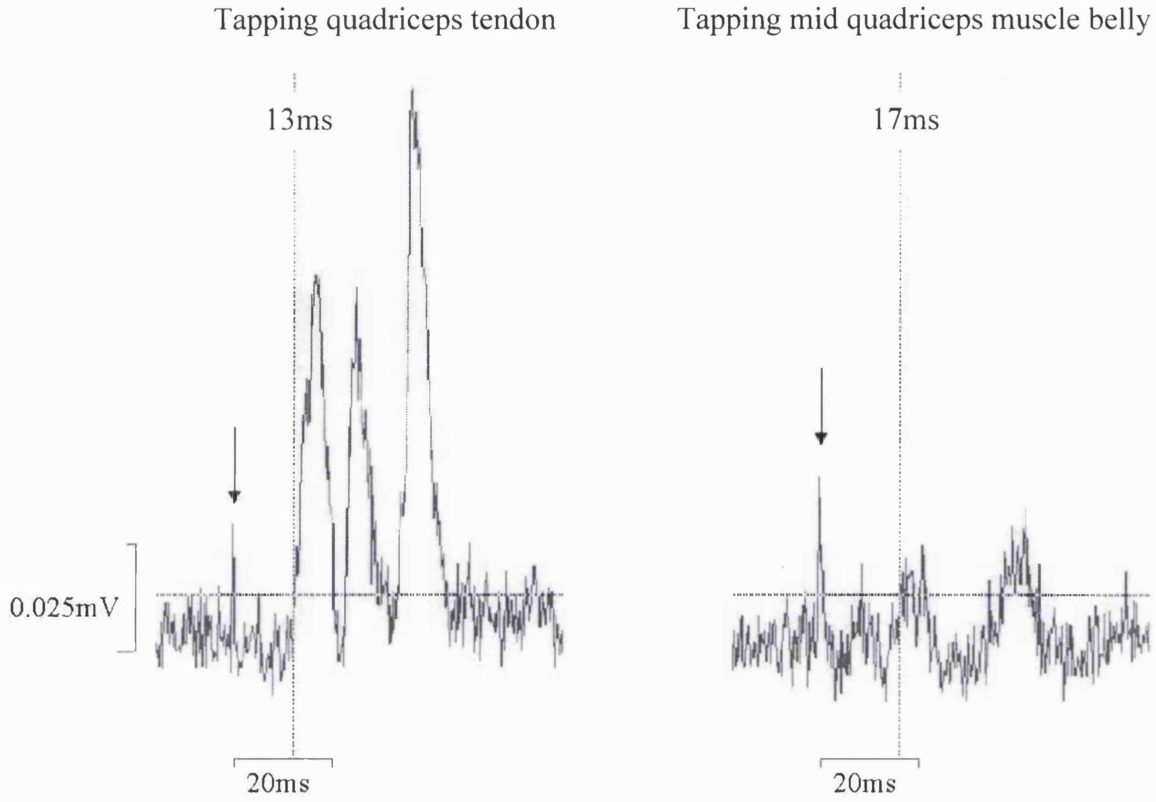


Figure 41. The effect of tap position on reflex amplitude. An example of the average rectified quadriceps tendon jerk evoked from a mechanical tap to the muscle's tendon (left) and a mechanical tap to the mid muscle belly (right). The latency of the reflex evoked by the tendon jerk is 4ms faster. The amplitude of the first peak of the reflex evoked by the tendon jerk is 273% above mean activity. The amplitude of the first peak of the reflex evoked by a tap to the muscle belly is 70% above mean activity. This represents a near 4 fold increase in the amplitude of the response when the stretch is applied from the tendon rather than the muscle belly. The arrows mark the stimulus onset. Each average is constructed from the result of 20 stimuli. The vertical cursor shows the reflex latency. The horizontal cursor lies on the mean + 95% confidence interval.

3.4.2 Long latency reflexes.

Returning to serratus anterior, a second, longer latency reflex was evoked in the homonymous muscle at a mean latency of 50.4 ± 11.1ms. This reflex seems to be the equivalent of other long latency reflexes evoked by muscle stretch. There has been some uncertainty of the pathway of these long latency reflexes. They may be evoked by fast afferents using a transcortical pathway or by slow afferents using a spinal pathway.

To add to the confusion, a tap to human leg muscles has been demonstrated to evoke three responses. The three reflexes are the short latency monosynaptic reflex, a medium latency response and a longer latency response. Schieppati & Nardone (1997) demonstrated that the medium latency reflex slowed to a greater degree than the monosynaptic reflex when the limb was subjected to cooling. They concluded that this was due to the differential effect of cooling large and small afferents. Schieppati & Nardone (1997) believed their results to be consistent with the medium latency reflex originating from the smaller group II spindle afferents mediated spinally. Darton *et al.* (1985) also concludes that this medium latency reflex is not transcortical. They demonstrated a difference between short and long latency reflexes when evoked from arm muscles, as compared to those evoked from leg muscles. The central delay was the same whether the reflex was evoked from the arm or the leg. Therefore, this reflex could not be transcortical as the difference in central delay would be longer when evoked from the leg (because of the greater conduction distance from the leg to the cortex) than that evoked from the arm.

The third and longest latency reflex evoked by a stretch to leg muscles has been investigated by Petersen *et al.* (1998). They used an MEP evoked by magnetic stimulation of the relevant motor cortex to condition this reflex. The MEP was reported to facilitate this long latency stretch reflex at an appropriate test-condition interval and they concluded that this was due to its transcortical nature. So to summarise, the short and medium latency reflexes evoked by a stretch to leg muscles have a spinal path and the longest latency reflex is transcortical.

These three reflexes evoked in the leg tend not to be reported in the arm. Typically, a short latency monosynaptic reflex is evoked along with one long latency response. The origin of this long latency reflex has also been investigated (Palmer & Ashby, 1992; Taylor *et al.*, 1995; Matthews, 1991). Taylor *et al.* (1995) demonstrated that at least a part of the long latency reflex evoked from a stretch of the long finger flexors is mediated transcortically. They used the inter-hemispheric inhibition evoked by magnetic stimulation of the motor cortex that had been demonstrated by Ferbert *et al.* (1992), to condition the long latency reflex. This ipsilateral magnetic stimulation inhibited the incoming volley. Thus, they concluded that the long latency reflex had been inhibited at a cortical level and so must be transcortical in nature.

These long latency reflexes are thought to be evoked by muscle afferents. However, Corden *et al.* (2000) has attempted to evoke the long latency reflex by tapping the muscle without permitting muscle stretch. They demonstrate that the long latency reflex is evoked without muscle stretch and so they conclude that it is mediated by afferents other than those from muscle. Indeed, as previously suggested, the tap also evokes cutaneous afferent activity (Burke *et al.*, 1983). Long latency facilitation of muscle from cutaneous afferents from electrical stimulation has been well described. Some of these reflexes are also thought to have a transcortical path (Jenner & Stephens, 1982), although, Macefield *et al.* (1996) suggest that they are served by several pathways that vary according to the task.

Whether the long latency reflex evoked in serratus anterior is a) transcortically mediated and b) evoked by muscle or cutaneous afferents is difficult to conclude from the present data alone. Some indication of whether it is transcortically mediated can be determined by estimating the expected latency of such a reflex. This can be estimated by the addition of the latency of the somatosensory evoked potential from serratus anterior, the cortical relay time (Michels *et al.*, 1993) and the latency of the MEP evoked from stimulation of the serratus anterior motor cortex. There appear to be no published figures for the somatosensory evoked potential from serratus anterior in the literature. So, a reasonable conduction time from this muscle to the cortex can be estimated by the addition of a) the conduction time of serratus anterior Ia afferents to the spinal cord and b) the conduction time of afferent input from the same spinal segment to the cortex. The addition of the Ia conduction time from serratus anterior to the spinal cord at 4ms (see p.108) and the conduction time of other shoulder afferents to the motor cortex at 15ms (Macefield & Gandevia, 1992), gives a conduction time of 19ms. Thus, this represents the conduction time from serratus anterior to the cortex. With the addition of approximately 8ms for the cortical relay time (Michels *et al.*, 1993) and the fastest conduction time from the cortex to serratus anterior of 17.8ms (from the data in table 6), a transcortical reflex could have a conduction time approximating 45ms. The actual latency of the long latency reflex was 50.4ms. Thus, this timing opens up the possibility that the second, longer latency ipsilateral reflex has a transcortical path.

A bilateral corticospinal input upon the motoneurone pools of serratus anterior has been demonstrated here (see table 6). Thus, if the ipsilateral long latency serratus anterior reflex were transcortical in nature, one might expect that this cortical input would evoke bilateral reflex responses. Indeed, this was the case as the tap to the serratus anterior not only evokes a reflex ipsilaterally at a latency of 50.4 ± 11.1ms but also a crossed serratus anterior reflex at a mean latency of 50.8 ± 16.9ms on 42% of occasions. Therefore, that these long latency reflexes are bilateral, in this case, suggests that they are transcortically mediated.

Other approaches have been used to investigate the nature of a transcortical pathway. To confirm this pathway, Taylor *et al.* (1995) conditioned the long latency reflex of the long finger flexors using magnetic stimulation of the ipsilateral motor cortex. The ipsilateral magnetic stimulation evoked an inter-hemispheric inhibition, which inhibited the incoming volley, thus suggesting a transcortical path (Ferbert *et al.*, 1992). Presuming inter-hemispheric inhibition exists between the serratus anterior muscle pair, the magnetic stimulation of the ipsilateral serratus anterior motor cortex may inhibit the long latency reflex. However, this magnetic stimulation also evokes an ipsilateral MEP (see figure 40 and table 6, section 3.3.2). This large ipsilateral response would confound any analysis of a change in amplitude of the serratus anterior long latency reflex (see figure 42).

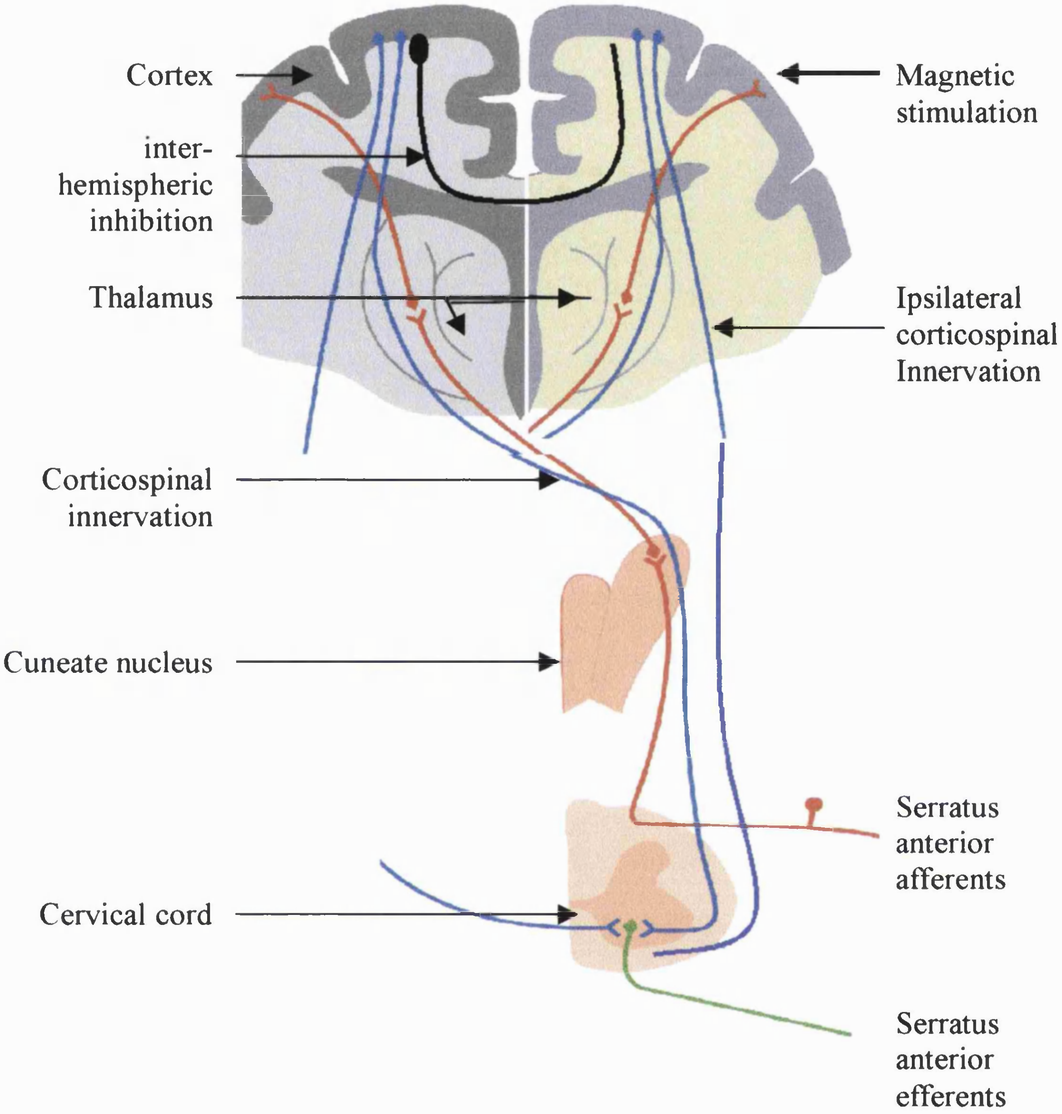


Figure 42. Diagrammatic representation of the inter-hemispheric inhibition of a transcortical reflex evoked from serratus anterior. Theoretically, the long latency serratus anterior reflex relays at the cuneate nucleus and the thalamus before arriving at the cortex. Here, ipsilateral (right) magnetic stimulation evokes inter-hemispheric inhibition, thus inhibiting the transcortical reflex. The magnetic stimulation would also evoke an ipsilateral corticospinal volley, facilitating the serratus anterior motoneurone pool. This is at such latency that the MEP would conflict with the long latency reflex.

Unlike trapezius, no short latency crossed serratus anterior reflex was evoked by the tap to the ipsilateral serratus anterior muscle. The difference in this control begs the question of the functional significance of the short and long latency crossed reflexes. One must presume that the monosynaptic crossed trapezius reflex helps to closely co-ordinate the activity of one side to the other. The bilateral function of the trapezius muscle pair seems to be integral to normal movement. The bilateral function of the serratus anterior muscles is not as well defined. Certainly during normal function of the arm one might expect crossed control mechanisms but the polysynaptic nature of these reflexes allows greater opportunity for their modification by other inputs. Thus, the existence of the long latency crossed serratus anterior reflex is consistent with greater separation of the control of the two serratus anterior muscles during movement of the arm, when compared to the control of the trapezius muscle. Indeed, the modification of these reflexes must be task specific because, as discussed in the Introduction (section 3.1), the serratus anterior does not always work bilaterally during unilateral arm function. Yet, the serratus anterior has been revealed to have strong bilateral corticospinal connections. This suggests a task specific nature of these connections.

In conclusion, a short latency serratus anterior reflex was evoked by a mechanical tap to the 5th digitation of the muscle at a mean latency of 18.4 ± 5.7ms. Taking the mean latency at face value, this is a little slow to be consistent with a monosynaptic reflex. However the fastest reflex was evoked at 9ms which is consistent with this pathway. A long latency reflex was also evoked ipsilaterally at 50.4 ± 11.1ms. Magnetic stimulation of the serratus anterior motor cortex demonstrated a bilateral corticospinal input to the serratus anterior muscles. In addition, a tap to the ipsilateral muscle also evoked bilateral reflex responses with the same mean latencies. This suggests that both the ipsilateral and crossed serratus anterior long latency reflexes are transcortically mediated.

4 REFLEXES BETWEEN TRAPEZIUS AND SERRATUS ANTERIOR

4.1 Introduction

The lower trapezius and serratus anterior muscles on one side act together to a) stabilise the scapula and b) to rotate the scapula during movements of the arm. The synergistic action of these muscles has been established elsewhere in this thesis (section 1.2.2.2). In addition, a tendency for the substitution of trapezius activity by serratus anterior activity during a fatiguing protraction task reveals their closely linked function and control (Hurley *et al.*, 1999).

It is known that reflex connections exist between other synergists helping to control their co-ordinated action (section 1.3). In particular, reflexes that help to control arm movement have been demonstrated in humans (Cavallari & Katz, 1989; Creange *et al.*, 1992; Gielen *et al.*, 1988; Marchand-Pauvert *et al.*, 2000a; Marchand-Pauvert *et al.*, 2000b; McClelland *et al.*, 2001). As described in section 1.3 of the Introduction, synergistic reflexes between two muscles may be stronger in one direction than the other; that is, they can be skewed or even unidirectional. Caicoya *et al.* (1999) and Fritz *et al.* (1989) suggest that these skewed or unidirectional reflexes tend to serve those muscles that act over a joint but may pull in different directions. On the other hand, bi-directional Ia reflex connections between synergists described in human and animal studies seem to exist between those muscles that act together to produce single movements (Cavallari & Katz, 1989; Cavallari *et al.*, 1992; Caicoya *et al.*, 1999; Fritz *et al.*, 1989).

So, although the closely associated action of trapezius and serratus anterior has been investigated, the reflex connections between this synergistic pair have not been explored. The action of trapezius and serratus anterior produce different movements in different directions. Thus, this particular situation contrasts with that described for the balanced bi-directional reflex connections described above. However, as the action of trapezius and serratus anterior results in a single movement, that of rotation of the scapula, reflex connections between these muscles are likely to exist. Thus, the aim of this investigation was to explore the reflex connections between trapezius and serratus anterior.

4.2 Methods

4.2.1 Reflexes in serratus anterior evoked by electrical stimulation of the afferent nerve to trapezius.

With the local ethical approval and the informed consent of ten healthy subjects aged between 21 and 51 years, a lower trapezius, mid amplitude H reflex was electrically evoked as described in section 2.2.2. Surface EMG of the ipsilateral and contralateral serratus anterior and lower trapezius muscles were recorded using adhesive electrodes. The electrodes were positioned over the relevant muscle bellies as described elsewhere (section 2.2.1 and 3.2.1). The EMG was amplified, filtered and stored (see section 2.2.1). The cervical nerve of C3/4 was stimulated 30 times at an inter-stimulus interval of 3 seconds. In six (of the ten) subjects, the procedure was repeated on separate occasions (n=19). If a response could be clearly recognised, its latency was taken to occur from the first clear deflection from the baseline in the unrectified EMG. The waveforms were rectified and averaged, and the size of the reflex recorded as the percentage of peak activity above the mean. If a clear deflection could not be visualised from the unrectified waveform, the latency was taken from the point where the reflex deflected from the pre-stimulus mean ± 95% confidence interval. As the procedure was repeated with some subjects, each subject's mean latency was used to construct the final results.

4.2.2 Reflexes in trapezius evoked by a mechanical tap to serratus anterior.

Recordings were made, with local ethical approval and informed consent from nineteen healthy subjects aged between 21 and 51years.

Reflexes in trapezius were evoked by tapping the belly of the 5th digitation of the serratus anterior muscle (section 3.2.1). Using audio and light biofeedback devices, a maximum voluntary contraction (MVC) of the bilateral lower trapezius fibres was established as the maximum EMG produced during a maximum depression/retraction of the scapula. A low grade (approximately 20% MVC), stable contraction of the lower fibres of trapezius was maintained throughout the recording period. Thirty taps were delivered to serratus anterior with an inter-stimulus interval of 3 seconds. The procedure was repeated on fifteen of the nineteen subjects on separate occasions (n=39). The waveforms were rectified and averaged and the latency of any evoked reflex was recorded from where it deflected from the pre-stimulus mean ± 95% confidence interval. As the procedure was repeated with some subjects, each subject's mean latency was used to construct the final results. The amplitude of the rectified reflexes was recorded as the percentage of peak rectified amplitude above the mean activity.

4.3 Results

4.3.1 Reflexes in serratus anterior evoked by electrical stimulation of the afferent nerve to trapezius.

The electrical stimulation of the afferent supply to trapezius evoked reflexes in both ipsilateral and contralateral serratus anterior muscles.

Short latency reflexes were evoked in the ipsilateral serratus anterior in 7 of 19 trials. Of these 5 had clearly defined onsets. An example of a clearly defined reflex can be seen in figure 43. This reflex in serratus anterior could be visualised without rectification. Two of the seven short latency facilitations however, did need rectifying to be visualised. The latency of this reflex ranged from 9.7ms to 16.3ms and had a mean of 13.1 ± 2.9ms. This serratus anterior reflex did occur at a shorter latency than the trapezius H reflex. However, despite the short latency of the serratus anterior reflex, it still may be too long for the reflex to be compatible with a monosynaptic connection (see discussion).

This short latency reflex evoked in the ipsilateral serratus anterior was not the most frequently evoked response. The most frequently evoked response was a long latency facilitation (seen in 11 of 19 experiments; see figure 44), which were best visualised once rectified (see insert to figure 44).

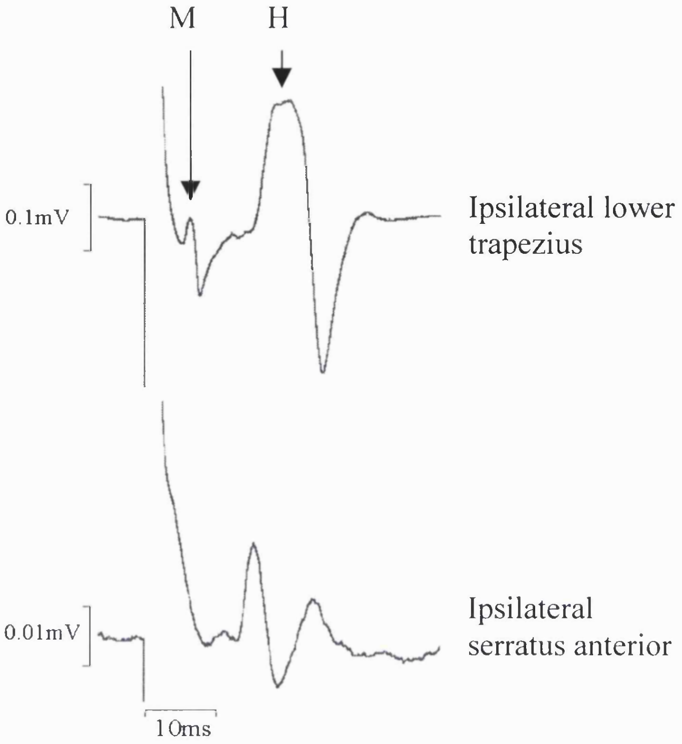


Figure 43. The short latency reflex response of serratus anterior to electrical stimulation of the afferent nerve supply to trapezius. The average M response and H reflex of trapezius (top) and the reflex evoked in serratus anterior (bottom). These responses were recorded simultaneously. The artifact marks the stimulus onset. The averages were constructed from the result of 30 stimuli.

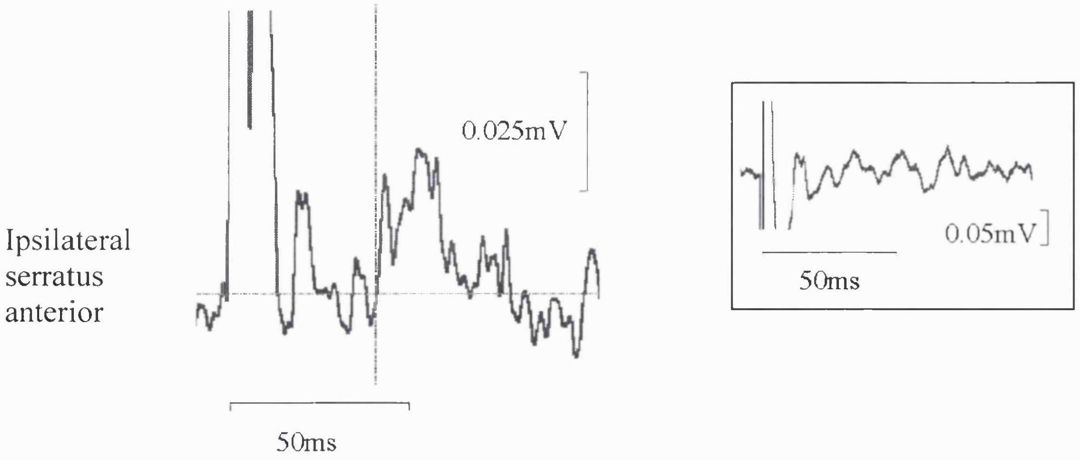
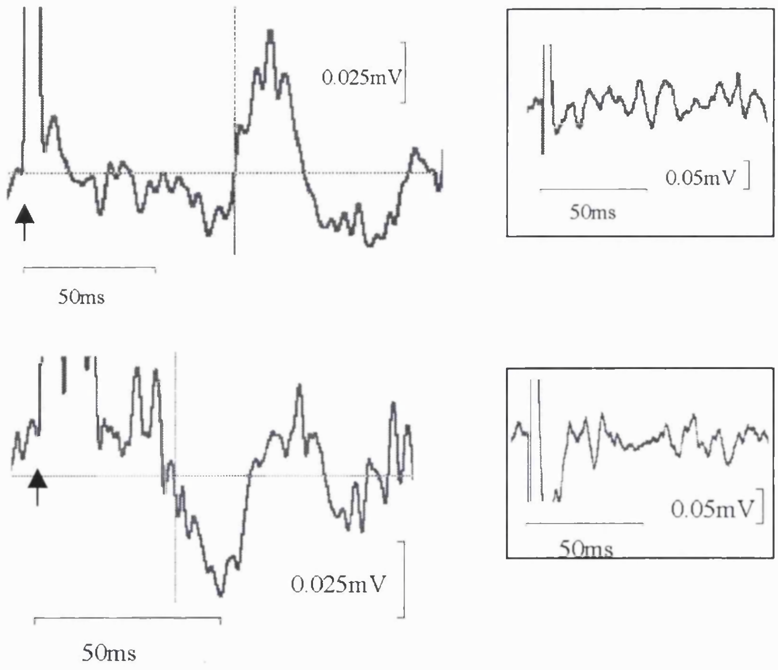


Figure 44. An example of the ipsilateral long latency reflex evoked in serratus anterior from the stimulation of the afferent supply of trapezius. The reflex was the average of 30 sweeps. The stimulus artifact marks the stimulus onset. The horizontal cursor marks the mean + 95% confidence interval. The vertical cursor marks the onset of the reflex determined using the 95% confidence interval. The same averaged unrectified reflex is inset. This unrectified reflex illustrates that they are more easily visualised once rectified.

Reflexes were also evoked in the contralateral serratus anterior muscle (see figure 45). Two different responses were seen. A contralateral long latency facilitation was evoked in 5 of 16 experiments. A contralateral late inhibition was also evoked in 5 of 16 experiments. These were also better visualised once rectified. Sometimes the facilitation and sometimes the inhibition could be evoked on different occasions in the same subject. It is notable that no short latency reflexes were observed in the contralateral serratus anterior.



Contralateral serratus anterior facilitation

Contralateral serratus anterior inhibition

Figure 45. Facilitatory and inhibitory reflexes evoked in the contralateral serratus anterior muscle evoked by the stimulation of the afferent supply of trapezius in two different subjects. The average rectified facilitatory reflex (top) and inhibitory reflex (bottom) were the average of 30 sweeps. The artifact (see arrows) marks the stimulus onset. The horizontal cursors mark the mean + 95% (top) and –95% (bottom) confidence intervals. The vertical cursors mark the onset of the reflexes as determined using the 95% confidence intervals.

As can be seen in figure 45, the latency of the reflexes may have been recorded later than one might have done manually. That is, using the 95% confidence interval might over estimate the reflex latency. This is, however, a method of objectively marking the onset of the reflex with this rather noisy data (Wohlert, 1996).

The latency, amplitude and frequency of these reflexes are summarised in table 7.

	Ipsilateral serratus anterior			*Crossed serratus anterior*		
	short latency facilitation	long latency facilitation	inhibition	short latency facilitation	long latency facilitation	inhibition
latency (ms) mean ± S.D.	13.1 ± 2.9	45.2 ± 14.0	54.2 ± 8.9	-	55.3 ± 14.1	47.7 ± 10.0
amplitude	335%	79%	66%	-	63%	62%
occurrence	37%	58%	11%	0%	31%	31%
	(7/19)	(11/19)	(2/19)	(0/16)	(5/16)	(5/16)

Table 7. The latency, amplitude and occurrence of the ipsilateral and contralateral serratus anterior reflexes evoked by electrical stimulation of the afferent supply to trapezius. The amplitude of the reflex is displayed as the percentage increase of mean activity. The occurrence of the reflex is displayed as the number of reflexes evoked over the total number of trials.

4.3.2 Reflexes in trapezius evoked by a tap to serratus anterior.

A mechanical tap of the serratus anterior muscle evoked reflexes in ipsilateral trapezius, albeit at a long latency. This reflex had a mean latency of 46.8 ± 11.1ms and was evoked 30 times in 39 experiments. The reflexes had a mean amplitude of 85% above the pre-stimulus mean activity. This reflex was more easily visualised if the waveform was rectified. An example of the late facilitation of trapezius is displayed in figure 46. In contrast to those reflexes evoked in serratus anterior by stimulation of the cervical nerve of C3/4, no significant crossed reflexes were evoked in trapezius by tapping serratus anterior (see figure 46).

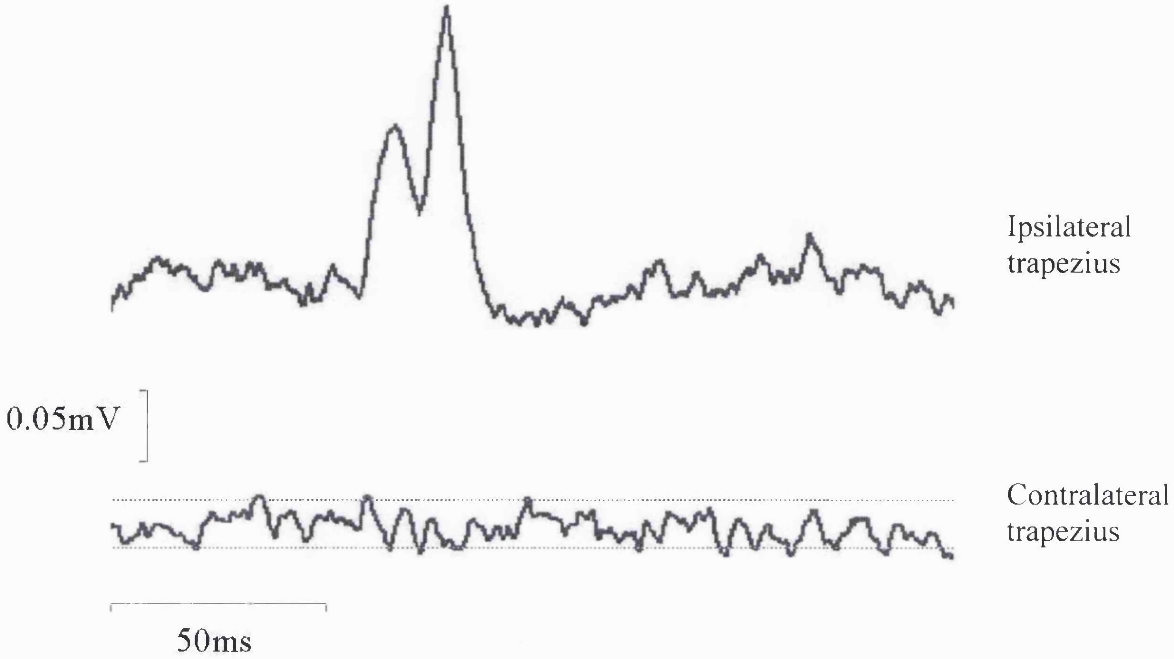


Figure 46. The ipsilateral and contralateral trapezius reflex in response to a mechanical tap to the ipsilateral serratus anterior muscle. The reflexes were the average of 30 rectified sweeps. The stimulus occurred at the onset of each trace. The horizontal cursor marks the mean ± 95% confidence intervals.

4.4 Discussion

Reflexes were evoked in both trapezius and serratus anterior from the stimulation of the synergistic muscle afferents. That reflexes were evoked between these muscle pairs is consistent with the findings of Caicoya *et al.* (1999) and McClelland *et al.* (2001). These authors, amongst others (see Introduction to this section), have demonstrated reflex connections between synergistic muscles in studies of both animals and man.

4.4.1 Short latency reflexes.

In contrast to the long latency reflexes evoked in trapezius by a mechanical tap to serratus anterior, electrical stimulation of the afferent nerve to trapezius evoked a short latency serratus anterior reflex. The latency of this short latency reflex ranged from 9.7ms to 16.3ms and had a mean of 13.1ms ± 2.1. Thus, this response is consistent with being a spinally mediated reflex. Knowledge of the central delay involved in this reflex can lead to a greater understanding of the central pathway. The central delay can be estimated if estimates are taken of peripheral conduction time. This peripheral conduction time is dependent upon the reflex's afferent origin. If it is assumed that this reflex originates from group I afferents, the afferent conduction time from the site of stimulation of the cervical nerve to C3 or C4, can be estimated at 1ms (see section 2.4.1). The efferent conduction time can be estimated at 4ms (see section 3.4.1), so with 1ms estimated as the time for the transmission across the neuromuscular junction, the peripheral conduction time can be estimated at 6ms. With the fastest reflex in serratus anterior being evoked at 9.7ms, the central delay can be estimated at approximately 4ms. This delay could represent a) the synaptic delay involved in an oligosynaptic connection between these two muscles and/or

b) the inter-segmental conduction distance between point of entry to the spinal cord of the afferents and the motoneurones of their synergist. At its shortest, the conduction distance from the point of entry of the trapezius afferents to the serratus anterior motoneurone pool is one spinal level from C4 to C5. This short conduction distance is unlikely to have a long conduction time and so, this 4ms central delay might suggest an oligosynaptic connection.

It is interesting to note that a central delay of 4ms is similar to that of the non-monosynaptic reflexes serving forearm muscles in man (Pauvert *et al.*, 1998). These are thought to be relayed through a system of premotoneurones, which may be located at the upper part of the cervical enlargement (Pierrot-Deseilligny, 1996; Gracies *et al.*, 1994). If this system of interneurones helps to co-ordinate a pattern of upper limb movement, then input from scapulothoracic muscles could well add to this control.

4.4.2 Long latency reflexes.

4.4.2.1 Facilitation.

Long latency facilitatory reflexes were evoked in both ipsilateral trapezius and serratus anterior muscles from stimulation of their synergist. Long latency reflexes were also evoked contralaterally in the serratus anterior muscle. It is interesting to relate the bilateral long latency reflexes in serratus anterior to the bilateral corticospinal input upon the serratus anterior motoneurone pools (see section 3.3.2). If the ipsilateral long latency reflex in serratus anterior is transcortically mediated, then given that the corticospinal output is directed bilaterally, a contralateral serratus anterior reflex might automatically follow. This line of argument receives further support from the observations in section 3.3.1, that contralateral long latency reflexes were also evoked in serratus anterior by tapping the ipsilateral serratus anterior muscle. Thus, if a long latency reflex is evoked ipsilaterally in serratus anterior, it follows that a long latency reflex will also be evoked contralaterally in the serratus anterior muscle. Correspondingly, where in trapezius these strong bilateral corticospinal projections were not present (see section 2.3.3.4), bilateral long latency reflexes have not been observed in any of the experiments reported in this thesis. Consequently, where a mechanical tap to serratus anterior evoked a long latency reflex in the ipsilateral trapezius muscle, it followed that no long latency reflex was evoked in the contralateral trapezius muscle.

4.4.2.2 Inhibition.

On occasion, evidence of a long latency contralateral inhibition in serratus anterior was revealed by the stimulation of the ipsilateral trapezius afferents. This inhibition seems less functionally relevant than the stabilising action of a bilateral facilitation during elevation of one side. However, that both facilitatory and inhibitory contralateral reflex pathways were evoked by the stimulation of trapezius afferents, might indicate that various pathways are available to serve different tasks. Indeed, this functional specificity of reflex outcomes has been demonstrated by McClelland *et al.* (2001). They showed that both excitation and inhibition of the biceps and triceps could occur from stimulation of shoulder muscle afferents. The balance of these responses changed with different positions of the elbow. It is conceivable that such positional changes could alter the reflexes evoked here. If this is the case, bilateral serratus anterior connections from trapezius may help to co-ordinate and modify varying inter-limb activity.

The contralateral inhibitory reflex in serratus anterior may be mediated at cortical or spinal level. As discussed in section 3.4.2, inter-hemispheric inhibition has been revealed between peripheral muscle pairs (Ferbert *et al.*, 1992). In Ferbert's experiments, the interhemispheric inhibition was established by the conditioning of a motor evoked response from the magnetic stimulation of the opposite motor cortex. If such connections exist for the serratus anterior muscle pair, it would be surprising if the single shock stimulation of the cervical nerve to trapezius (compared to condition testing) would be strong enough to evoke this crossed inhibition. Instead, the contralateral inhibition may be as a result of corticospinal input upon inhibitory interneurones at spinal level (Iles & Pisini, 1992; de Noordhout *et al.*, 1999). Once more, this long latency contralateral reflex may be a reflection of the bilateral corticospinal input to the serratus anterior motoneurone pools.

4.5 Summary

In conclusion, that bi-directional facilitatory reflexes were evoked ipsilaterally is unsurprising as trapezius and serratus anterior are synergists, contracting together to stabilise and rotate the scapula during movements of the arm (see section 1.2.2). The pattern of the long latency reflexes evoked may reflect the pattern of corticospinal projections to the ipsilateral and contralateral serratus anterior and trapezius muscles. Thus, long latency reflexes are evoked bilaterally in serratus anterior as a consequence of strong bilateral corticospinal projections from the serratus anterior motor cortex. Whereas, long latency reflexes are evoked just ipsilaterally in trapezius as a consequence of weaker bilateral corticospinal projections from the trapezius motor cortex. Finally, if the long latency contralateral reflexes are mediated transcortically, then it follows that the long latency ipsilateral reflexes are also mediated transcortically.

5 REFLEX CONNECTIONS FROM THE AFFERENTS OF THE ARM AND HAND TO SHOULDER GIRDLE MUSCLES

5.1 Introduction

As previously described (section 1.2), the arm needs a stable base of support to be able to position the hand in space (Peat, 1986; Paine & Voight, 1993). This base of support is provided by anchoring the scapula to the chest wall, which is dependent upon the action of trapezius and serratus anterior. The altered strength of these muscles or even altered timing of their activation, can lead to painful pathologies such as impingements and instabilities (Host, 1995; Ludewig & Cook, 2000; Wadsworth & Bullock-Saxton, 1997; David *et al.*, 2000). Indeed, even when pain is not apparent but altered kinematics of the shoulder girdle is evident – termed a dysfunction – a precursor to a painful pathology may be present (Belling Sorensen & Jorgensen, 2000).

Given this requirement for a stable base of support (Sjogaard *et al.*, 2000), one might expect that central control mechanisms exist between muscles of the upper limb and the muscles that control the stability of the scapula. Indeed, as described in the Introduction (section 1.2.2.1) both the upper and lower fibres of trapezius are active during hand activities. These include finger tapping or when pressing a button even when those muscles that move the shoulder are inactive (Kitahara *et al.*, 2000; Roman-Liu *et al.*, 2001; Schnoz *et al.*, 2000). There is evidence of facilitatory connections between the lateral triceps and serratus anterior in the cat (Caicoya *et al.*, 1999). There is also evidence for bi-directional reflex connections between biceps and triceps in the arm and pectoralis major and deltoid around the shoulder in infants and adults (McClelland *et al.*, 2001; O'Sullivan *et al.*, 1991).

However, there have been no investigations examining the reflex connections from afferents originating in the upper limb to motoneurones of the muscles controlling the shoulder girdle in normal adults and in those adults with dysfunctions that relate to the control of the shoulder girdle muscles.

This chapter investigates the reflex connections from muscles supplied by the median, ulnar and radial nerves to the trapezius and serratus anterior muscles in normal adult subjects and in those subjects with various dysfunctions and pathologies of the shoulder complex.

5.2 Methods

With local ethical committee approval and informed consent, recordings were made from a core group of twenty healthy subjects aged between 21 and 50. Twelve subjects returned on further occasions for additional recording sessions. Whilst sitting, surface EMG was recorded using adhesive electrodes placed edge to edge with the recording area 3cm apart. The electrodes were positioned over the upper and lower fibres of trapezius and along the 6th digitation of serratus anterior just anterior to the mid axillary line as described previously in section 2.2.1 and 3.2.1. The EMG was amplified and filtered with a bandwidth of 30Hz - 3KHz. The data was collected at a sampling frequency of no less than 10KHz and stored as previously described (section 2.2.1). Using audio and light biofeedback devices, a maximum voluntary contraction (MVC) of the lower trapezius fibres was established as the maximum EMG produced during a maximum depression/retraction of the scapula. The MVC of serratus anterior was established as the maximum EMG produced during a maximum resisted protraction of the scapula with the arm in 90° flexion. A low grade (approximately 20% MVC), stable contraction of the lower fibres of trapezius or serratus anterior was maintained throughout the recording periods. Electrical, 1ms square wave pulses were delivered percutaneously every three to five seconds (Digitimer DS7A stimulator) to the median, ulnar and radial nerves sequentially, in varying order. On stimulation of the median and ulnar nerves the anode (a metal plate smeared with electrode gel) was strapped over the bicipital groove. When stimulating the radial nerve, the anode was placed over the lateral side of the upper arm below the level of the deltoid tubercle. The cathode (a Medicotest disk, pre-gelled electrode) was adhered to the skin over the appropriate nerve at the elbow. A recording of surface EMG activity from a muscle supplied by each of these peripheral nerves (flexor carpi radialis (FCR) for the median nerve, flexor carpi ulnaris (FCU) for the ulnar nerve and brachioradialis (Br) for the radial nerve) was used to monitor the intensity of the stimulation. The intensity was varied and ranged up to 4 MT. After 30 stimuli, the EMG from trapezius and serratus anterior was averaged and the latency of any reflex evoked from these muscles was taken from the first clear deflection from base line (Hodges & Bui, 1996). The EMG was rectified and averaged. A reflex was considered to be present if there was activity above the 95% confidence interval for the pre-stimulus mean (Wohlert, 1996). The duration of the response was recorded and the size of the reflex was expressed as a proportion of the peak activity to the pre-stimulus mean activity of the rectified response.

5.2.1 Conduction velocity of the afferents mediating shoulder girdle reflexes.

In order to calculate the conduction velocity of the afferent fibres responsible for the reflex, the median, ulnar and/or radial nerves of nine subjects were stimulated at different points along their length. The median and ulnar nerves were stimulated at the elbow and wrist. When stimulating at the wrist, the anode was placed just proximal to the cathode. The radial nerve was stimulated at the shoulder and at the elbow. When stimulating at the shoulder the cathode was placed between the long head and lateral head of triceps. The distance between the two sites of stimulation was measured. Knowledge of a) the distance between the two sites of stimulation and b) the difference in the latency of the reflex when evoked from the two sites was then used to calculate the conduction velocity of the afferents mediating the trapezius and serratus anterior reflexes. The frequency of evoking the reflex in the upper and lower fibres of trapezius and in serratus anterior was expressed as a percentage. Wilcoxon's matched pairs test was used to examine any statistical differences in the frequency of evoking the reflex in the different parts of trapezius.

5.2.2 Investigation of the possible contribution of cutaneous afferents to reflexes of shoulder girdle muscles.

To assess the possibility of a cutaneous afferent contribution to reflexes of trapezius and serratus anterior, various cutaneous nerves were stimulated. In order to stimulate cutaneous afferents from the forearm, the digital nerves of fourteen subjects were stimulated at between 2 and 3 times perception threshold (PT). In order to stimulate the cutaneous afferents of the median nerve, ring electrodes were placed around the thumb, index and middle finger on the distal side of the proximal interphalangeal joints. These electrodes were connected together and were used as the cathode. An adhesive electrode over the cutaneous palmar branch of the median nerve was used as the anode. In order to stimulate the cutaneous afferents of the ulnar nerve, ring electrodes were placed around the 4th and 5th finger and similarly connected together. In order to assess for a cutaneous effect from radial nerve afferents, the superficial terminal branch of the radial nerve in thirteen subjects was stimulated at between 2 and 3PT as it winds around the lateral border of the radius.

In all experiments EMG from thirty stimuli was averaged, stored and analysed. On some occasions a further 70 stimuli were delivered to confirm the result. In the majority of subjects multiple recordings were taken on separate occasions and the latency of the trapezius and the serratus anterior reflex from each subject on each occasion was averaged. In general there was no response to cutaneous stimulation but on the few occasions that a reflex was evoked, a mean latency was calculated for individual subjects.

5.2.3 Investigation of possible short latency reflex connections between arm afferents and shoulder girdle muscles using monosynaptic reflex testing.

To assess whether short latency reflexes were present from these arm afferents to trapezius, which may not have been revealed using the methodology described above, a mid-amplitude trapezius test H reflex was conditioned with appropriately timed stimuli from the median and ulnar nerves using six subjects. Two stimuli were delivered, one to the cervical nerve of C3/4 (to evoke the test H reflex) and a further stimulus (the conditioning stimulus) to either the median or ulnar nerve at the level of the elbow at 1.2MT. The test-condition time interval was controlled by the CED 1401, which triggered both the stimuli and the start of the EMG recording. 50 test stimuli and 50 conditioning stimuli were randomly delivered. The amplitude of the conditioned reflexes was compared to the unconditioned reflexes using an unpaired Student's t test assuming equal variance. The averaged conditioned reflex was expressed as a percentage of the averaged un-conditioned reflex at each test-condition interval.

5.2.4 Preliminary investigation of a transcortical pathway mediating the reflexes evoked in the trapezius muscle by stimulation of arm afferents.

To investigate the pathway mediating the reflex evoked in trapezius by stimulation of arm afferents, EMG recordings were made whilst conditioning this trapezius reflex with magnetic stimulation of the relevant motor cortex. Upper and lower trapezius EMG was recorded bilaterally from one subject. A 70mm double coil from the magnetic stimulator was positioned over the motor area of trapezius on one side (see section 2.2.3.3). Ipsilateral cortical stimulation, at 65% of the stimulator output, randomly conditioned a series of 100 trapezius reflexes, evoked from stimulation of the median nerve at 1.5MT at the wrist, at a test-condition interval of 20ms. If the ipsilateral transcortical stimulation evoked an inhibitory interhemispheric response, this would be expected to inhibit the transcortical component of the trapezius reflex (Taylor *et al.*, 1995). The amplitude of the conditioned reflex was expressed as a percentage of the test reflex. Any change in the amplitude of the test reflex was compared to the conditioned reflex.

5.2.5 Reflex control of shoulder girdle muscles in subjects with shoulder dysfunctions and pathologies.

The reflex control of trapezius and serratus anterior in subjects with shoulder dysfunctions was also investigated. The median, ulnar and radial nerves were stimulated at the elbow (as previously described) using a core group of twenty-six subjects with various shoulder dysfunctions and pathologies. Lower trapezius activity was recorded from eighteen of these subjects and serratus anterior activity was recorded from eight subjects. The EMG from 30 stimuli at 1.2MT was averaged and the latency of any evoked reflex was recorded. Again, on some occasions a further 70 stimuli were delivered to confirm the result. When recording from trapezius, the 'good' side of two subjects was also investigated in this way.

5.3 Results

Stimulation of the median, ulnar or radial nerves typically evoked excitatory reflexes in the upper and lower muscle fibres of trapezius and in the serratus anterior muscle. Examples of these reflexes can be seen in figure 47.

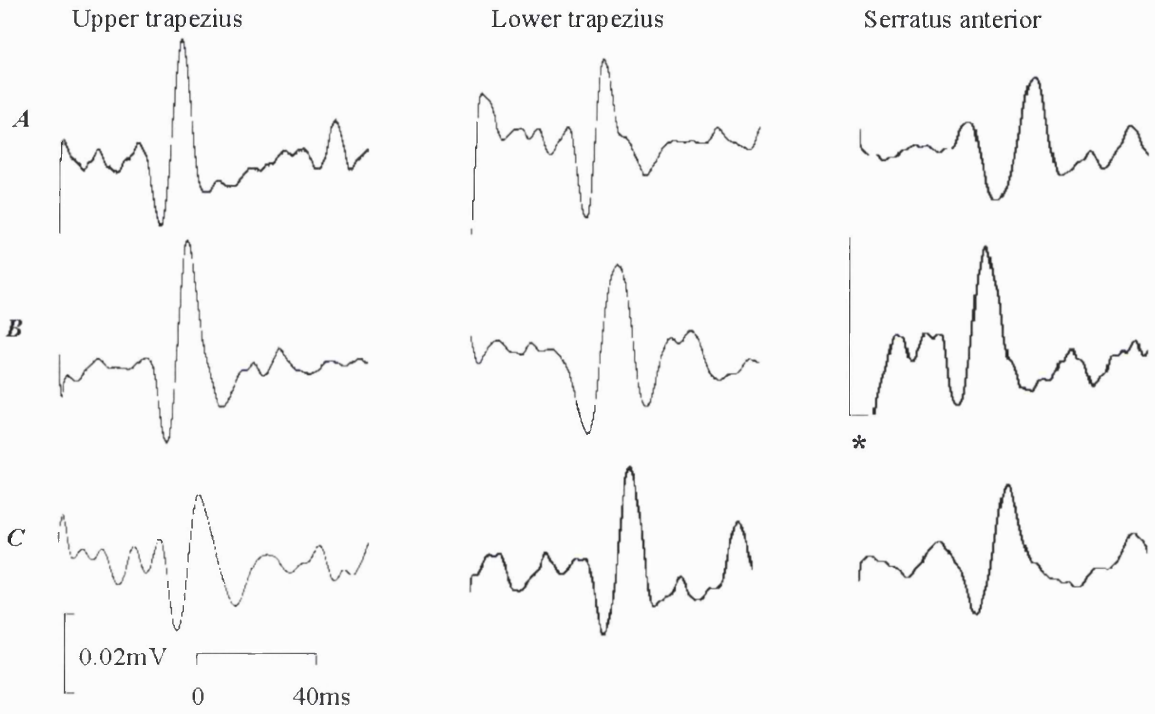


Figure 47. Reflexes in trapezius and serratus anterior evoked from arm afferents. Average reflexes evoked in the upper fibres of trapezius (left), the lower fibres of trapezius (middle), and serratus anterior (right) upon stimulation at 1.2MT of A) the median nerve, B) the ulnar nerve and C) the radial nerve at elbow level. Each average was constructed from the result of 30 stimuli. The stimulus occurred at the onset of each trace. The * indicates truncation of the downward going deflection of the stimulus artifact.

5.3.1 The amplitude and frequency of occurrence of these reflexes.

Figure 48 and 49 detail the size of the trapezii reflex and serratus anterior reflex which, if present, ranged between 14% and 767% above the mean activity. Of the reflexes evoked in trapezius, the median percentage increase in its activity was 61% above the mean background EMG activity. A reflex was evoked in the lower fibres of trapezius with greater frequency than that evoked in the upper fibres ($p = 0.04$). For example, a reflex evoked in 94% of subjects in the lower fibres when stimulating the median nerve at the elbow, was evoked in only 75% of subjects in the upper fibres (see table 8).

Of the reflexes evoked in serratus anterior, the median percentage increase in serratus anterior activity was 51.6% above the mean background EMG activity. Like the reflexes of trapezius, reflexes in serratus anterior were not always observed. For example, the reflex was evoked on 89% (or 16/18) of occasions by stimulation of the ulnar nerve, whereas it was evoked on 100% (22/22) of occasions by stimulation of the radial nerve (see table 8).

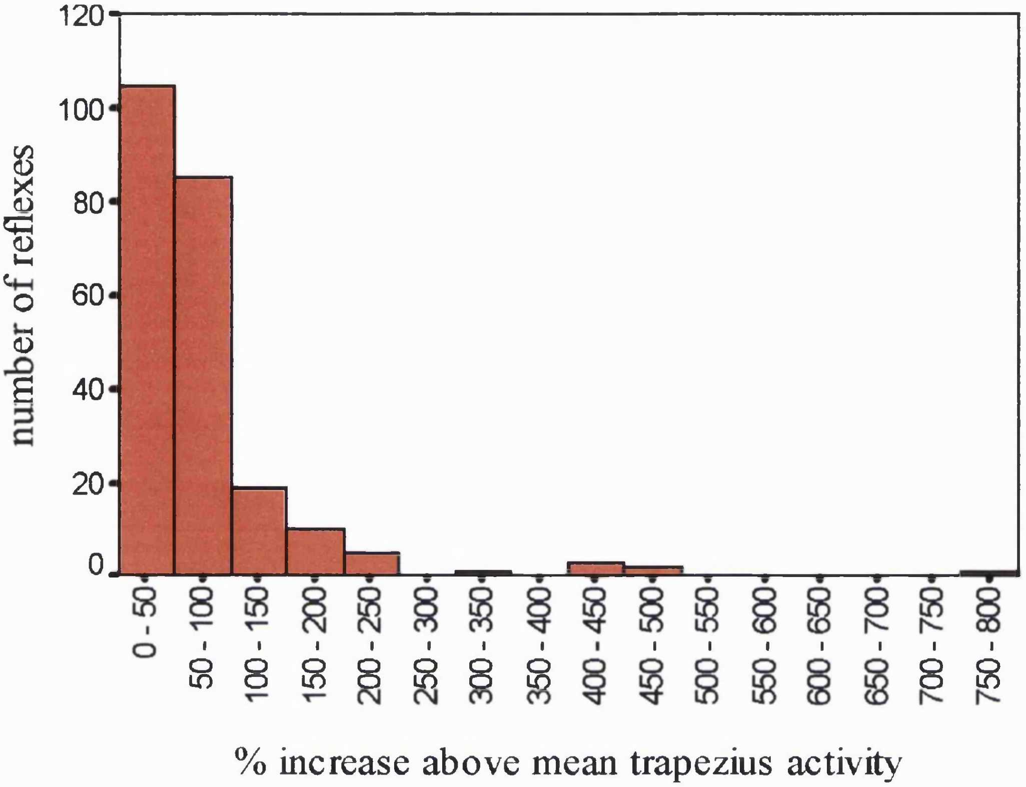


Figure 48. The distribution of trapezius reflex amplitude evoked from arm afferents. The histogram displays the size of the trapezii reflexes evoked from stimulation of the three arm nerves at two points along their length. The size is expressed as a percentage increase above the mean EMG activity of trapezius. Given that activity above 2 standard deviations from the mean was considered a reflex, it is conceivable that some small reflexes may have been present but not detected. These reflexes are reported as 36 of the 105 responses between 0% and 50% above mean trapezius activity.

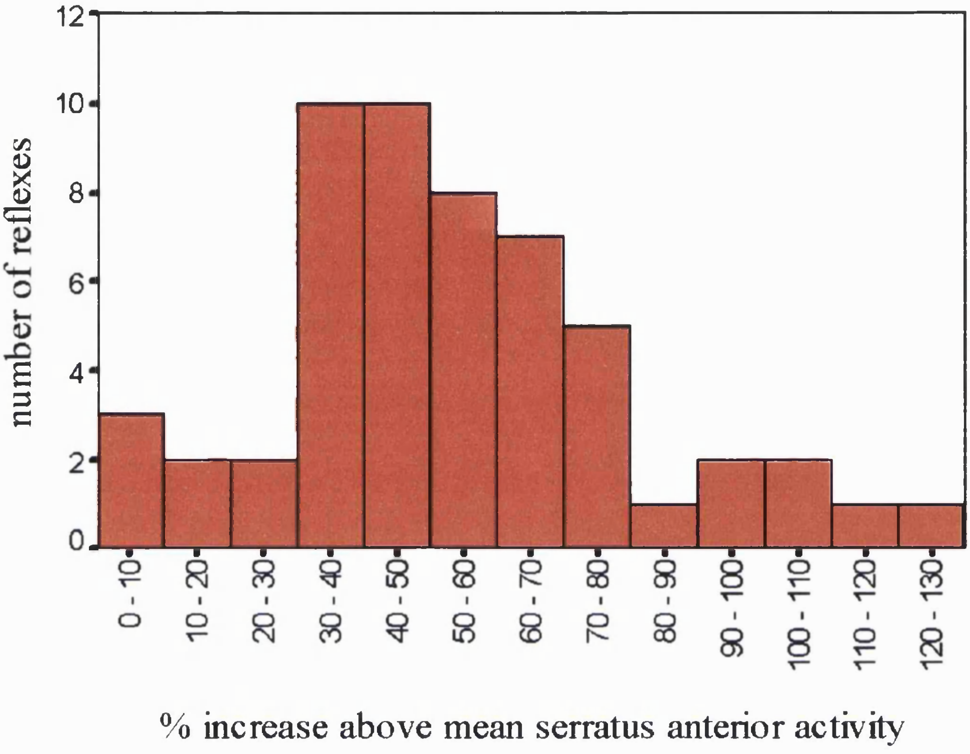


Figure 49. The distribution of serratus anterior reflex amplitude evoked from arm afferents. The histogram displays the size of the serratus anterior reflexes evoked from stimulation of the three arm nerves at two points along their length. The size is expressed as a percentage increase above the mean activity of serratus anterior.

	Site of stimulation	Occurrence of serratus anterior reflex	Occurrence of upper trapezius reflex	Occurrence of lower trapezius reflex
Median nerve	Elbow	12/12 (100%)	9/12 (75%)	31/33 (94%)
	Wrist	10/11 (91%)	9/20 (45%)	19/20 (95%)
Ulna nerve	Elbow	10/11 (91%)	13/15 (87%)	26/30 (87%)
	Wrist	6/7 (86%)	15/22 (87%)	20/22 (91%)
Radial nerve	Shoulder	10/10 (100%)	7/10 (70%)	11/12 (92%)
	Elbow	12/12 (100%)	9/9 (100%)	48/48 (100%)

Table 8. Frequency of occurrence of the trapezius and serratus anterior reflexes evoked from the median, ulnar and radial nerves (occurrence/trials). The percentages in brackets indicate the frequency with which a reflex was observed.

5.3.2 Reflex latency.

The mean latency of the reflex observed in the lower fibres of trapezius evoked from the median and ulnar nerves at the elbow was similar at 35.7 and 35.5ms respectively. The mean latency of the reflex evoked from the radial nerve at the elbow was a little longer at 38.6ms. This longer latency from stimulation of the radial nerve was also reflected in the latency of the reflex in serratus anterior (see table 9). The mean latency of the reflex evoked in the upper fibres of trapezius was, in the main, shorter than that in the lower fibres, presumably because of a shorter conduction distance. For example, the latency of the reflex evoked in the upper and lower fibres when evoked from the ulnar nerve at the elbow was 31.4ms and 35.5ms respectively.

Nerve	**Sight of stimulation**	**Reflex details**	**Serratus anterior**	**Upper trapezius**	**Lower Trapezius**
Median	Elbow	Latency	35.7 ± 4.0	35.7 ± 5.6	35.8 ± 3.6
		Size	58 ± 25	97 ± 79	74 ± 37
		Duration	32.0 ± 7.0	25.7 ± 12.5	22.5 ± 9.1
	Wrist	Latency	44.7 ± 7.0	42.3 ± 2.9	42.9 ± 3.6
		Size	60 ± 25	85 ± 44	53 ± 7
		Duration	35 ± 10	29.4 ± 12.2	29.2 ± 7.7
Ulnar	Elbow	Latency	36.5 ± 3.4	31.4 ± 3.1	35.5 ± 3.6
		Size	58 ± 27	241 ± 146	62 ± 40
		Duration	39.0 ± 18.0	18.6 ± 3.4	23.5 ± 7.9
	Wrist	Latency	42.5 ± 5.1	39.2 ± 5.2	43.6 ± 2.5
		Size	51 ± 29	69 ± 58	45 ± 18
		Duration	27.0 ± 8.0	24.0 ± 5.3	28 ± 8.0
Radial	Shoulder	Latency	34.2 ± 3.1	24.8 ± 5.1	33.0 ± 9.0
		Size	54 ± 32	121 ± 65	74 ± 17
		Duration	32.0 ± 8.0	15.1 ± 1.1	23.7 ± 8.3
	Elbow	Latency	39.7 ± 3.7	37.4 ± 6.8	38.6 ± 4.0
		Size	50 ± 10	52 ± 23	46 ± 16
		Duration	27 ± 7	24.7 ± 14.4	23.7 ± 8.8

Table 9. The mean latency (ms), amplitude (% increase above mean EMG activity) and duration (ms) of the serratus anterior and trapezius reflex evoked from the median, ulnar and radial nerves (mean ± S.D.). The mean latency and duration are expressed in ms.

5.3.3 Conduction velocity of the afferents mediating shoulder girdle reflexes.

As might be expected, the latency of reflexes evoked at a more distal location on the same nerve was greater than that evoked proximally. When reflexes were evoked from proximal and distal sites in the same subject, estimates could be made of the conduction velocity of the afferent fibres responsible for evoking the reflex. For example, figure 50 depicts a reflex in the lower fibres of trapezius evoked from stimulation of the median nerve at the elbow (top trace) and the wrist (bottom trace).

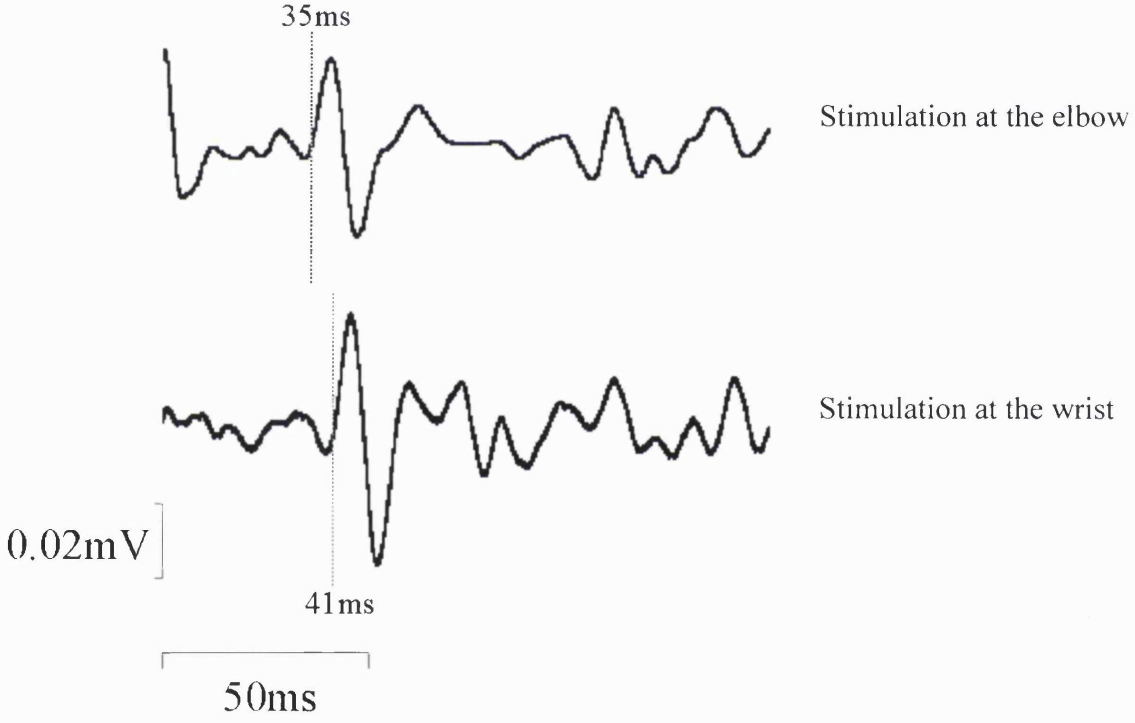


Figure 50. The average reflex evoked in the lower fibres of trapezius by the stimulation of the median nerve at elbow level (top) and at the wrist (bottom). Each average was constructed from the result of 30 stimuli. The stimulus occurred at the onset of each trace. The latency of the reflex evoked distally is 6ms later than that evoked proximally.

The difference in reflex latency was 6ms and the distance between the two sites of stimulation in this subject was 0.24m. This results in a conduction velocity of the afferents involved in the reflex of 40m/s. Mean conduction velocities for the effective afferents evoking reflexes in both upper and lower trapezius were 47 ± 12m/s (n=9), 44 ± 11m/s (n=9) and 54 ± 18m/s (n=5) for the median, ulnar and radial nerves respectively. The conduction velocity of the afferents evoking a reflex in serratus anterior were 51 ± 45m/s (n=9), 45 ± 24m/s (n=5) and 84 ± 42m/s (n=8) for the median, ulnar and radial nerves respectively. The fastest conduction velocity of the afferents that evoked the upper trapezius reflex was 79m/s, the lower trapezius reflex was 59m/s and finally, that which evoked the serratus anterior reflex was 107m/s.

The standard deviation of the afferent conduction velocities evoking reflexes in serratus anterior is high. This may be due to the range in size of the afferents stimulated. It may also be due to the various sources of measurement error, such as the resolution of distance and latency measurements. However, another factor is that the reflexes were not evoked at exactly the same amplitudes. As latency of other reflexes has been shown to vary with amplitude (see section 2.3.3.1), this will affect the difference in latency of two reflexes evoked at different points along the arm. This source of error is illustrated by figure 51 and 52. Figure 51 is of two reflexes evoked from stimulation of the median nerve. The reflexes are of very similar amplitude and their latencies result in a conduction velocity of 96m/s.

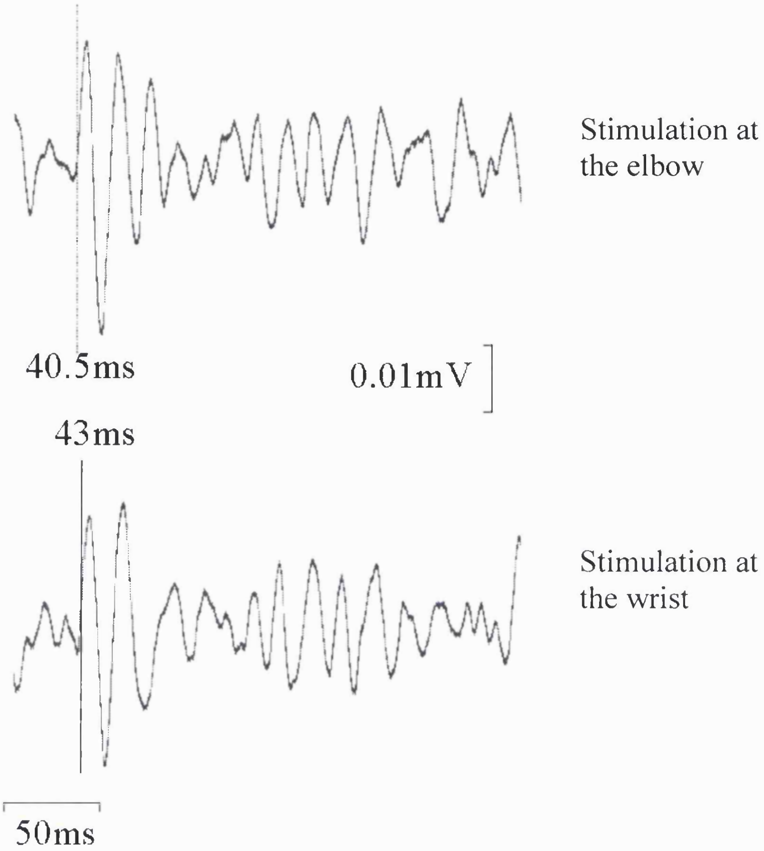


Figure 51. Serratus anterior reflexes evoked from stimulation of the median nerve at the elbow (top) and wrist (bottom). Each average was constructed from the result of 30 stimuli. The stimulus occurred at the onset of each trace. The vertical cursors mark the reflex latency.

On the other hand figure 52 illustrates two reflexes of different amplitudes evoked from the stimulation of the ulnar nerve at the elbow and the wrist. The amplitude of the reflex from stimulation at the level of the elbow is larger than that evoked from the wrist. The latency measurements may not be therefore comparable, with the smaller response being unduly low. This, in turn, produces a latency difference of 10.5ms, which results in a conduction velocity of only 24m/s.

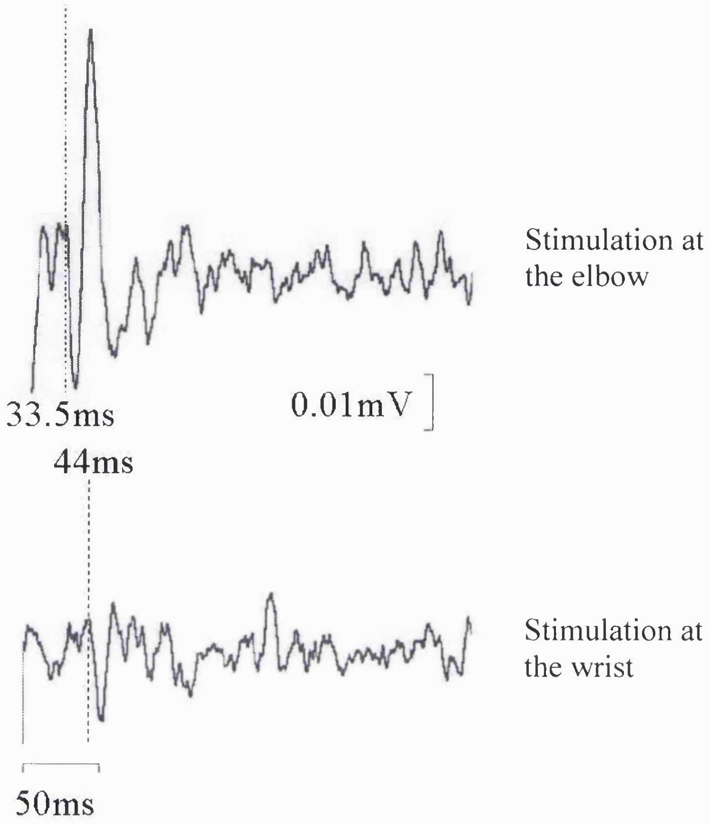


Figure 52. Serratus anterior reflexes evoked from stimulation of the ulnar nerve at the elbow (top) and wrist (bottom). Each average was constructed from the result of 30 stimuli. The stimulus occurred at the onset of each trace. The vertical cursors mark the reflex latency.

5.3.4 Electrical threshold of afferent fibres responsible for evoking shoulder girdle reflexes.

Given that these conduction velocities are in the group I range, it is to be expected that low stimulus intensities are required to evoke these reflexes. Indeed, the lowest stimulation intensity required to activate the afferent fibres responsible and therefore to evoke a reflex in the lower fibres of trapezius from stimulation of the median, ulnar and radial nerves at the elbow was 0.6, 0.5 and 0.6 MT respectively. The lowest stimulation intensity required to evoke a reflex in serratus anterior from stimulation of the median, ulnar and radial nerves at the elbow was 0.5, 0.3 and 0.6 MT respectively. Moreover, as exemplified in figure 53 the afferents responsible for the reflex are mainly confined to the low threshold range. Thus, upon increasing the stimulus strength the upper trapezius reflex is just visualised at 0.5MT and becomes maximal at about 0.7MT. Further increases in stimulus strength produce no further increase in amplitude.

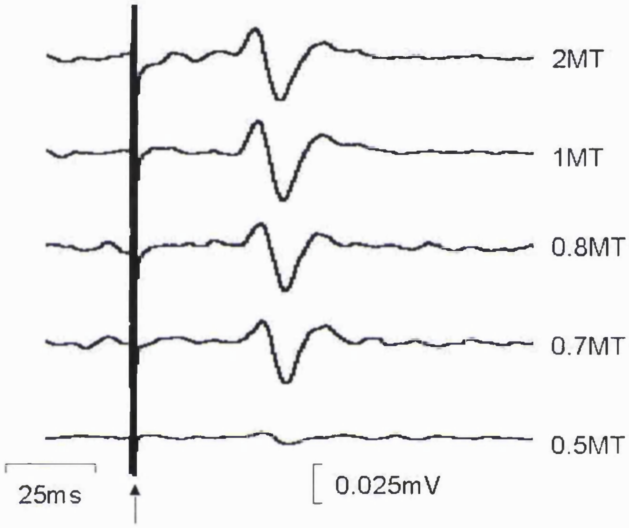


Figure 53. The effect of stimulation intensity on reflex amplitude. Average reflexes evoked in the upper fibres of trapezius evoked from stimulation of the ulnar nerve at the elbow. Increasing the stimulus intensity from 0.5MT to 2MT of flexor carpi ulnaris. The stimulus onset is indicated with an arrow.

5.3.5 Investigation of the possible contribution of cutaneous afferents to reflexes of shoulder girdle muscles.

In order to consider the possibility that the trapezius and serratus anterior reflexes were evoked by the activation of cutaneous afferents, cutaneous nerves were independently stimulated. In accordance with the recordings of Nadler (2001) in relation to trapezius, cutaneous reflexes were generally difficult to evoke. Indeed, in our experiments no cutaneous reflex responses were evoked in trapezius in all fourteen subjects tested. For example, figure 54 illustrates that while shoulder girdle reflexes were evoked from the stimulation of upper limb nerves at proximal and distal sites, this reflex is not evoked from combined stimulation of the individual digital nerves of the hand i.e. from cutaneous afferents alone.

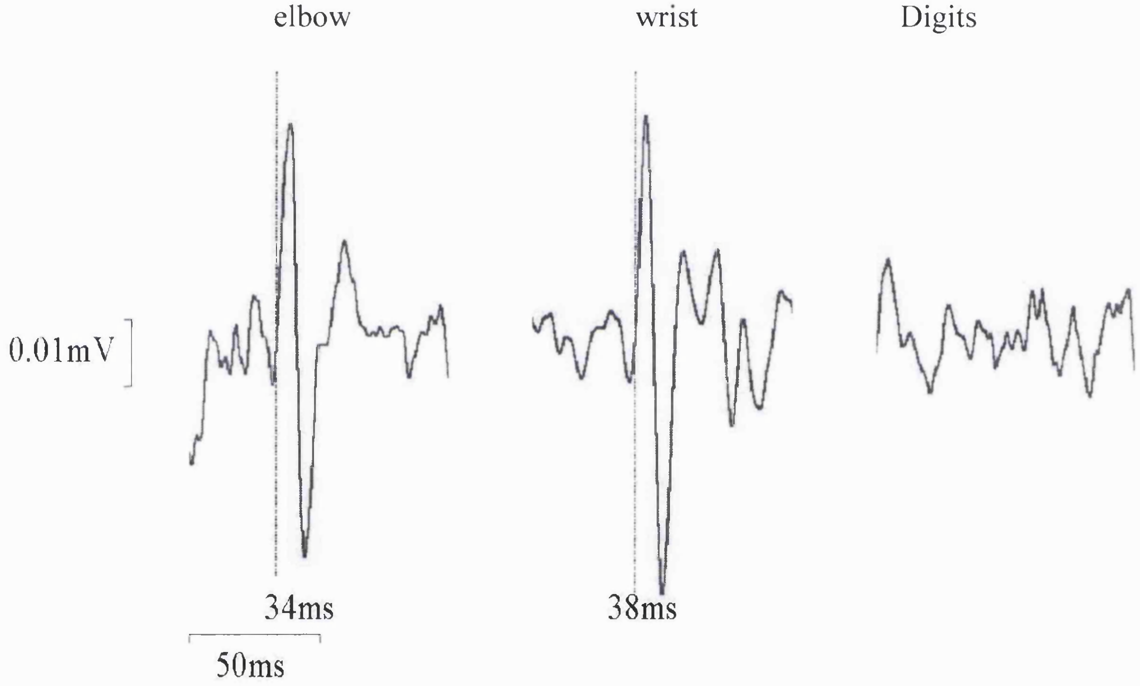


Figure 54. The response of trapezius to arm and hand afferent stimulation. The average lower trapezius reflex evoked at progressively longer latencies from stimulation of the median nerve at the elbow and wrist. No reflex was evoked from digital nerve stimulation. Each reflex was the result of 30 stimuli. The vertical cursors mark the reflex onset. The stimulus occurred at the onset of each trace.

In relation to serratus anterior, once again these reflexes were not evoked with digital nerve stimulation. Occasionally reflex responses were observed but these were at a longer latency. In one subject, combined stimulation of a) the digital nerves supplying the thumb, index and middle finger and b) the digital nerves supplying the ring and fifth finger evoked reflexes at a latency of 62ms and 72ms respectively. In two other subjects, stimulation of the cutaneous branch of the radial nerve evoked reflexes at latencies of 63ms and 64ms. Some of these responses were more easily visualised once rectified (see figure 55). This contrasts with the typical reflex responses obtained by stimulating the median, ulnar and radial nerves, which were evoked at approximately 35 to 40ms. Thus, these results imply that the reflexes evoked by stimulation of the mixed nerve are due to the activation of muscle afferents rather than cutaneous afferents.

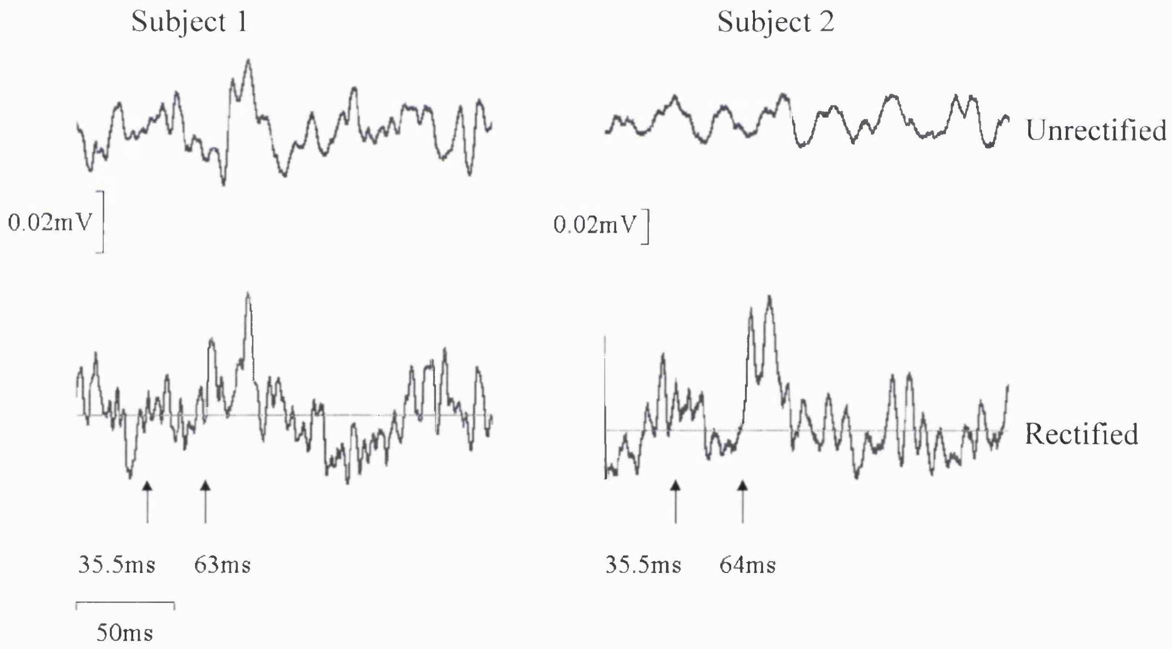


Figure 55. The musculocutaneous reflex of serratus anterior evoked from stimulation of the radial nerve at the elbow from two subjects. Each reflex is constructed from the result of 30 stimuli. The stimulus occurred at the onset of each trace. The reflex is more easily visualised (particularly in subject 2) once rectified (lower traces). The first arrow indicates the expected latency of the reflex evoked from stimulation of the mixed nerve. The second arrow indicates the presumed onset of the cutaneous reflex. The horizontal cursor represents the mean + 95% confidence interval.

5.3.6 Investigation of possible short latency reflex connections between arm afferents and shoulder girdle muscles using monosynaptic reflex testing.

The modulation of a test trapezius H reflex, conditioned from both the median and ulnar nerves, was assessed at test-condition intervals of 0ms, 3ms, 5ms, 7ms, 10ms, 15ms and 20ms. The results revealed little modulation of the trapezius reflex across these intervals tested that are consistent with a short latency reflex (test-condition interval of approximately 8ms). Conditioning of the trapezius H reflex by stimulating the median nerve in six subjects revealed only one significant change. At a test-condition interval of 0ms there was a 10% inhibition ($p < 0.04$, see figure 56). However, given the number of data points (26) it is to be expected that 1/26 or 4% would be significant. Hence, this single significant change is not thought to be important. Figure 56 demonstrates that, on average there was no consistent change with median nerve stimulation throughout these test-condition intervals.

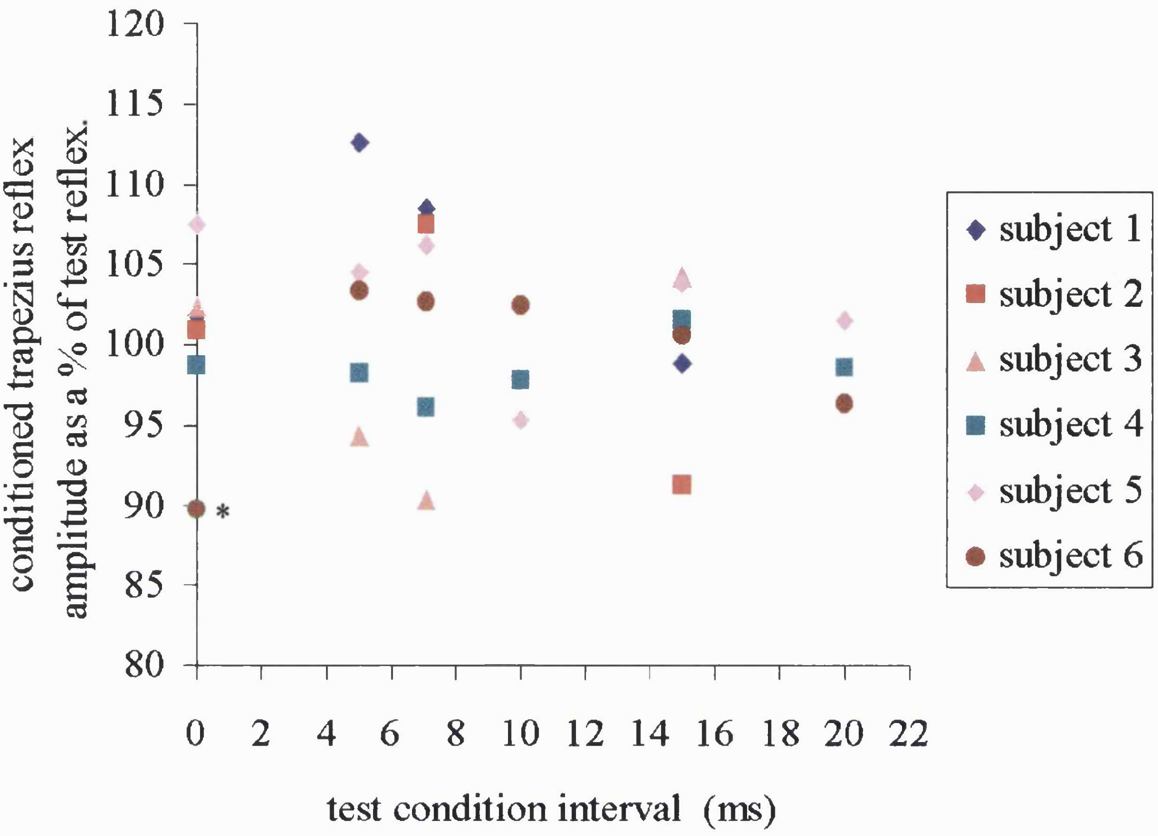


Figure 56. The trapezius H reflex was conditioned by median nerve stimulation at various test-condition intervals. The percentage change at each test-condition interval is represented. The * marks the significant change.

Conditioning the trapezius H reflex from stimulation of the ulnar nerve in four subjects revealed five significant changes. These are marked in figure 57. These changes are small and inconsistent at the test-condition times consistent with monosynaptic reflex connections.

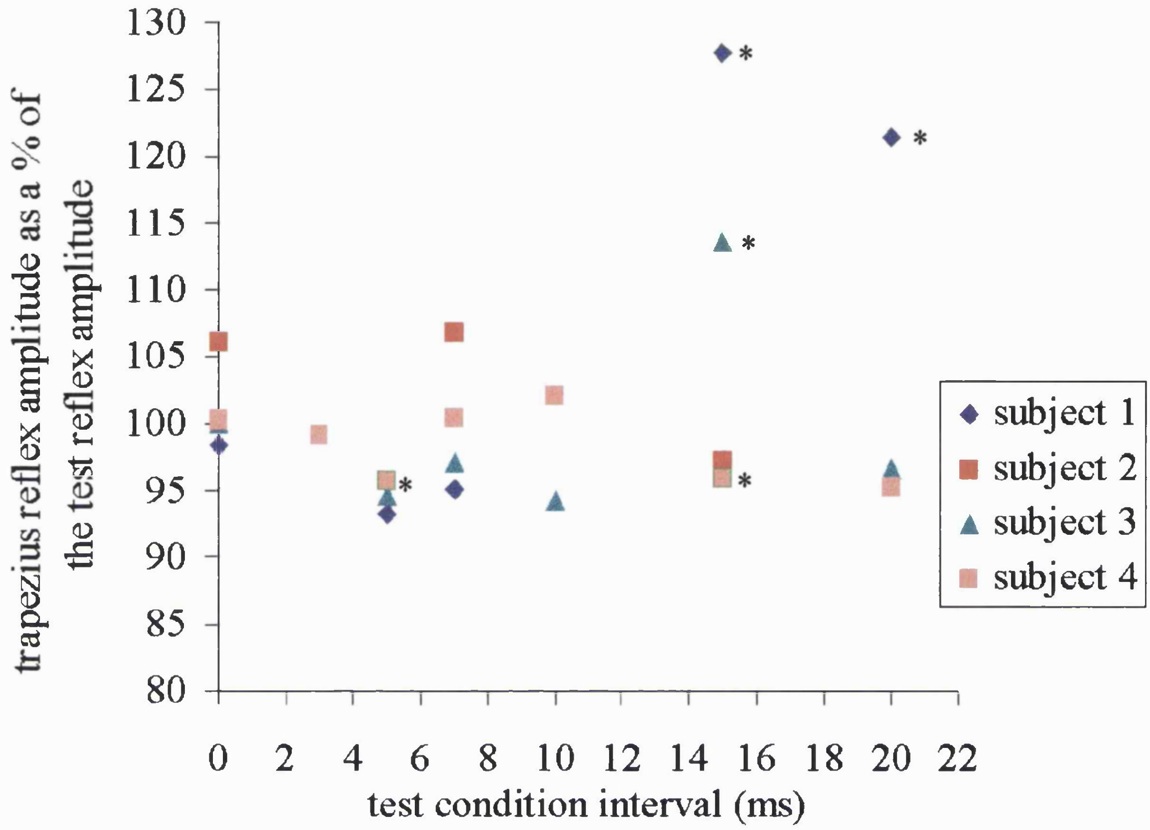


Figure 57. The trapezius H reflex was conditioned by ulnar nerve stimulation at various test-condition intervals. The percentage change at each test-condition interval is represented. * marks a significant change in amplitude of the test reflex.

An indication of a monosynaptic connection between arm and hand afferents upon shoulder girdle muscle motoneurones would be an increase in test reflex amplitude at a test-condition interval of around 8ms. However, the only obvious variation in amplitude was at longer test-condition intervals. This facilitation of test reflex amplitude may be consistent with either an oligosynaptic connection or one originating from slower arm and hand afferents.

5.3.7 Preliminary investigation of a transcortical pathway mediating reflexes evoked in the trapezius muscle by stimulation of arm afferents.

Given that the reflex latencies are longer than might be expected for a spinally mediated reflex, the possibility is raised that they are transcortically mediated. This can be investigated by conditioning long latency reflexes with magnetic stimulation to the relevant motor cortex (Taylor *et al.*, 1995). In order to assess the feasibility of this approach here, preliminary experiments were made using one subject. At a test-condition interval of 20ms, the reflex evoked in trapezius from stimulation of the median nerve at the wrist increased in amplitude (rather than the expected decrease in amplitude – see discussion) by 18% during magnetic stimulation of the ipsilateral motor cortex (see figure 58).

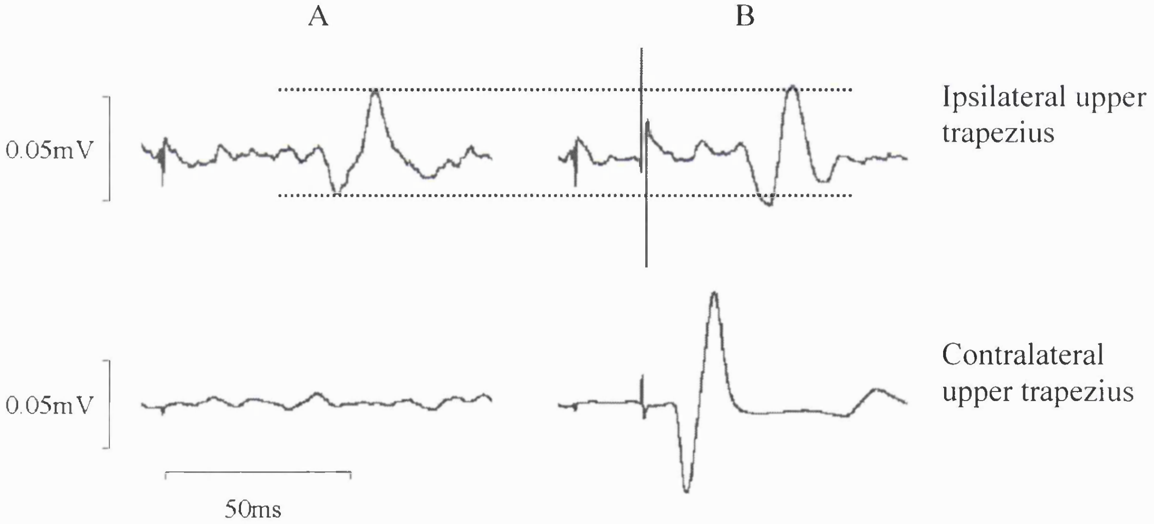


Figure 58. Investigation of the transcortical pathway of the reflex evoked in trapezius by stimulation of arm and hand afferents. A. Average reflex of the ipsilateral trapezius muscle evoked from the stimulation of the median nerve at the wrist (upper trace). No contralateral reflex was evoked (lower trace). B. The average ipsilateral upper trapezius reflex conditioned by magnetic stimulation of the ipsilateral trapezius motor cortex at a test-condition interval of 20ms (upper trace). The contralateral response to magnetic stimulation is seen (lower trace). The horizontal cursors mark the amplitude of the unconditioned trapezius reflex.

Thus, facilitation of the trapezius reflex rather than the expected inhibition occurred. However, it was clear that stimulation of the trapezius motor cortex evoked a response in the ipsilateral trapezius muscle. The influence of an ipsilateral response of trapezius to magnetic stimulation of the trapezius motor cortex may need to be taken into account during the analysis of these and any future results (see section 2.3.3.4). To examine whether the trapezius reflex evoked by stimulation of the median nerve might be conditioned at a level which does not evoke the ipsilateral trapezius motor evoked potential, the threshold of this response was determined. The lowest threshold for both the ipsilateral and contralateral responses occurred together at 40% of the output of the stimulator (see figure 59). Thus, this experimental paradigm may not prove effective in establishing if the reflex of trapezius is indeed transcortical.

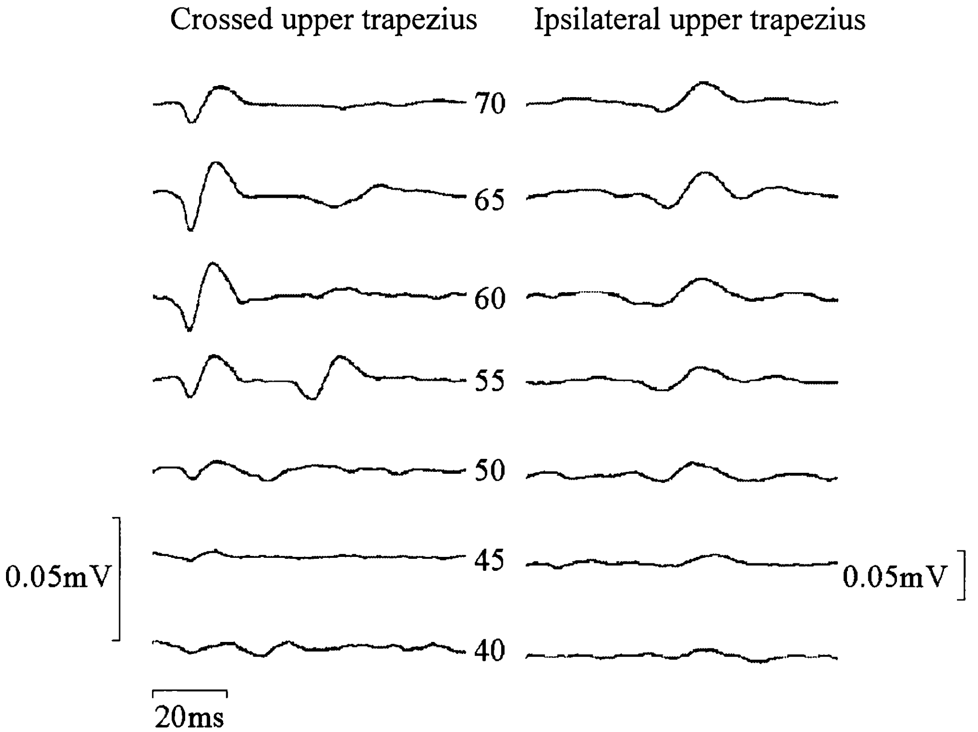


Figure 59. The effect of varying the intensity of magnetic stimulation on the trapezius response. The average crossed and ipsilateral responses of the upper trapezius to ipsilateral cortical stimulation with increasing stimulation intensity from 40% of the magnetic stimulator output to 70% output. Each average was constructed from the result of 25 stimuli. The stimulus occurred at the onset of each trace.

5.3.8 Reflex control of shoulder girdle muscles in subjects with shoulder dysfunctions and pathologies.

The reflexes of subjects with shoulder girdle problems were examined to investigate if these reflexes were different from the normal. Table 10 shows the wide range of dysfunctions and pathologies of the subjects investigated.

	number of subjects
Recurrent gleno-humeral dislocations without surgical intervention	6
Recurrent gleno-humeral dislocations with surgical intervention	3
Instability of the gleno-humeral joint	3
Rotator cuff tendonitis	6
Adhesive capsulitis	1
Winging scapula on abduction	7

Table 10 depicts the range and distribution of dysfunctions and pathologies of the subjects under investigation.

The reflexes to both trapezius and serratus anterior in these individuals were either absent or of a longer latency than those seen in a normal population. Indeed, these reflexes were more often absent than present. For example, the serratus anterior reflex was only evoked in one of nine subjects from stimulation of the ulnar nerve. The most frequently evoked reflex was that of trapezius, which was only evoked in eight of twenty-one subjects by the stimulation of the median nerve (see table 11). Thus, where the reflexes of the lower trapezius and serratus anterior were evoked on 86% to 100% of occasions in a normal population, at their most frequent they were only evoked on 38% of occasions in subjects with shoulder problems. Indeed, when a reflex was evoked in these subjects, it was at a longer latency. An example of this is illustrated in figure 60, which shows the difference in latency of a reflex evoked in a normal subject (see figure 60 A) when compared to that evoked in a subject with a shoulder pathology (see figure 60 B). Here, the difference in latency is 15ms, although the latency increase ranged from 7.7ms to 55.9ms. Where 5 or more reflexes were evoked, an unpaired Student's t-test revealed that the reflexes evoked from these subjects were significantly longer than those evoked from normal subjects ($p>0.02$).

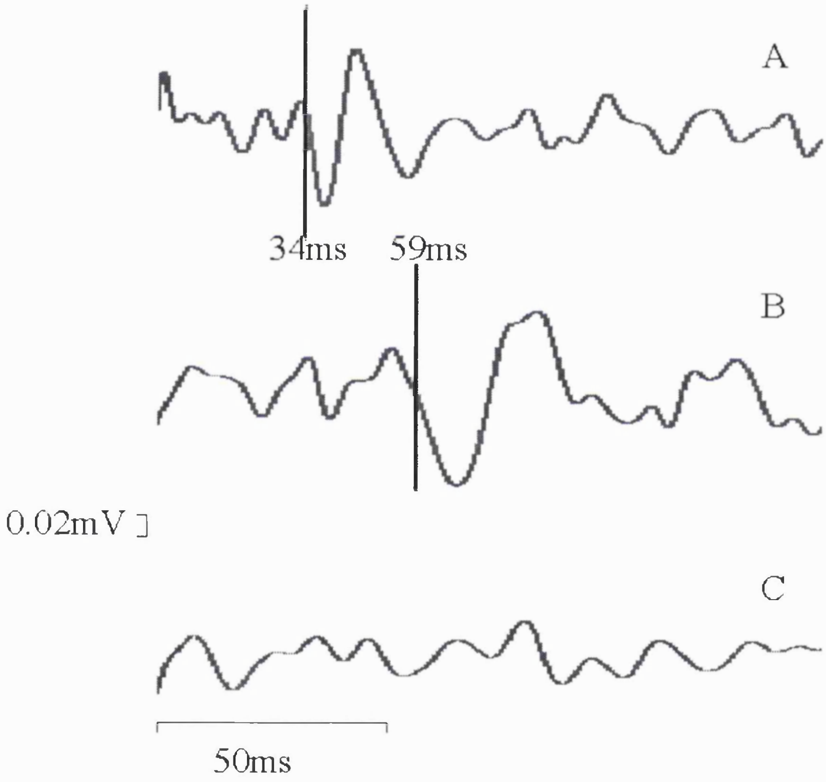


Figure 60. The effect of pathology on the trapezius reflex evoked from arm afferents. A. An average serratus anterior reflex evoked by the electrical stimulation of the radial nerve at the elbow in a normal subject. B. An average serratus anterior reflex evoked by the electrical stimulation of the radial nerve at the elbow in a patient suffering with a recurrent supraspinatus tendonitis. C. No reflex was evoked by the electrical stimulation of the radial nerve at the elbow in a patient who suffers recurrent dislocations of the glenohumeral joint. The average reflexes were constructed from the result of 30 stimuli at an intensity of 1.5MT. The stimulus occurred at the onset of each trace.

One subject had good scapula control with most movements but was able to wing her scapula in an unstable fashion on command. Recordings were taken of trapezius whilst a) the scapula was held stable by the correct action of trapezius and serratus anterior and b) when held with a markedly winging scapula. When she tried to maintain a stable scapula during the experiment a reflex was evoked at a long latency (48ms). When the nerve was stimulated whilst she was winging her scapula, the reflex was absent (figure 61). Caution needs to be taken in drawing conclusions from this data since the subject had difficulty in maintaining the same background EMG in the two experimental situations. Thus, the test conditions were not entirely identical. Never the less, there is a marked difference in the reflex response relative to the background EMG activity.

Trapezius reflexes were also investigated from the 'good' side of one patient when stimulating the ulnar and radial nerves, and the 'good' side of two patients when stimulating the median nerve. Interestingly, in only one of these experiments was a reflex evoked on the 'good' side, which was at 41.3ms on stimulation of the radial nerve at the elbow.

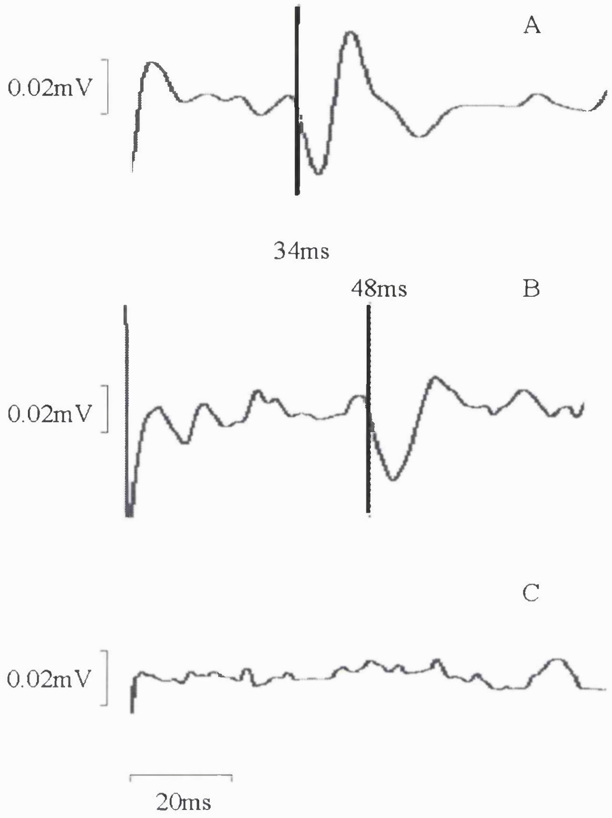


Figure 61. The effect of scapula position on the trapezius reflex evoked from arm afferents. A. An average lower trapezius reflex evoked by the electrical stimulation of the median nerve at the elbow in a normal subject. B. An average lower trapezius reflex evoked by the electrical stimulation of the median nerve at the elbow in a patient suffering with a chronic shoulder impingement. C. No reflex was evoked by electrical stimulation of the median nerve at the elbow in this subject whilst she actively subluxed her shoulder. The average reflexes were constructed from the result of 30 stimuli at an intensity of 1.5MT. The stimulus occurred at the onset of the trace.

A summary of the latency and occurrence of the serratus anterior and lower trapezius reflexes evoked by the stimulation of arm afferents in individuals with shoulder dysfunctions and pathologies are presented in table 11.

Nerve stimulated	Details of reflex	Serratus anterior	Lower trapezius
Median nerve	Latency (ms)	55.5 ± 9.9	45.7 ± 3.9
	Occurrence	3/9 (33%)	8/21 (38%)
Ulnar nerve	Latency (ms)	92.4	52.5 ± 13.3
	Occurrence	1/9 (11%)	4/17 (24%)
Radial nerve	Latency (ms)	54 ± 4.9	46.3 ± 4.4
	Occurrence	2/8 (25%)	5/14 (36%)

Table 11. The latency (mean ± S.D.) and occurrence of the reflex evoked from stimulation of the median, ulnar and radial nerves in those patients with shoulder dysfunctions and pathologies. The occurrence is expressed as the number of reflexes evoked over the total number of trials as well as a percentage.

5.4 Discussion

The results of this study have revealed the presence of a facilitatory reflex in the trapezius and serratus anterior muscles upon stimulation of the median, ulnar and radial nerves. The same reflex was evoked from the elbow and the wrist on stimulation of the median and ulnar nerves indicating that they originate from afferents distal to the wrist, that is, from within the hand. The distal site of stimulation of the radial nerve was at the elbow. Thus, the origin of the afferents involved in this reflex are distal to the elbow, that is, from the forearm or hand.

The latency of these reflex responses, being approximately 35ms, is longer than might be expected if they are mediated by fast conducting afferents with a short central delay. Consequently, we need to consider whether these reflexes are mediated from slow afferents with a short central delay or faster afferents with a long central delay, or indeed a combination of the two.

That the reflex was evoked at low stimulus intensities suggests that it is mediated by large diameter and therefore fast conducting afferents. Indeed, calculations made of the conduction velocity of the effective afferent fibres of the trapezius and serratus anterior reflex support this. Thus, if it is assumed that the conduction velocity of the nerve remains consistent along its length, the afferents mediating these reflexes conduct at a mean of approximately 50m/s, the fastest conducting at 107m/s. The fastest conduction velocity of human group I afferents in the median and ulnar nerves has previously been reported at between 68 and 70m/s (Marchand-Pauvert *et al.*, 2000a). Therefore our calculations indicate that the afferents responsible for the reflexes demonstrated here are within the group I range of conduction velocities.

5.4.1 The peripheral afferent origin of these reflex connections.

Muscle and cutaneous afferents of the human median nerve have similar conduction velocities and so may have a similar threshold to stimulation (Macefield *et al.*, 1989). Therefore, although the reflex was evoked at low stimulation intensities, the origin could not be assumed. Thus, this sheds no light on whether the reflexes are of cutaneous or muscle origin. In relation to any possible cutaneous origin, Nadler (2001) failed to consistently evoke cutaneous reflexes from the human hand to the upper fibres of trapezius. This work was extended and confirmed here. Thus, electrical stimulation of the cutaneous nerves did not evoke any effect in either the upper or lower fibres of trapezius and evoked a reflex in serratus anterior only at a longer latency and infrequently. This was so even with the combined stimulation of the palmar branch and digital nerves to three digits, at a stimulus intensity sufficient to typically evoke cutaneous reflexes in the intrinsic muscles of the hand. In addition, the reflexes observed were clearly seen with an average of as few as 30 sweeps. This starkly contrasts with investigations of cutaneous reflexes, which typically require the averaging of 250 sweeps for a reflex to be observed (Nadler, 2001). Thus, the reflexes seen here are an order of magnitude larger than typically reported for cutaneous reflexes. Hence, in the absence of a substantial cutaneous component, these results imply that the trapezius and serratus anterior reflexes are mediated by group I muscle afferents rather than by cutaneous afferents. This result is unsurprising since lifting an object (or even lifting the arm alone) would always demand stabilisation of the scapula and therefore the facilitation of shoulder girdle muscles, whereas, this would not necessarily activate cutaneous afferents. Therefore, a muscle origin of these reflexes is more appropriate.

5.4.2 Estimate of the central processing time of these reflex connections.

From knowledge of the peripheral conduction time and the total reflex latency, the central processing time can be deduced. The peripheral conduction time can be estimated by the addition of the afferent and efferent conduction times, plus the synaptic delay at the neuromuscular junction. If the conduction velocity of the fastest arm afferents evoking reflexes in the lower fibres of trapezius is used to calculate the afferent conduction time, then action potentials travelling at 59m/s over a distance of 0.55m from the elbow to the lower cervical spine take 9.3ms. The conduction velocity of the efferent supply, travelling in the spinal accessory nerve, has been measured at 54m/s (Priori *et al.*, 1991). The conduction distance of this pathway to the lower fibres of trapezius were measured in four cadavers, giving a mean distance of 0.39 m. The efferent conduction latency can therefore be estimated at 7.2ms. Assuming 1ms delay for the neuromuscular junction, the peripheral processing time is approximately 17.5ms. Using the median nerve as an example, the mean lower trapezius reflex latency was 35.7ms, leaving a central delay of 18.2ms. This clearly mitigates against short latency reflex pathways, including a group Ia monosynaptic reflex.

5.4.3 Investigation of possible short latency reflex connections between arm afferents and shoulder girdle muscles using monosynaptic reflex testing.

While single shock electrical stimulation has failed to reveal short latency reflex pathways, further confirmation was sought using monosynaptic reflex testing. The appropriate test-condition time intervals were set as follows. As previously indicated, the conduction time from the elbow to the lower cervical spine can be estimated at 9.3ms. The conduction time from the site of stimulation to C3/4 is 1ms. The most caudal position of the incoming afferents from the arm is C5 and together with the addition of 1ms conduction time from C5 to C4, this suggests a test-condition interval of approximately 8 to 10ms is appropriate. No consistent changes to the trapezius H reflex occurred at these test-condition intervals.

5.4.4 Investigation of a transcortical pathway mediating the reflexes evoked in the trapezius muscle from stimulation of arm afferents.

With a central delay of approximately 18.2ms, the question arises of whether or not this reflex is transcortical. To help clarify this, an estimate can be made of the latency expected if this reflex is transcortical. The sum of the latencies of the somatosensory potential evoked from the median nerve at the wrist (20.5ms; Iwasaki *et al.*, (2001)), the cortical relay time (8ms; Michels *et al.*, (1993)), and from our results, the latency of the cortically evoked response to the lower fibres of trapezius (11.2ms) adds up to 39.7ms. This is close to the mean latency of the trapezius reflex evoked from the median nerve at the wrist (42.9ms). Therefore, this is consistent with this reflex being transcortical.

As previously discussed (see section 3.4), magnetic stimulation of the motor cortex has been used to investigate other transcortical reflex pathways (Palmer & Ashby, 1992; Taylor *et al.*, 1995). Taylor *et al.* (1995), investigated the transcortical nature of the long latency stretch reflex evoked from the long finger flexors. They confirmed that this reflex was transcortical by conditioning it at appropriate test-condition intervals, with an ipsilateral cortical stimulation. This ipsilateral stimulation evoked an inter-hemispheric inhibition of the incoming volley to the contralateral side (Ferbert *et al.*, 1992). Using the same methodology, we sought to confirm whether the trapezius reflex was indeed transcortical. The reflex in trapezius evoked from stimulation of the median nerve at the wrist was conditioned by an ipsilateral cortical stimulation. Rather than this conditioning stimulus evoking an inhibition, it facilitated the reflex. However, this approach was confounded since magnetic stimulation of the relevant ipsilateral motor cortex evoked facilitatory ipsilateral trapezius and serratus anterior responses at a latency that may interfere with the reflex evoked from the arm afferents. Therefore, when an attempt was made to condition the trapezius reflex with stimulation of the ipsilateral cortex, the ipsilateral cortically evoked response may interfere with the trapezius reflex making the results uninterpretable, thereby confounding the elegant approach used by others (Taylor *et al.*, 1995).

The presence of these ipsilateral responses raises the issue of whether the neural organisation controlling these axial muscle pairs differs from that controlling the hand. It may be that, one way in which axial muscle pairs differ is that inter-hemispheric inhibition does not exist for these muscle pairs. Functionally, one might expect a predominant facilitation rather than inhibition as the muscle pairs work so closely together. Indeed, Abbruzzese *et al.* (1999) have revealed that cortico-cortical inhibition and facilitation in proximal and distal arm muscles vary. This may be due to their differing functions.

5.4.5 Reflex control of shoulder girdle muscles in subjects with shoulder dysfunctions and pathologies.

Reflexes evoked in individuals with shoulder dysfunctions and pathologies were absent or where present occurred at a longer latency when compared to a normal population. This absence or increase in latency of the shoulder girdle reflexes could be due to altered peripheral conduction and/or an alteration in central processing.

Changes in this reflex control from altered peripheral conduction could be due to compression or ischaemia of the afferent nerve supply within the arm and/or the motor supply to trapezius and serratus anterior. This would impede impulse propagation and therefore affect reflex generation. The slowing of an action potential or conduction failure during compression and ischaemia has been investigated by Fern & Harrison (1991,1994a, 1994b), who distinguished the separate effects of compression and ischaemia on nerve conduction. As these individuals suffered a range of shoulder problems associated with a positional change of the scapula (Ludewig & Cook, 2000; Ludewig *et al.*, 1996; Paine & Voight, 1993), compression of the afferent nerve supply driving these reflexes could have occurred. Indeed, the individuals investigated often had protracted shoulder girdles. This can lead to the compression of the brachial plexus against its surrounding structures. Therefore, afferent compression could lead to the absence or slowing of the reflexes in trapezius and serratus anterior. In terms of the motor supply, protracted scapulae would also alter the position of the spinal accessory nerve and the long thoracic nerve with respect to the surrounding tissue. This could also result in compression of the respective nerves. On the other hand, it seems less likely that conduction failure of the efferent supply to the shoulder girdle muscles was the main cause of the change, since the shoulder girdle reflexes were sometimes present when evoked from one nerve and not when evoked from the others. Regardless of the precise point of compromise, it is entirely possible that these reflex changes may be due to nerve compression.

An alternative, though not necessarily exclusive, explanation is that the altered control of these shoulder girdle muscles may also be due to central factors. The change to central control may be activated directly by the pathology or it may be activated by a change to the balance of peripheral or descending input upon the shoulder girdle motoneurone pools. Either way, the absence of these reflexes may reflect a change in the modulation of inhibition, which has been reported in subjects where pathology has been experimentally induced. Iles *et al.* (1990) injected saline into the joint space of the knee, which resulted in a localised inhibition of the quadriceps motoneurones. Svensson *et al.* (2000) also evoked inhibitory changes when they injected a painful volume of hypertonic saline into masseter. In addition, Wang *et al.* (1999) evoked polysynaptic brain stem reflexes that induce periods of inhibition in masseter - the exteroceptive suppression period. With the addition of experimentally induced pain, the reflex latency was increased and the amplitude was reduced. It is possible that the reflexes evoked here in trapezius and serratus anterior were acting under some central influence that modifies, indeed reduces the effect of the afferent input to the shoulder girdle motoneurone pools.

As the shoulder girdle reflexes are probably transcortically mediated, a change to the descending modulation of the motoneurone pool may have caused the change in reflex control reported here. This modification to descending control has been previously reported in those with low back pain, work related myalgia and knee pathologies. Muscle activity is delayed, more variable or changed by the substitution of one muscle for another (Elert *et al.*, 1992; Hodges & Richardson, 1998; Hodges & Richardson, 1999; O'Sullivan *et al.*, 1998; Hurley *et al.*, 1999). In addition, a change to descending control has also been demonstrated in those with shoulder problems (Barrett *et al.*, 2000; Wadsworth & Bullock-Saxton, 1997). In particular, Wadsworth & Bullock-Saxton (1997) investigated individuals who had a unilateral impingement of the rotator cuff muscles. They demonstrated an increased variability in the onset of both trapezius and serratus anterior activity during elevation. In addition, and perhaps more surprisingly, they also demonstrated delays to the onset of serratus anterior recruitment during the same task in the unaffected, 'good' side. Returning to this investigation, the change in the reflex control of trapezius was also seen in the 'good' side of three subjects examined. These alterations affecting the 'good' side have been thought to be mediated through central mechanisms (Koltzenburg *et al.*, 1999). Thus, that changes in control of the 'good' side occurred, adds strength to the belief that a central factor may also be involved in the change to the reflex control seen here.

5.4.6 The functional significance of these reflexes.

The functional significance of these trapezius and serratus anterior reflexes might be to stabilise the scapula during use of the hand. Other muscles involved in stability in other situations seem to contract independently of the direction of the movement. For example, feed-forward mechanisms to transversus abdominis, that aid stabilisation of the trunk when moving the arm or leg, occur whether this movement is in flexion, abduction or extension (Hodges & Richardson, 1997a; Hodges & Richardson, 1997b). Feed-forward mechanisms to the rotator cuff muscles that aid stabilisation of the gleno-humeral joint occur before either internal or external rotation of the arm (David *et al.*, 2000). The reflex control of the shoulder girdle muscles described here seems to complement these findings as these reflexes are evoked from afferents of muscles controlling movements in different directions. For example, the radial nerve supplies extensors of the wrist whereas the median nerve supplies the flexors of the wrist and fingers. This indicates that just like the other muscles of stability, the reflexes of shoulder girdle muscles act independently of the direction of movement. That is, the direction of movement of the limb is irrelevant to the need for stability. To enable this stability, group I muscle afferents will be active during any movement of the arm. Indeed, during gripping of the hand co-activation of the flexor and extensor muscles will increase the afferent barrage to the shoulder girdle muscles. Thus, when stability is required during movement of the arm and especially whilst lifting an object, this feedback mechanism will drive scapula stability.

That the reflex was evoked with greater frequency in the lower fibres might suggest a differential strength of input upon different parts of the trapezius motoneurone pool. In the cat and rat, the motoneurones of the upper fibres of trapezius tend to be more rostrally placed (Liinamaa *et al.*, 1997; Vanner & Rose, 1984; Kitamura & Sakai, 1982). Presuming that a similar situation exists in humans, this might facilitate different strengths of input upon different parts of the motoneurone pool. This could assist in controlling the functional subdivisions of the different parts of trapezius. Johnson *et al.* (1994) proposed that because the upper fibres attach to the distal end of the clavicle, which is beyond the axis of rotation of scapula movement, activation of these fibres create a moment about the clavicle. This, through the clavicle's attachment to the scapula, rotates it during elevation of the arm. In contrast, the lower fibres attach on the scapula upon its axis of rotation so, rather than generating movement, activation of these fibres would stabilise the scapula. This anatomical arrangement matches with the possibility for differential input upon the two parts of trapezius. This could lead to the results observed here, that is, a stronger input from the arm afferents to motoneurones of the lower fibres of the muscle. This is entirely in accordance with the view that the function of these reflexes is to anchor the scapula during use of the hand rather than to move the arm. This functional sub-division within a muscle, as described in the Introduction of this thesis (section 1.2.2.1), has been demonstrated before in cats and humans (Chanaud *et al.*, 1991b; Wickham & Brown, 1998). Indeed, functional sub-division has already been demonstrated within the upper fibres of trapezius in humans where differing tasks lead to activation of independently controlled motor units (Jensen & Westgaard, 1997).

That the reflexes are delayed or absent in subjects with various shoulder problems indicates that the feedback mechanisms that generate shoulder girdle stability are not as proficient in these subjects. One could hypothesis that central changes lead to an abolition of these reflexes and therefore to a lack of stability of the scapula. In turn, these changes may add to or produce the dysfunctional conditions evident in these subjects. The individuals had a wide range of shoulder conditions and the results did not indicate that the reflex alteration is independent of the type of dysfunction or pathology.

In summary, by taking into account the reflex latency, the length of the conduction path, that the reflex was mediated by low threshold, fast conducting afferents and the latency of the cortically evoked responses, it is proposed that group I muscle afferents from the forearm and hand evoke a transcortical reflex to trapezius and serratus anterior. It appears that the functional significance of these reflexes is to aid in the stability of the shoulder girdle. These stability mechanisms are absent or delayed in subjects with shoulder dysfunctions.

6 SUMMARY OF PRESENT FINDINGS AND POSSIBLE INVESTIGATIONS FOR THE FUTURE

The aim of this series of investigations was to explore the reflex control of the shoulder girdle muscles, trapezius and serratus anterior. A short stretch to trapezius and electrical stimulation of the trapezius afferent nerve supply revealed homonymous short latency reflexes. Both stimuli also evoked short latency crossed trapezius reflexes. These crossed reflexes were evoked at such a latency and at such strength that the earliest part of the reflex may be monosynaptically mediated. Voluntary activity of the ipsilateral trapezius increased the amplitude of both mechanically and electrically evoked ipsilateral and crossed reflexes; vibration of the ipsilateral trapezius decreased the amplitude of both reflexes. These results together suggest that the earliest parts of both ipsilateral and crossed reflexes are monosynaptic in origin. If the crossed reflex is, in part, due to a common Ia presynaptic input, correlation of bilateral trapezius activity should produce a peak in the cross correlogram. Indeed, cross correlation of the bilateral trapezius activity during elevation of the arms produced a short duration peak. Moreover, this was significantly larger when compared to that constructed from activity of the upper and lower fibres of trapezius from one side. These results imply that muscle spindle afferents from the ipsilateral trapezius monosynaptically activate motoneurones contralaterally.

It is unsurprising that facilitatory homologous reflexes exist that mirror those between other synergists as the trapezii co-contracts during bilateral tasks. While initially the finding that these connections are monosynaptic was surprising, with hindsight it is not surprising as their co-activation is secure even during unilateral actions such as elevation of the arm.

A short stretch to serratus anterior evoked both short and long latency homonymous reflexes. In contrast to trapezius, no short latency crossed reflex was evoked but a long latency facilitatory crossed serratus anterior reflex was evoked. This long latency reflex is consistent with a transcortical pathway. In future investigations it may be appropriate to examine the reflex activity of serratus anterior electrically. Given that the long thoracic nerve is superficially positioned upon the lateral aspect of the chest wall, this makes it accessible for electrical stimulation. If an H reflex of serratus anterior can be evoked, it lays open the possibility of further investigation of its homonymous and heteronymous projections. Whether these reflexes are evoked by muscle and/or cutaneous afferents could be explored in future investigations using electrical stimulation of the skin overlying serratus anterior.

Afferent projections from both serratus anterior and trapezius connect with the ipsilateral motoneurone pool of its synergist. A pattern of short and long latency reflexes were evoked from these muscle pairs. Functionally, they must help to co-ordinate their synchronous co-contraction during stabilising and movement of the scapula.

Exploration of reflexes between the arm afferents and the shoulder girdle muscles revealed long latency reflexes. It is proposed that group I afferents from the hand and forearm evoke transcortical reflexes that function to help stabilise the scapula during upper limb movements. Further investigation of the reflexes from the arm to the trapezius and serratus anterior muscles may reveal a predictable pattern of contralateral responses. Long latency contralateral reflexes evoked in this muscle group seem to be driven by the pattern of their corticospinal projections (see section 4.4.2). Stimulation of the serratus anterior motor cortex revealed strong corticospinal projections to the bilateral serratus anterior motoneurone pools. Thus, one could predict that if these reflexes evoked from the arm are transcortically mediated then, contralateral reflexes would be evoked in serratus anterior. Stimulation of the trapezius motor cortex revealed weaker corticospinal projections to the bilateral trapezius motoneurone pools. Thus, one could also predict that contralateral reflexes would not be evoked in trapezius.

As it is proposed that these reflexes are a requirement of stability of the shoulder girdle, further investigation of reflexes from the arm to the shoulder complex may reveal other facilitatory input upon the motoneurones of the rotator cuff muscles that act to stabilise the glenohumeral joint.

Although establishing the transcortical nature of these pathways was not successful using the approach of Taylor *et al.* (1995), further exploration using transcortical magnetic stimulation may reveal results of interest. This may be so despite the ipsilateral corticospinal responses described here. For example, the approach of Taylor *et al.* (1995) relies upon ipsilateral magnetic stimulation inhibiting an MEP evoked from the contralateral side. However, Kujirai *et al.* (1993) evoked intra-cortical, rather than inter-cortical inhibition and facilitation of the first dorsal interosseous muscle. This was evoked by pairing contralateral magnetic stimuli at different test-condition intervals. The pattern of responses they recorded has been used to condition transcortical afferent input (Ridding & Rothwell, 1999). For example, musculocutaneous reflexes evoked by electrical stimulation of the nerves of the hand have been used to condition MEPs evoked by contralateral magnetic stimulation at an appropriate test-condition interval. This MEP is then itself conditioned by a preceding magnetic stimulus at a level that is sub motor threshold. The effect is dependent upon the test-condition time between the magnetic stimuli. That is, shorter test-condition intervals inhibited the reflex whilst longer intervals evoked a facilitation (Ridding & Rothwell, 1999). If it is established that this intra-cortical inhibition and facilitation can be evoked in the trapezius and serratus anterior muscles, this approach could be used to examine the reflex pathways of the arm afferent projections to this shoulder girdle muscle group.

That the shoulder girdle reflexes are absent or delayed in those with shoulder dysfunctions and pathology, suggests that the stability of the scapula is compromised. Further investigation of the reflex response of the 'good' side will lead to a greater understanding of the central control of this reflex action. Measurements of conduction velocity of the afferents from both the problem and 'good' sides will also give insight to the understanding of the mechanisms leading to alterations of this reflex control. An investigation of the possible return of this reflex function with the rehabilitation of these shoulder problems is now pertinent.

The investigations presented here explore the reflex control of two muscles that play an important role in the movement and stability of the shoulder complex. The bilateral connections between the trapezius muscles and between the serratus anterior muscles demonstrate how these muscle pairs can act together during movements of the arm. The close monosynaptic connection between the bilateral trapezius muscle pair suggests that this muscle, in contrast to serratus anterior, may play an important role in the correcting or maintenance of axial posture during movement of an arm. The bi-directional reflexes between trapezius and serratus anterior demonstrate a mechanism by which they can work synergistically to move and stabilise the scapula. Finally, reflexes from the arm to the trapezius and serratus anterior muscles demonstrate that the feedback from arm afferents to these muscles may function to help efficient movement of the arm whilst maintaining a stable base of support.

7 APPENDIX I

7.1 Examination of any possible cross talk between the trapezii muscle pair.

Lower trapezius reflexes were recorded with surface electrodes that were placed near to the mid-line. This leaves open the possibility that the reflex recorded by the contralateral electrodes was as a result of cross talk from the ipsilateral side.

Cross talk is the contamination of the signal from one muscle by the activity of an adjacent muscle, as the signal travels by volume conductance through the muscle and fat layers. These tissues act as a low pass filter allowing the low frequency components to be recorded at a distance (Turker & Miles, 1990). This is especially evident when muscle activity is high.

To explore the contribution of cross talk to surface EMG recordings, De Luca & Merletti (1988) recorded from adjacent muscles whilst electrically stimulating the tibialis anterior. By normalising the activity of the adjacent muscles with respect to the activity of tibialis anterior, they suggest that if the peak to peak amplitude of the signal from an adjacent muscle is 16.6% or greater than that of the target muscle, then cross talk may be a factor in the recording. As long as the two adjacent muscles can be functionally differentiated, functional tests can be used to investigate the contribution of cross talk to the recording (Turker, 1993). As it is impossible to activate one trapezius muscle without the other, a functional test for this muscle pair is impracticable.

In order to avoid cross talk, careful placement of the surface electrode pairs is also vital especially when the muscles are synergists and so cannot be functionally differentiated effectively. The distance between recording electrode pairs influences the recording of cross talk. As described by Winter *et al.* (1994) and Fuglevand *et al.* (1992), with 1cm between surface electrode pairs, the quantity of cross talk, as measured by the cross correlation of model motor units, is 49% of the surface signal. This decreases steeply with inter-electrode distance. With a 2cm separation the cross talk reduces to 13% and at 4cm it is only 4%. When the model was compared to 'real' quadriceps motor units, these results are only slightly modified as a 4% contribution was recorded at an inter-electrode distance of 5cm. So, even with the crossed trapezius reflex being greater than 20% of the ipsilateral reflex, with the inter-electrode distance being at its closest 6cm, the likelihood of cross talk significantly contributing to the crossed reflex is greatly reduced.

Winter *et al.* (1994) and Fuglevand *et al.* (1992) used cross correlation as one technique to explore the contribution of cross talk to a given signal. Other techniques are also used to investigate the effect of cross talk. Firstly, surface recording can be compared to an intramuscular recording. Secondly, filters can be used to split a given signal into its constituent parts by the cross correlation of the signal until there is no peak in a cross correlogram. This is especially useful when there is no likelihood of common presynaptic input between the adjacent muscles (Baker *et al.*, 1998). Thirdly, individual motor unit activity from one muscle is used to trigger the surface recording of the adjacent muscle. If the surface EMG is then averaged, spike triggered averaging, the activity that occurs from both muscles at the same time will be revealed about time zero.

If cross talk is inevitable, a double differential recording technique, where the signal from one muscle is compared to another and simultaneously arriving signals are subtracted in order to reduce the contribution from distant muscles or motor units, can be utilised (Turker, 1993).

Some of these methods were employed here to investigate any possible contribution of cross talk to the generation of trapezius crossed reflexes. First, the activity from the trapezius muscle pair was cross-correlated. If the activity recorded contralaterally did originate from the ipsilateral muscle, it would result in a large peak centred about time zero. Second, single spikes of activity from the ipsilateral muscle was used as a trigger to average the gross EMG activity from the contralateral and ipsilateral side (spike triggered averaging). In addition, the presence of a crossed reflex was confirmed by recording contralateral trapezius activity using concentric needle electrodes.

7.1.1 Methods

7.1.1.1 Cross correlation of voluntary activity from the ipsilateral and contralateral lower fibres of trapezius.

Randomised, sequential recordings were made from the lower fibres of trapezius muscle pairs (seven subjects, see section 2.2.3.2). Subjects were asked to maintain a weak contraction of trapezius by abducting the arms to approximately 90°. This was aided by visual and auditory feedback of the EMG signal. Surface EMG recordings were collected as detailed elsewhere (with the electrode pairs positioned 5cms apart when at their closest) and stored on a PC using CED Spike software. Large amplitude spikes (approximately

3700) were selected from the EMG of both muscles using level detectors (Neurolog NL200) and these trigger pulses were also converted to a digital signal (CED 1401) and stored on the PC using Spike software. This method was repeated using spikes generated from the lower trapezius muscle on the ipsilateral side from one subject. Cross correlograms were constructed from the spikes using a 1ms bin width and a recording period of100ms before and after the triggering period. The size of any peak within the correlogram was measured in terms of peak bin count divided by the mean bin count (κ), the number of extra bins above the mean divided by the mean (E/M) and the duration of the peak. To ensure an accurate reflection of the mean, the mean bin count was measured away from any central feature. The statistical significance of the peak was calculated using the criteria of (Davey *et al.*, 1986).

7.1.1.2 Spike triggered averaging.

Spike triggered averaging is a method by which single unit activity acts as a trigger to time lock the activity from a second source for a fixed time period (Shefner, 2001; Fortier, 1994). The activity generated from the second source is averaged. Any response is therefore dependent upon the triggering activity of the single unit.

EMG recordings were made, with local ethical approval and informed consent, from 3 healthy subjects aged between 35 and 45. The recordings were made using both surface electrodes and a concentric needle electrode. The needle electrode was positioned, with the aid of ultrasound scanning, in the belly of the lower trapezius on one side. In a seated position, the subject was asked to bilaterally abduct the arms to approximately 20° until a unit was audible and this EMG was monitored using an oscilloscope. Firstly, the unit triggered the collection of EMG from the surface electrodes, placed over the ipsilateral lower fibres of trapezius and secondly, placed over the contralateral lower trapezius fibres.

7.1.1.3 Recording crossed reflexes with concentric needle electrodes.

Recordings were made, with local ethical approval and informed consent, from two healthy subjects aged 35 and 41. Reflex responses of trapezius were evoked by an electrical stimulus applied to the cervical nerve of C3/4 as previously described. The ipsilateral reflex was recorded using surface electrodes previously described. The crossed reflex was recorded using a concentric needle positioned as previously described. The resulting EMG activity was collected as individual sweeps of data and also averaged and stored for future analysis.

7.1.2 Results

7.1.2.1 Cross correlation of voluntary activity from the ipsilateral and contralateral lower fibres of trapezius.

When the activity of the two bilateral lower trapezii muscle pairs was cross correlated, a significant central peak centred on time zero was revealed in seven subjects (see section 2.3.3.3). The activity generated from the ipsilateral lower trapezius recorded from two sites closely situated was also cross correlated in one subject. This was to encourage cross talk and so compare the cross correlogram generated from the ipsilateral and bilateral trapezii. This generated a central peak that was approximately four times larger than those generated from activity of the left and right trapezius muscle pair (see figure 62). It was also only 2ms wide rather than 5.6 ± 1.6ms wide peak of that generated from the right and left trapezii.

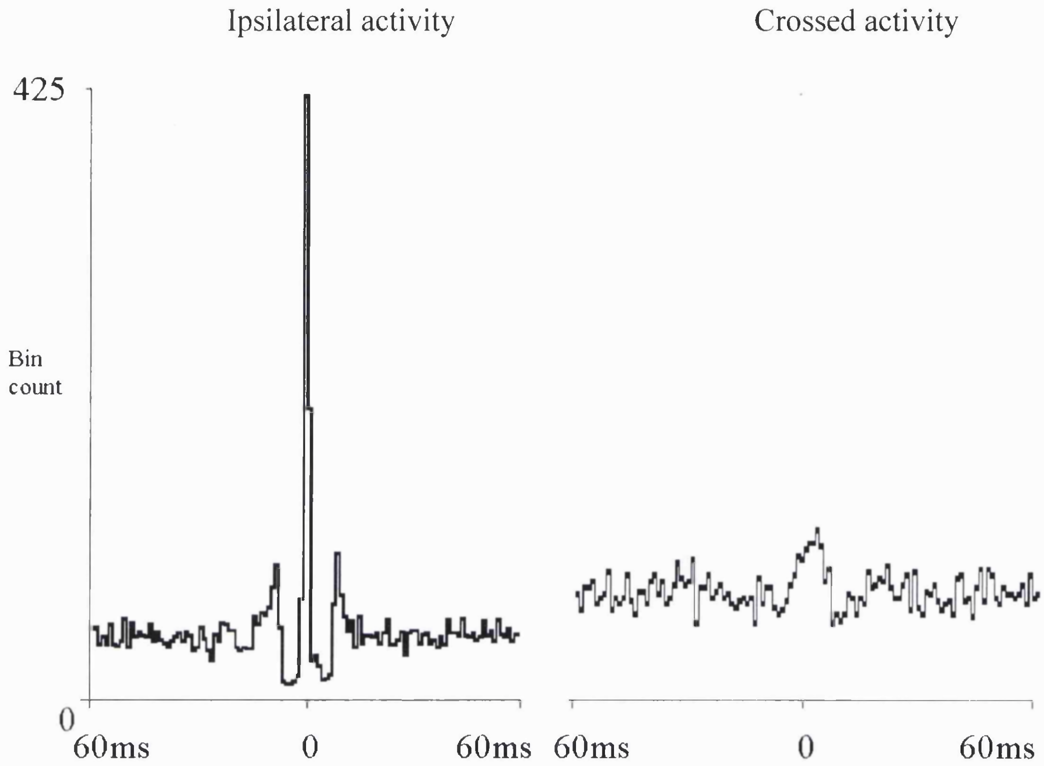


Figure 62. Two cross correlograms generated from the activity of two sites upon the ipsilateral lower trapezius (left) and the left and right lower trapezius (right).

7.1.2.2 Spike triggered averaging.

In three subjects, spike triggered averaging, triggered from single units recorded by the concentric needle electrode, the ipsilateral and contralateral trapezius muscles were averaged. This revealed a marked reduction in amplitude of the averaged contralateral muscle activity when compared to the ipsilateral side (see figure 63). This contralateral activity could be due to cross talk. It could also be due to common excitation. However even if it were cross talk, it is only 7% of the activity recorded on the ipsilateral side.

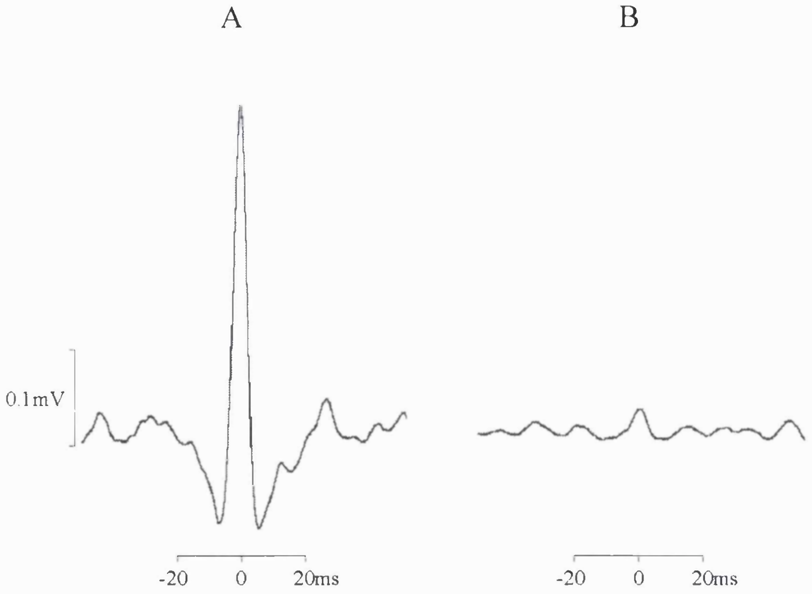


Figure 63. Spike triggered averaging of the ipsilateral and contralateral trapezius muscles. The ipsilateral trapezius EMG was triggered from single unit activity using a concentric needle and a) recorded using surface electrodes over the same muscle and b) using surface electrodes over the contralateral lower fibres of trapezius.

7.1.2.3 Recording crossed reflex using concentric needle electrodes.

The crossed trapezius activity was recorded from two subjects using a concentric needle (see figure 64). This crossed reflex can be seen with every sweep (see figure 65).

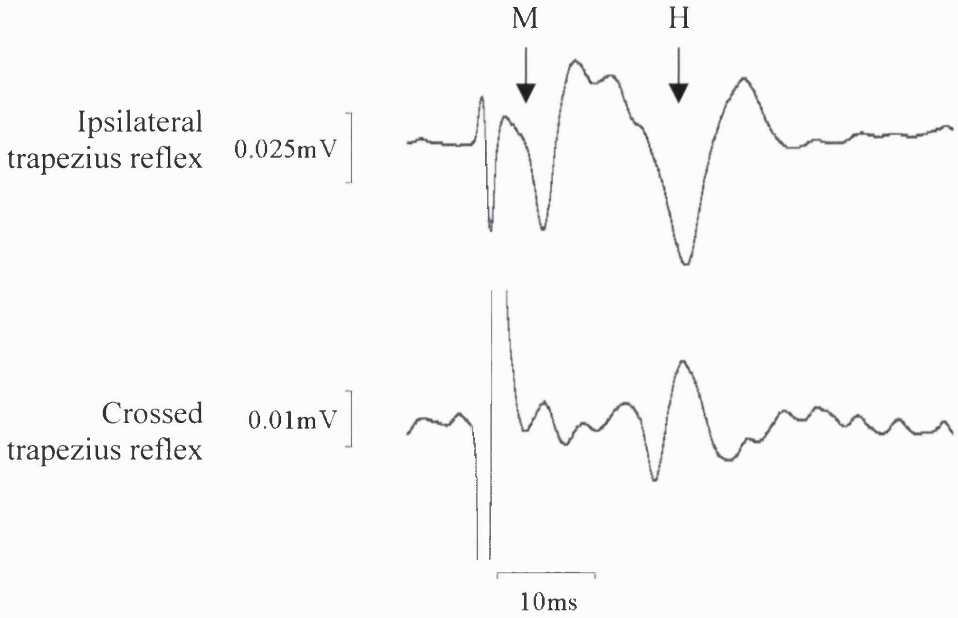


Figure 64. The crossed trapezius reflex recorded using a concentric needle electrode. A surface electrode recording of a single sweep of EMG of the lower trapezius reflex evoked using electrical stimulation of the cervical nerves of C3/4 (top). A single sweep recording of the lower trapezius crossed reflex recorded using a concentric needle (bottom). The stimulus artifact marks the stimulus onset.

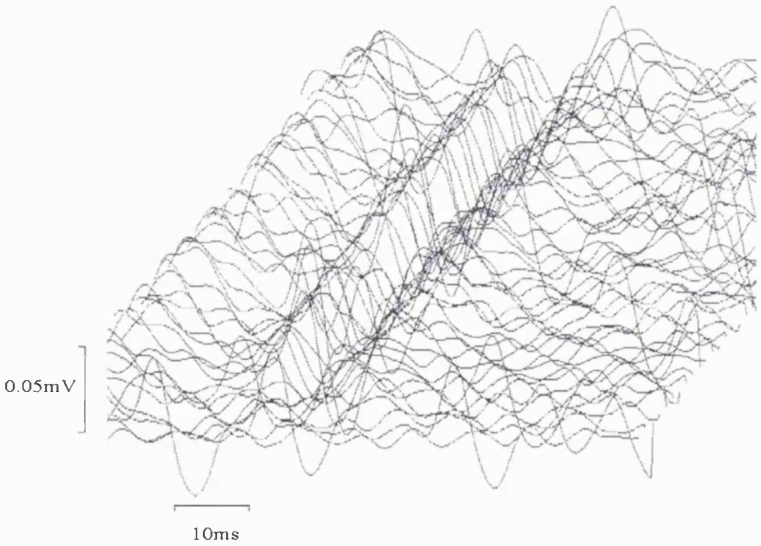


Figure 65. A series of individual sweeps of the crossed lower trapezius reflex recorded using a concentric needle. The start of the sweep marks the stimulus onset.

7.1.3 Discussion

The combination of the results presented here suggests that the crossed trapezius activity is not cross talk from the ipsilateral side. The most compelling evidence that the crossed reflexes are genuine is that the crossed reflex can be recorded using needle rather than surface electrodes. This needle was positioned with the aid of ultrasound scanning and so one can be confident of its correct placement. The significant peak in the cross correlogram and the small peak from spike triggered averaging, reiterate the inability of one trapezius to contract independently of the other rather than the existence of cross talk from the ipsilateral side.

7.2 The contribution of trapezius and rhomboid activity to recordings using surface electrodes.

As previously discussed, a criticism of recording with surface electrodes is that activity from other local muscles may contaminate the records. Rhomboid major lies directly beneath the upper portion of the lower part of trapezius. It attaches from the medial edge of the scapula and inserts onto the thoracic vertebrae of T2 to T5. The cross sectional area of the lower fibres of trapezius is small so, as trapezius is thin as well as directly superficial to rhomboid major, an investigation was needed to ensure that surface electrodes were recording from trapezius and not rhomboid major (see figure 66).

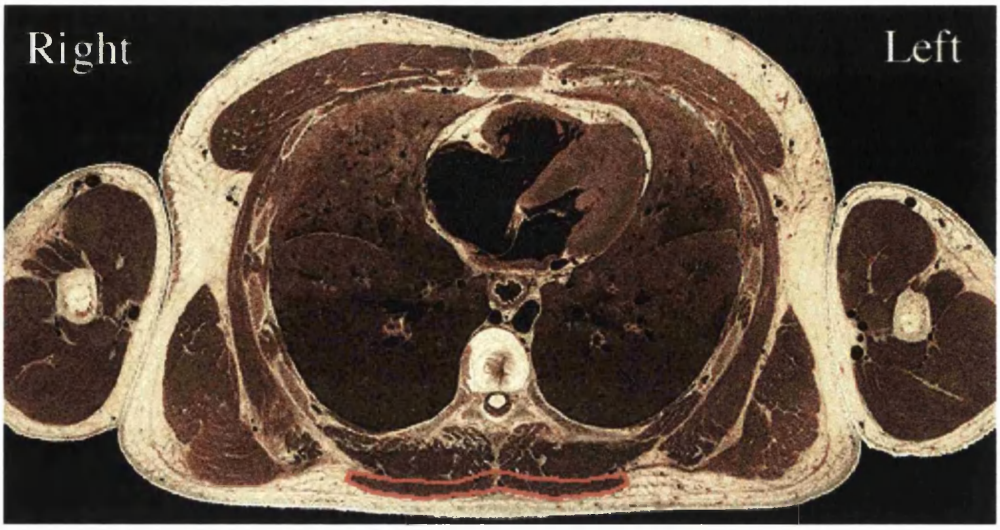


Figure 66. A cross section of the trunk at the level of the lower fibres of trapezius. Trapezius is outlined in red. This illustrates that rhomboid major lies directly anterior to trapezius. This picture has been taken from the Visible Human Project, Mediatheque Sante, Lyon 1 University (2001).

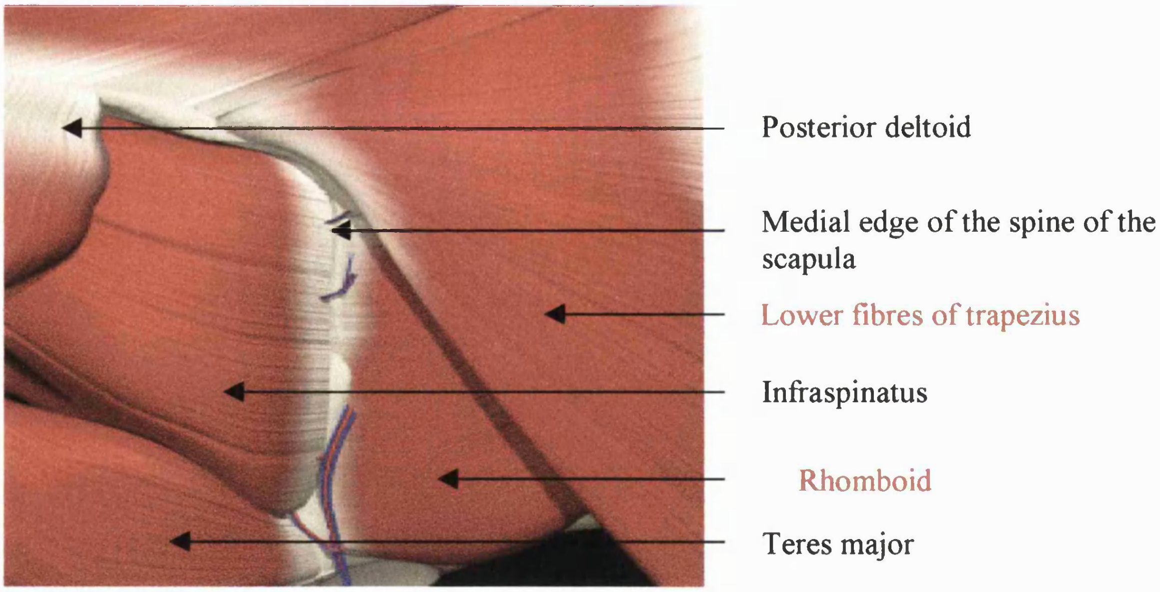


Figure 67. A posterior view of the left shoulder region. Rhomboid major and trapezius can be seen with other scapula muscles demonstrating their contrasting muscle fibre orientation. The picture has been adapted from Copeland *et al.* (2000).

Figure 67 demonstrates that the rhomboid major fibres are orientated approximately 90° to the line of the lower trapezius fibres. In the experiments reported here the electrodes were aligned in the direction of the trapezius muscle fibres, which is the orientation expected to produce the largest signal (Basmajian, 1989). This differential orientation leaves open the possibility of investigating the origin of the response. Rotating the electrode position by 90° should decrease the signal if the activity originates from trapezius, but increase the signal if the activity is from rhomboid major.

7.2.1 Methods

In this experiment, using one subject, the trapezius reflex response was electrically evoked. Ten stimuli were delivered and the surface EMG averaged with the electrodes placed edge to edge and with the recording area 3cm apart. The electrodes were orientated in two directions, a) along the length of the lower trapezius fibres and b) along the rhomboid fibres (see figure 68). The amplitude of the averaged reflex recorded with these two electrode placements was compared.

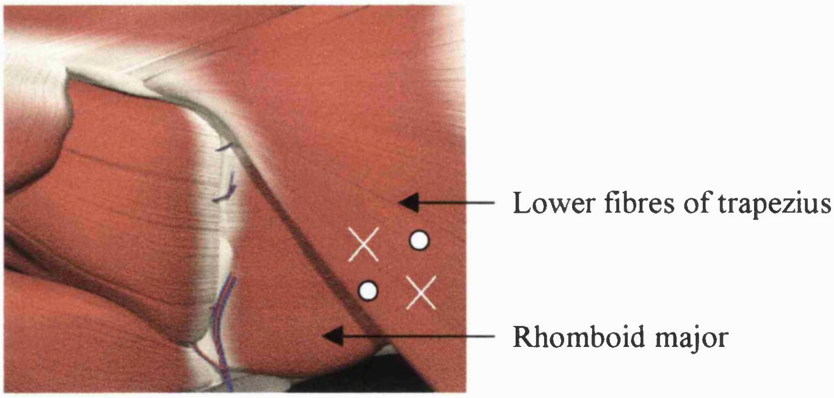


Figure 68. Electrode location and fibre orientation of the trapezius and rhomboid major muscles. The electrodes recording from trapezius (x) are orientated approximately 90° to the electrodes recording rhomboid major (o). This picture has been adapted from Copeland *et al.* (2000).

7.2.2 Results

The following records reveal that a trapezius reflex evoked electrically from stimulation of the cervical nerve of C3/4, can be visualised clearly when the electrodes are orientated along the trapezius fibres but the signal decreased profoundly in amplitude when orientated along the line of the rhomboid fibres.

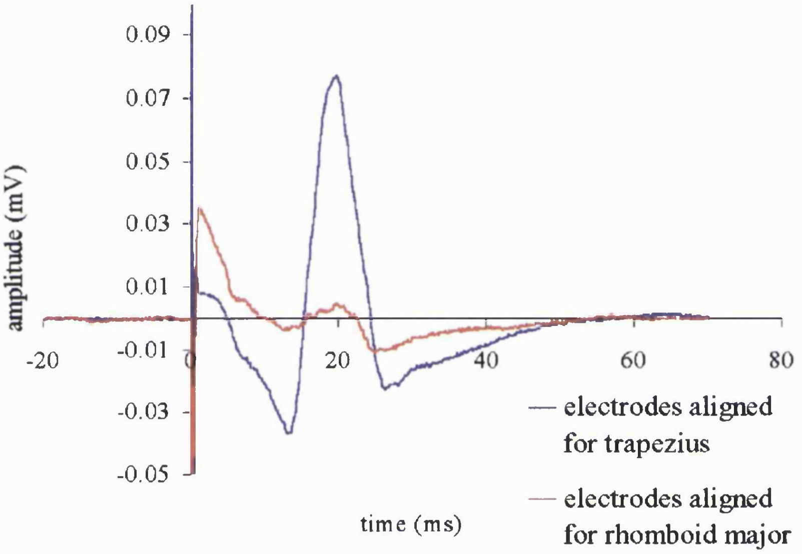


Figure 69. The effect of electrode position on reflex amplitude. The average surface EMG from 10 stimuli of the cervical nerve of C3/4. The EMG was recorded with the electrodes orientated along the line of the lower trapezius fibres (blue) and the line of the rhomboid major fibres (red). The reflex is reduced in amplitude if the electrodes are aligned in the direction of rhomboid major.

7.2.3 Discussion

The reduction in amplitude when aligning the electrodes along the length of the fibres of rhomboid major, indicates that the EMG recorded is from the lower fibres of trapezius and not from the muscle that so closely underlies it. There was though, a small amplitude response when the electrodes were orientated in the direction of the fibres of rhomboid major. This residual activity could be due to either a less than optimal recording from trapezius or it could be due to reflex activity being evoked in rhomboid major itself. Indeed, it is possible that rhomboid major acts synergistically with trapezius as both muscles act to move the scapula and therefore this small response may actually be recorded from rhomboid major. Nevertheless, it is clear that the main response can be attributed to trapezius and not rhomboid major when the electrodes are placed along the line of the lower fibres.

8 APPENDIX II

8.1 Pulse width of stimulus.

Traditionally, the accepted pulse width used to evoke an H reflex in peripheral muscles is 1ms (Pierrot-Deseilligny & Mazevet, 2000; Burke & Gandevia, 1999). Impulse generation is dependent upon the intensity of stimulus and pulse width. With a reduced stimulus intensity, an increase in pulse width is required to generate action potentials. This can be represented graphically by plotting a strength-duration curve, where pulse width is plotting against stimulus intensity. As muscle and nerve have different levels of excitability, their rheobase and chronaxie have different values. So, the strength-duration curve of muscle and nerve will have the same shape but will be differently positioned along the x-axis (Low & Reed, 1994). As the site of stimulation of the trapezius nerve supply is on the anterior surface of the upper fibres of trapezius muscle, the strength-duration curve was plotted to investigate whether nerve fibres or the muscle fibres of the upper trapezius were being directly stimulated.

8.1.1 Methods

The strength-duration curve was plotted for the stimulation of the site of the cervical nerve of C3/4 four times in two subjects. The trapezius response was evoked and recorded as described elsewhere in this thesis (see section 2.2.2). The threshold for evoking the ipsilateral trapezius response was found at pulse widths of 2ms, 1ms, 0.5ms, 0.2ms, 0.1ms and 0.05ms.

8.1.2 Results

Figure 70 illustrates the results obtained. Measurements form the plot indicate that the rheobase is ≈ 0.32mA and the chronaxie is ≈ 0.35ms.

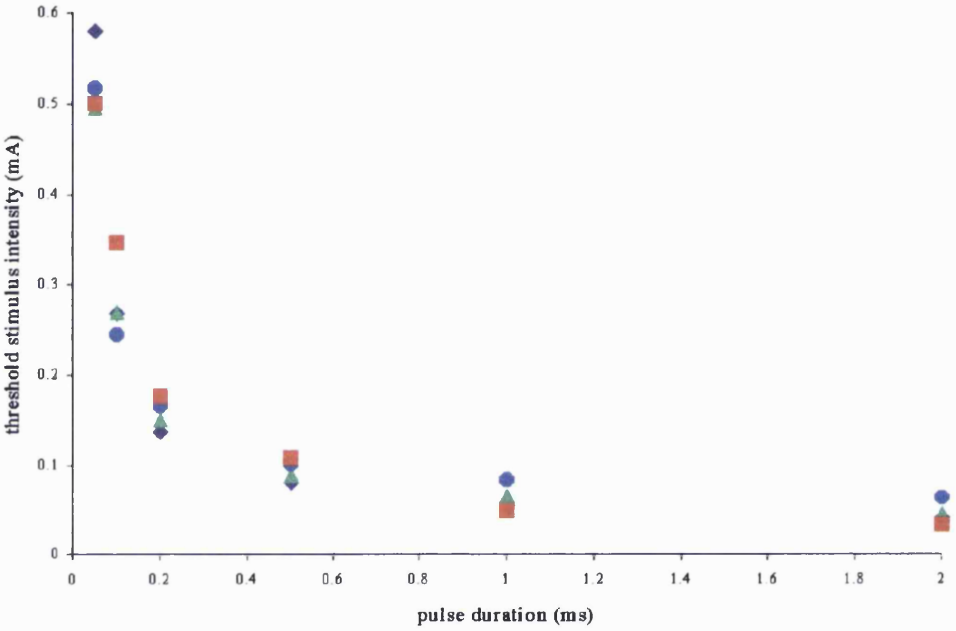


Figure 70. Four strength-duration curves of the lower trapezius H reflex evoked from the stimulation of the cervical nerve of C3/4. The threshold of the H reflex was determined from two subjects.

8.1.3 Discussion

The chronaxie is substantially less when stimulating nerve fibres than when stimulating a muscle. This is illustrated by the difference in the chronaxie of a denervated muscle, which has a chronaxie of over 10ms. Low & Reed (1994) describe the chronaxie of nerve at around 1ms so with a chronaxie as low as 0.35ms, this implies that nerve fibres and not muscle are directly activated by this electrical stimulation. Thus, with a chronaxie of 0.35ms, this allows for a 1ms pulse width to be used when electrically stimulating the cervical nerve of C3/4 with the confidence that this is not evoking a response directly from the upper fibres of trapezius.

8.2 The effect of inter-stimulus interval upon trapezius H reflex amplitude.

The amplitude of the soleus H reflex decreases with an increase in the frequency of stimulation (Pierrot-Deseilligny & Mazevet, 2000; Van Boxtel, 1986; Crone & Nielsen, 1989). Hence, a balance needs to be achieved between a) the need to collect multiple sweeps of data and b) a loss of reflex amplitude. Since the reflexes described in this thesis have not been previously described, the effect of this post stimulation depression upon the trapezius reflex has not been explored. Thus, the inter-stimulus interval was varied to examine the dependency of the reflex on frequency of stimulation and consequently examine the inter-stimulus interval that could be used in these experiments.

8.2.1 Methods

Ten stimuli were delivered at four different inter-stimulus delays delivered in a varying order (six subjects). These intervals were nine, seven, five and three seconds. The EMG was averaged for each interval and analysed using a two way ANOVA without replication, to assess whether any significant difference in average trapezius reflex amplitude occurred at the different inter-stimulus delays.

8.2.2 *Results*

The amplitude of the soleus reflex does not begin to decrease to a large degree until the stimulus frequency is greater than one stimulus every three seconds (Van Boxtel, 1986). To explore if the trapezius reflex amplitude was stable at such an inter-stimulus interval of 3 seconds, it was measured across a number of inter-stimulus intervals. As can be seen in figure 71, there was no significant difference in amplitude of the average lower trapezius H reflex at these four different inter-stimulus intervals (p>0.84).

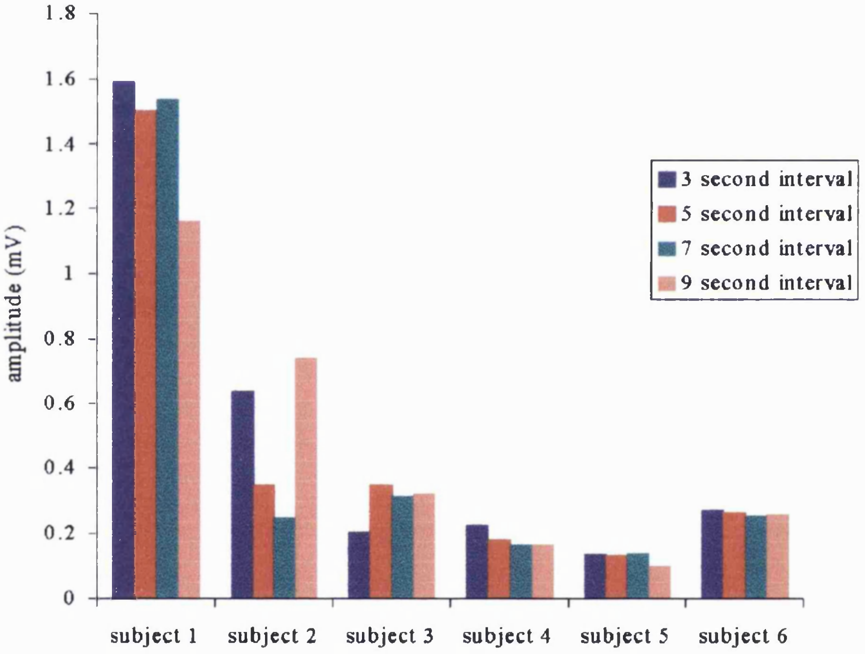


Figure 71. The effect of inter-stimulus interval on reflex amplitude. The amplitude of the average lower trapezius H reflex collected using 4 different inter-stimulus intervals repeated with six subjects.

8.2.3 *Discussion*

Burke *et al.* (1989) investigated how the amplitude of H reflexes evoked from the forearm flexor muscles varied with inter-stimulus interval. They demonstrated that, with the muscles at rest, the H reflex reduced in amplitude with increasing frequency of stimulation. This forearm flexor H reflex was 100% when collected at 0.1Hz, however, the amplitude decreased to 20% at a stimulus frequency of 4Hz. The post stimulus depression produced at higher frequencies of stimulation, is thought to be due to a depletion of neurotransmitter with repeated stimulations (Burke *et al.*, 1989; Van Boxtel, 1986; Pierrot-Deseilligny & Mazevet, 2000). The neurotransmitter is replenished after three seconds such that the greatest drop in amplitude occurs at faster frequencies than one every three seconds (Van Boxtel, 1986). On the basis of this, Pierrot-Deseilligny & Mazevet (2000) suggests that an inter-stimulus frequency of between 0.2 and 0.3Hz is acceptable. At this point the amplitude of a soleus H reflex has dropped by approximately 25% (Van Boxtel, 1986). Certainly the results presented here, suggest that no significant difference in trapezius H reflex amplitude could be demonstrated when collected at inter-stimulus intervals ranging between nine and three seconds. Therefore an inter-stimulus interval of three seconds is an acceptable frequency with which to assess trapezius reflex activity.

9 APPENDIX III

9.1 Publications.

The following is a list of publications originating in part or from this thesis (in reverse chronological order).

Alexander CM & Harrison PJ. (2001) The bilateral reflex control of the trapezius muscle in humans. Experimental Brain Research (in press).

Alexander CM & Harrison PJ. (2001) Reflex connections from afferents of the arm to the shoulder girdle muscle in humans. Submitted to J Physiol (Lond).

Alexander CM & Harrison PJ. (2001) Reflexes from arm afferents contribute to shoulder girdle stability. 31st Annual meeting of the Society for Neuroscience. San Diego, Ca. 936.7.

Harrison P.J & Alexander C.M. (2001) Group I muscle afferent reflexes from the arm and hand to the trapezius muscle in humans. Proceedings of the 34th IUPS meeting, Vol. XX, Christchurch, N.Z.

Alexander CM & Harrison PJ. (2000) Reflex connections from forearm muscles to trapezius. Proceedings of the 7th Scientific Conference of IFOMT. Ed K. Singer. Pub. UWA p15-17.

Harrison P.J, Alexander C.M., Beith I.D., Myriknas S.E., Zheng R. (2000) Crossed reflexes in the human shoulder girdle and trunk muscles – is there a monosynaptic component? The J Physiol (Lond) 523 69P.

Alexander C.M., Zheng R, & Harrison P.J. (1999) Ipsilateral and crossed stretch reflexes of the trapezius muscle in humans. 29th Annual meeting of the Society for Neuroscience. Miami, Fl. 52.3

REFERENCE LIST

Abbruzzese, G., Assini, A., Buccolieri, A., Schieppati, M., & Trompetto, C. (1999). Comparison of intracortical inhibition and facilitation in distal and proximal arm muscles in humans. *J Physiol (Lond)* **514 (3)**, 895-903.

Abbruzzese, M., Reni, L., Minatel, C., & Favale, E. (1998). Presynaptic and postsynaptic mechanisms underlying H-reflex changes produced by a selective voluntary contraction. *Muscle and Nerve* **21**, 439-453.

Abrahams, V. C. & Keane, J. (1984). Contralateral, midline, and commissural motoneurons of neck muscles: a retrograde HRP study in the cat. *J Comp Neurol.* **223**, 448-456.

Alfonsi, E., Moglia, A., Sandrini, G., Pisoni, M. R., & Arrigo, A. (1986). Electrophysiological study of long thoracic nerve conduction in normal subjects. *Electromyography and Clinical Neurophysiology* **26**, 63-67.

Alstermark, B., Kummel, H., Pinter, M. J., & Tantisira, B. (1987). Branching and termination of C3-C4 propriospinal neurones in the cervical spinal cord of the cat. *Neuroscience Letters* **74**, 291-296.

Alstermark, B., Kummel, H., Pinter, M. J., & Tantisira, B. (1990). Integration in descending motor pathways controlling the forelimb in the cat. Axonal projection and termination of C3-C4 propriospinal neurones in the C6-Th1 segments. *Exp Brain Res* **81**, 447-461.

Arroyo, J. S., Hershon, S. J., & Bigliani, L. (1997). Special considerations in the athletic throwing shoulder. *Orthopaedic Clinics of North America* **28 (1)**, 69-78.

Baker, S. N., Kilner, J. M., Ahmed, A., Fitzgerald, W. J., Mayston, M. J., & Lemon, R. N. (1998). Use of blind separation algorithem to remove electrical cross-talk from multiple EMG recordings. *J Physiol (Lond)* **509P**, p168.

Baldissera, F., Hultborn, H., & Illert, M. (1981). Integration of spinal neuronal systems. In *Handbook of physiology the nervous system II.* The American Physiological Society. Bethesda. pp. 509-595.

Barrett, C., Emery, R., Wallace, A., & Davey, N. J. (2000). Altered corticospinal control of shoulder musculature in shoulder instability - a case study. Singer, K. p.52-56. Perth Australia, University of Western Australia. IFOMT 2000.

Basmajian, J.V. (1989) *Biofeedback, Principles and Practice for clinicians.* 3rd Ed. Baltimore. Williams and Wilkins.

Belling Sorensen, A. K. & Jorgensen, U. (2000). Secondary impingement in the shoulder. An improved terminology in impingement. *Scand. J. Med. Sci. Sports* **10**, 266-278.

Berardelli, A., Priori, A., Inghilleri, M., Cruccu, G., Mercuri, B., & Manfredi, M. (1991). Corticobulbar and corticospinal projections to neck muscle motoneurons in man. A functional study with magnetic and electric transcranial brain stimulation. *Exp Brain Res* **87**, 402-406.

Bernhardt, P., Wilke, H. J., Wenger, K. H., Jungkunz, B., Bohm, A., & Claes, L. E. (1999). Multiple muscle force simulation in axial rotation of the cervical spine. *Clinical Biomechanics* **14**, 32-40.

Bull, M. L., de Freitas, V., & Vitti, M. (1990). Electromyographic study of the trapezius (pars superior) and serratus anterior (pars inferior) in free movements of the arm. *Anatomischer Anzeiger* **171**, 125-133.

Bull, M. L., Vitti, M., & de, F., V (1985). Electromyographic study of the trapezius (upper portion) and levator scapulae muscles in some movements of the shoulders. *Anatomischer Anzeiger* **159**, 21-27.

Bull, M. L., Vitti, M., & de, F., V (1989). Electromyographic study of the trapezius (pars superior) and serratus anterior (pars inferior) muscles in free movements of the shoulder. *Electromyography and Clinical Neurophysiology* **29**, 119-125.

Burke, D., Adams, R. W., & Skuse, N. F. (1989). The effects of voluntary contraction on the H reflex of human limb muscles. *Brain* **112**, 417-433.

Burke, D. & Gandevia, S. C. (1999). Properties of human peripheral nerves: implications for studies of human motor control. *Progress in Brain Research* **123**, 427-435.

Burke, D., Gandevia, S. C., & McKeon, B. (1983). The afferent volleys responsible for spinal proprioceptive reflexes in man. *J Physiol (Lond)* **339**, 535-552.

Burke, D., Gandevia, S. C., & McKeon, B. (1984). Monosynaptic and oligosynaptic contributions to human ankle jerk and H-reflex. *J. Neurophysiol.* **52**, 435-448.

Burke, D., Gracies, J. M., Mazevet, D., Meunier, S., & Pierrot-Deseilligny, E. (1992). Convergence of descending and various peripheral inputs onto common propriospinal-like neurones in man. *J Physiol (Lond)* **449**, 655-671.

Caicoya, A. G., Illert, M., & Janike, R. (1999). Monosynaptic Ia pathways at the cat shoulder. *J Physiol (Lond)* **518 (3)**, 825-841.

Carr, L. J., Harrison, L. M., & Stephens, J. A. (1994). Evidence for bilateral innervation of certain homologous motoneurone pools in man. *J Physiol (Lond)* **475**, 217-227.

Carrasco, D. I. & English, A. W. (1999). Mechanical actions of compartments of the cat hamstring muscle, biceps femoris. *Progress in Brain Research* **123**, 397-403.

Cavallari, P. & Katz, R. (1989). Pattern of projections of group I afferents from forearm muscles to motoneurones supplying biceps and triceps muscles in man. *Exp Brain Res* **78**, 465-478.

Cavallari, P., Katz, R., & Penicaud, A. (1992). Pattern of projections of group I afferents from elbow muscles to motoneurones supplying wrist muscles in man. *Exp Brain Res* **91**, 311-319.

Chalmers, G. R. & Bawa, P. (1997). Synaptic connections from large afferents of wrist flexor and extensor muscles to synergistic motoneurones in man. *Exp Brain Res* **116**, 351-358.

Chanaud, C. M. & Macpherson, J. M. (1991). Functionally complex muscles of the cat hindlimb. III. Differential activation within biceps femoris during postural perturbations. *Exp Brain Res* **85**, 271-280.

Chanaud, C. M., Pratt, C. A., & Loeb, G. E. (1991a). Functionally complex muscles of the cat hindlimb. II. Mechanical and architectural heterogenity within the biceps femoris. *Exp Brain Res* **85**, 257-270.

Chanaud, C. M., Pratt, C. A., & Loeb, G. E. (1991b). Functionally complex muscles of the cat hindlimb. V. The roles of histochemical fiber-type regionalization and mechanical heterogeneity in differential muscle activation. *Exp Brain Res* **85**, 300-313.

Charlton, C. G., Crowell, B., Jr., & Benson, R. (1988). Identification of motor neurons for accessory muscles of inspiration and expiration, pectoralis, trapezius and external oblique: comparison with non-respiratory skeletal muscle. *Synapse* **2**, 219-224.

Clavenzani, P., Scapolo, P. A., Callegari, E., Barazzoni, A. M., Petrosino, G., Lucchi, M. L., & Bortolami, R. (1994). Motoneuron organisation of the muscles of the spinal accessory complex of the sheep investigated with the fluorescent retrograde tracer technique. *J Anat.* **184 (2)**, 381-385.

Copeland, S., Bigliani, L., Emery, R., Amis, A., Chippindale, A., & Stoller, D. (2000). Interactive Shoulder. London, Primal Pictures Ltd.

Corden, D. M., Lippold, O. C., Buchanan, K., & Norrington, C. (2000). Long-latency component of the stretch reflex in human muscle is not mediated by intramuscular stretch receptors. *J Neurophysiol.* **84**, 184-188.

Creange, A., Faist, M., Katz, R., & Penicaud, A. (1992). Distribution of heteronymous Ia facilitation and recurrent inhibition in the human deltoid motor nucleus. *Exp Brain Res* **90**, 620-624.

Crone, C. & Nielsen, J. (1989). Methodological implications of the post activation depression of the soleus H-reflex in man. *Exp Brain Res* **78**, 28-32.

Cuadros, C. L., Driscoll, C. L., & Rothkopf, D. M. (1995). The anatomy of the lower serratus anterior muscle: a fresh cadaver study. *Plastic and Reconstructive Surgery* **95**, 93-97.

Culham, E. & Peat, M. (1993). Functional anatomy of the shoulder complex. *J Orthop. Sports Phys. Ther.* **18**, 342-350.

Curtis, D. R., Krnjevic, K., & Miledi, R. (1958). Crossed inhibition of sacral motoneurones. *J Neurophysiol.* **21**, 319-326.

Darton, K., Lippold, O. C., Shahani, M., & Shahani, U. (1985). Long-latency spinal reflexes in humans. *J Neurophysiol.* **53**, 1604-1618.

Davey, N. J., Ellaway, P. H., & Stein, R. B. (1986). Statistical limits for detecting change in the cumulative sum derivative of the peristimulus time histogram. *J Neurosci. Methods* **17**, 153-166.

David, G., Magarey, M. E., Jones, M. A., Dvir, Z., Turker, K. S., & Sharpe, M. (2000). EMG and strength correlates of selected shoulder muscles during rotations of the glenohumeral joint. *Clinical Biomechanics* **15**, 95-102.

De Luca, C. J. & Merletti, R. (1988). Surface myoelectric signal cross-talk among muscles of the leg. *Electroencephalography and Clinical Neurophysiology* **69**, 568-575.

de Noordhout, A. M., Rapisarda, G., Bogacz, D., Gerard, P., de, P., V, Pennisi, G., & Delwaide, P. J. (1999). Corticomotoneuronal synaptic connections in normal man: an electrophysiological study. *Brain* **122 (7)**, 1327-1340.

Deschuytere, J., Rosselle, N., & De Keyser, C. (1976). Monosynaptic reflexes in the superficial forearm flexors in man and their clinical significance. *J Neurol. Neurosurg. Psychiatry* **39**, 555-565.

Desmedt, J. E. & Godaux, E. (1978). Mechanism of the vibration paradox: Excitatory and inhibitory effects of tendon vibration on single soleus muscle motor units in man. *J Physiol (Lond)* **285**, 197-207.

Desmedt, J. E. (1983). Mechanisms of vibration induced inhibition or potentiation: Tonic vibration reflex and vibration paradox in man. In *Motor control mechanisms in health and disease.* Ed. Desmedt John E.. New York. Raven Press. pp. 671-683.

Dimitrijevic, M. R., Gregoric, M. R., Sherwood, A. M., & Spencer, W. A. (1980). Reflex responses of paraspinal muscles to tapping. *J Neurol. Neurosurg. Psychiatry* **43**, 1112-1118.

Dimitrijevic, M. R., Spencer, W. A., Trontelj, J. V., & Dimitrijevic, M. (1977). Reflex effects of vibration in patients with spinal cord lesions. *Neurology* **27**, 1078-1086.

Dindar, F. & Verrier, M. (1975). Studies on the receptor responsible for vibration induced inhibition of monosynaptic reflexes in man. *J Neurol. Neurosurg. Psychiatry* **38**, 155-160.

Donatelli, R. A. (1997). Functional anatomy and mechanics. In *Physical therapy of the shoulder.* Edinburgh. Churchill Livingstone. pp. 10-14.

Dvir, Z. & Berme, N. (1978). The shoulder complex in elevation of the arm: a mechanism approach. *J Biomech.* **11**, 219-225.

Elert, J. E., Rantapaa Dahlqvist, S. B., Henriksson Larsen, K., Lorentzon, R., & Gerdle, B. U. (1992). Muscle performance, electromyography and fibre type composition in fibromyalgia and work-related myalgia. *Scandinavian Journal of Rheumatology* **21**, 28-34.

Fahrer, H., Ludin, H. P., Mumenthaler, M., & Neiger, M. (1974). The innervation of the trapezius muscle. An electrophysiological study. *J Neurophysiol.* **207**, 183-188.

Ferbert, A., Priori, A., Rothwell, J. C., Day, B. L., Colebatch, J. G., & Marsden, C. D. (1992). Interhemispheric inhibition of the human motor cortex. *J Physiol (Lond)* **453**, 525-546.

Fern, R. & Harrison, P. J. (1991). The effects of compression upon conduction in myelinated axons of the isolated frog sciatic nerve. *J.Physiol (Lond)* **432**, 111-122.

Fern, R. & Harrison, P. J. (1994a). The contribution of ischaemia and deformation to the conduction block generated by compression of the cat sciatic nerve. *Exp.Physiol* **79**, 583-592.

Fern, R. & Harrison, P. J. (1994b). The relationship between ischaemic conduction failure and conduction velocity in cat myelinated axons. *Exp. Physiol* **79**, 571-581.

Fitzgerald, M. J., Comerford, P. T., & Tuffery, A. R. (1982). Sources of innervation of the neuromuscular spindles in sternomastoid and trapezius. *J.Anat.* **134**, 471-490.

Fortier, P. A. (1994). Use of spike triggered averaging of muscle activity to quantify inputs to motoneuron pools. *J Neurophysiol.* **72**, 248-265.

Fritz, N., Illert, M., de la, M. S., Reeh, P., & Saggau, P. (1989). Pattern of monosynaptic Ia connections in the cat forelimb. *J Physiol (Lond)* **419**, 321-351.

Fromm, S. (2001). The winging scapula. freespace.virgin.net/steven.fromm/index.htm.

Fuglevand, A. J., Winter, D. A., Patla, A. E., & Stashuk, D. (1992). Detection of motor unit action potentials with surface electrodes: influence of electrode size and spacing. *Biological Cybernetics* **67**, 143-153.

Gielen, C. C., Ramaekers, L., & van Zuylen, E. J. (1988). Long-latency stretch reflexes as co-ordinated functional responses in man. *J Physiol (Lond)* **407**, 275-292.

Gillies, J. D., Lance, J. W., Neilson, P. D., & Tassinari, C. A. (1969). Presynaptic inhibition of the monosynaptic reflex by vibration. *J Physiol (Lond)* **205**, 329-339.

Glousman, R., Jobe, F., Tibone, J., Moynes, D., Antonelli, D., & Perry, J. (1988). Dynamic electromyographic analysis of the throwing shoulder with glenohumeral instability. *J.Bone Joint Surg. [Am.]* **70**, 220-226.

Gottlieb, G. L. & Agarwal, G. C. (1973a). Modulation of postural reflexes by voluntary movement. II. Modulation at an inactive joint. *J Neurol. Neurosurg. Psychiatry* **36**, 540-546.

Gottlieb, G. L. & Agarwal, G. C. (1973b). Modulation of postural reflexes by voluntary movement. I. Modulation of the active limb. *J Neurol. Neurosurg. Psychiatry* **36**, 529-539.

Gottlieb, G. L. & Agarwal, G. C. (1976). Extinction of the Hoffmann reflex by antidromic conduction. *Electroencephalography and Clinical Neurophysiology* **41**, 19-24.

Gracies, J. M., Meunier, S., & Pierrot-Deseilligny, E. (1994). Evidence for corticospinal excitation of presumed propriospinal neurones in man. *J Physiol (Lond)* **475**, 509-518.

Grow, W. A., Kendall-Wassmuth, E., Grober, M. S., Ulibarri, C., & Laskowski, M. B. (1996). Muscle fiber type correlates with innervation topography in the rat serratus anterior muscle. *Muscle and Nerve* **19**, 605-613.

Guazzelli, F. J., de, F., V, & Furlani, J. (1994). Electromyographic study of the trapezius muscle in free movements of the shoulder. *Electromyography and Clinical Neurophysiology* **34**, 279-283.

Halder, A. M., Halder, C. G., Zhao, K. D., O'Driscoll, S. W., Morrey, B. F., & An, K. N. (2001). Dynamic inferior stabilizers of the shoulder joint. *Clinical Biomechanics* **16**, 138-143.

Harrison, P. J. & Taylor, A. (1981) Individual excitatory post-synaptic potentials due to muscle spindle Ia afferents in cat triceps surae motoneurones. *J Physiol (Lond)* **312**, 455-470.

Henneman, E., Somjen, G., & Carpenter D.O. (1965). Functional significance of cell size in spinal motoneurones. *J Neurophysiol.* **28**, 560-580.

Hess, S. A. (2000). Functional stability of the glenohumeral joint. *Manual therapy* **5 (2)**, 63-71.

Hodges, P. W. & Bui, B. H. (1996). A comparison of computer-based methods for the determination of onset of muscle contraction using electromyography. *Electroencephalography and Clinical Neurophysiology* **101**, 511-519.

Hodges, P. W. & Richardson, C. A. (1997a). Feedforward contraction of transversus abdominis is not influenced by the direction of arm movement. *Exp Brain Res* **114**, 362-370.

Hodges, P. W. & Richardson, C. A. (1997b). Contraction of the abdominal muscles associated with movement of the lower limb. *Physical Therapy* **77**, 132-142.

Hodges, P. W. & Richardson, C. A. (1998). Delayed postural contraction of transversus abdominis in low back pain associated with movement of the lower limb. *J Spinal Disord.* **11**, 46-56.

Hodges, P. W. & Richardson, C. A. (1999). Altered trunk muscle recruitment in people with low back pain with upper limb movement at different speeds. *Archives of Physical Medicine and Rehabilitation* **80**, 1005-1012.

Hoffmann, P. (1918). Uber die Beziehungen der Sehnenreflexe zur wilkurlichen Bewegung und zum Tonus. *Z. Biol.* **68**, 351-370.

Host, H. H. (1995). Scapular taping in the treatment of anterior shoulder impingement. *Physical Therapy* **75**, 803-812.

Hurley, D. A., Liebich, S. E., Jones, M. M., & Turker, K. S. (1999). EMG investigation of the activity of four scapula muscles during fatigue of serratus anterior-detection of muscle substitution. WCPT abstracts [PL-RR-335], 166-166. Japan.

Iles, J. F. (1976). Central terminations of muscle afferents on motoneurones in the cat spinal cord. *J Physiol (Lond)* **262**, 91-117.

Iles, J. F. & Pisini, J. V. (1992). Cortical modulation of transmission in spinal reflex pathways of man. *J Physiol (Lond)* **455**, 425-446.

Iles, J. F., Stokes, M., & Young, A. (1990). Reflex actions of knee joint afferents during contraction of the human quadriceps. *Clin. Physiol* **10**, 489-500.

Ishii, Y. (1989). Central afferent projections from the rat sternocleidomastoid and trapezius muscles. A study using transganglionic transport of horseradish peroxidase. *Osaka Daigaku Shigaku. Zasshi* **34**, 193-212.

Iwasaki, M., Nakasato, N., Kanno, A., Hatanaka, K., Nagamatsu, K., Nagamine, Y., & Yoshimoto, T. (2001). Somatosensory evoked fields in comatose survivors after severe traumatic brain injury. *Clinical Neurophysiology* **112**, 205-211.

Jack, J. J., Noble, D., & Tsien, R. W. (1985). *Electric current flow in excitable cells*, 1 ed.

Jankowska, E., McCrea, D., & Mackel, R. (1981). Oligosynaptic excitation of motoneurones by impulses in group Ia muscle spindle afferents in the cat. *J Physiol (Lond)* **316**, 411-425.

Jenner, J. R. & Stephens, J. A. (1982). Cutaneous reflex responses and their central nervous pathways studied in man. *J Physiol (Lond)* **333**, 405-419.

Jensen, C. & Westgaard, R. H. (1997). Functional subdivision of the upper trapezius muscle during low-level activation. *Eur. J Appl. Physiol* **76**, 335-339.

Johnson, G., Bogduk, N., Nowitzke, A., & House, D. (1994). Anatomy and actions of the trapezius muscle. *Clinical Biomechanics* **9**, 44-50.

Kapandji, I. A. (1986). *The Physiology of the Joints. Annotated diagrams of the mechanics of the human body.*, 5 ed. Edinburgh. Churchill Livingstone.

Kaplan, P. E. (1980). Electrodiagnostic confirmation of long thoracic nerve palsy. *J Neurol. Neurosurg. Psychiatry* **43**, 50-52.

Kendall, F. P., McCreary, E. K., & Provance, P. G. (1993). *Muscles, testing and function*, 4th ed., Baltimore. Williams and Wilkins.

Kent, B. E. (1971). Functional anatomy of the shoulder complex. A review. *Physical Therapy* **51**, 947.

Keshner, E. A., Campbell, D., Katz, R. T., & Peterson, B. W. (1989). Neck muscle activation patterns in humans during isometric head stabilization. *Exp Brain Res* **75**, 335-344.

Kitahara, T., Schnoz, M., Laubli, T., Wellig, P., & Krueger, H. (2000). Motor-unit activity in the trapezius muscle during rest, while inputting data, and during fast finger tapping. *Eur. J Appl. Physiol* **83**, 181-189.

Kitamura, S. & Sakai, A. (1982). A study on the localization of the sternocleidomastoid and trapezius motoneurons in the rat by means of the HRP method. *Anatomical Record* **202**, 527-536.

Kleine, B., Schumann, N., Stegeman, D. F., & Scholle, H. (2000). Surface EMG mapping of the human trapezius muscle: the topography of monopolar and bipolar surface EMG amplitude and spectrum parameters at varied forces and in fatigue. *Clinical Neurophysiology* **111**, 686-693.

Koltzenburg, M., Wall, P. D., & McMahon, S. B. (1999). Does the right side know what the left is doing? *Trends in Neurosciences* **22**, 122-127.

Krammer, E. B., Lischka, M. F., Egger, T. P., Riedl, M., & Gruber, H. (1987). The motoneuronal organization of the spinal accessory nuclear complex. *Advances in Anatomy, Embryology and Cell Biology* **103**, 1-62.

Krause, H. R., Bremerich, A., & Herrmann, M. (1991). The innervation of the trapezius muscle in connection with radical neck-dissection. An anatomical study. *Journal of Cranio-maxillo-facial Surgery* **19**, 87-89.

Krause, H. R., Kornhuber, A., & Dempf, R. (1993). A technique for diagnosing the individual patterns of innervation of the trapezius muscle prior to neck dissection. *Journal of Cranio-maxillo-facial Surgery* **21**, 102-106.

Kujirai, T., Caramia, M. D., Rothwell, J. C., Day, B. L., Thompson, P. D., Ferbert, A., Wroe, S., Asselman, P., & Marsden, C. D. (1993). Corticocortical inhibition in human motor cortex. *J Physiol (Lond)* **471**, 501-519.

Lance, J. W. (1965). The mechanism of reflex irradiation. *Proc. Aust. Assoc. Neurol.* **3**, 77-81.

Lear, L. J. & Gross, M. T. (1998). An electromyographical analysis of the scapular stabilizing synergists during a push-up progression. *J Orthop. Sports Phys. Ther.* **28**, 146-157.

Liinamaa, T. L., Keane, J., & Richmond, F. J. (1997). Distribution of motoneurons supplying feline neck muscles taking origin from the shoulder girdle. *J Comp Neurol* **377**, 298-312.

Lindman, R., Eriksson, A., & Thornell, L. E. (1991). Fiber type composition of the human female trapezius muscle: enzyme-histochemical characteristics. *Am. J. Anat.* **190**, 385-392.

Lisy, L. (1989). Reflex responses in the trapezius muscle after percussion of different parts of the body. *Cesk. Neurol. Neurochir.* **52**, 22-27.

Liu, J., Hughes, R. E., Smutz, W. P., Niebur, G., & Nan-An, K. (1997). Roles of deltoid and rotator cuff muscles in shoulder elevation. *Clinical Biomechanics* **12**, 32-38.

Lloyd, D. P. C. (1943). Conduction and synaptic transmission of the reflex response to stretch in spinal cats. *J Neurophysiol.* **6**, 317-326.

Lo Monaco, M., Di Pasquq, D., & Tonali, P. (1983). Conduction studies along the accessory, long thoracic, dorsal scapular and thoracodorsal nerves. *Acta Neurol Scand* **68**, 171-176.

Low, J. & Reed, A. (1994). Electrical stimulation of nerve and muscle. In *Electrotherapy explained. Principles and practice*. Oxford. Butterworth Heinemann. pp. 39-133.

Ludewig, P. M. & Cook, T. M. (2000). Alterations in shoulder kinematics and associated muscle activity in people with symptoms of shoulder impingement. *Physical Therapy* **80**, 276-291.

Ludewig, P. M., Cook, T. M., & Nawoczenski, D. A. (1996). Three-dimensional scapular orientation and muscle activity at selected positions of humeral elevation. *J Orthop. Sports Phys. Ther.* **24**, 57-65.

Lundh, B. & Rosen, I. (1979). On the physiological and clinical significance of a trapezius reflex evoked by tapping the spine. *Acta Neurol Scand* **59**, 211-220.

Macefield, G., Gandevia, S., & Burke, D. (1989). Conduction velocities of muscle and cutaneous afferents in the upper and lower limbs of human subjects. *Brain* **112**, 1519-1532.

Macefield, G. & Gandevia, S. C. (1992). Peripheral and central delays in the cortical projections from human truncal muscles. Rapid central transmission of proprioceptive input from the hand but not the trunk. *Brain* **115 (1)**, 123-135.

Macefield, V. G., Rothwell, J. C., & Day, B. L. (1996). The contribution of transcortical pathways to long-latency stretch and tactile reflexes in human hand muscles. *Exp Brain Res* **108**, 147-154.

Magarey, M. E., Jones, M. A., & Grant, E. R. (1996). Biomedical considerations and clinical patterns related to disorders of the glenoid labrum in the predominantly stable glenohumeral joint. *Manual Therapy* **1**, 242-249.

Magladery, J. W. & McDougal, D. B. (1950). Electrophysiological studies of nerve and reflex activity in normal man. I. Identification of certain reflexes in the electromyogram and the conduction velocity of peripheral nerve fibres. *Bulletin of the John Hopkins Hospital* **88**.

Marchand-Pauvert, V., Mazevet, D., Nielsen, J., Petersen, N., & Pierrot-Deseilligny, E. (2000a). Distribution of non-monosynaptic excitation to early and late recruited units in human forearm muscles. *Exp Brain Res* **134**, 274-278.

Marchand-Pauvert, V., Nicolas, G., & Pierrot-Deseilligny, E. (2000b). Monosynaptic Ia projections from intrinsic hand muscles to forearm motoneurones in humans. *J Physiol (Lond)* **525 (1)**, 241-252.

Matsushita, M. & Tanami, T. (1983). Contralateral termination of primary afferent axons in the sacral and caudal segments of the cat, as studied by anterograde transport of horseradish peroxidase. *J Comp Neurol.* **220**, 206-218.

Matthews, P. B. (1991). The human stretch reflex and the motor cortex. *Trends in Neurosciences* **14**, 87-91.

Matthews, P. (1972). *Mammalian muscle receptors and their central actions*, 1st Ed. London. Edward Arnold Ltd.

Mazevet, D. & Pierrot-Deseilligny, E. (1994). Pattern of descending excitation of presumed propriospinal neurones at the onset of voluntary movement in humans. *Acta Physiol Scand.* **150**, 27-38.

McClelland, V. M., Miller, S., & Eyre, J. A. (2001). Short latency heteronymous excitatory and inhibitory reflexes between antagonist and heteronymous muscles of the human shoulder and upper limb. *Brain Res* **899**, 82-93.

Mediatheque Sante Lyon 1 University (2001). Visible Human Project. http://rockefeller.univ-lyon1.fr/VisibleHumanProjectEnglish/VisibleHuman.html.

Mendell, L.M. & Henneman,E. (1971). Terminals of single Ia fibres: location, density and distribution within a pool of 300 homonymous motoneurones. *J Neurophysiol.* **34 (1)**, 171-187.

Michels, R., Wessel, K., Klohn, S., & Kompf, D. (1993). Long-latency reflexes, somatosensory evoked potentials and transcranial magnetic stimulation: relation of the three methods in multiple sclerosis. *Electroencephalography and Clinical Neurophysiology* **89**, 235-241.

Morgan, C., Nadelhaft, I., & de Groat, W. C. (1981). The distribution of visceral primary afferents from the pelvic nerve to Lissauer's tract and the spinal gray matter and its relationship to the sacral parasympathetic nucleus. *J Comp Neurol.* **201**, 415-440.

Myriknas, S. E., Beith, I. D., & Harrison, P. J. (2000). Stretch reflexes in the rectus abdominis muscle in man. *Exp. Physiol* **85**, 445-450.

Nadler, M. (2000). Central motor reorganisation following stroke and motor learning studied in man. University College London. PhD thesis. pp 274-283.

Nakajima, K., Maier, M. A., Kirkwood, P. A., & Lemon, R. N. (2000). Striking differences in transmission of corticospinal excitation to upper limb motoneurons in two primate species. *J Neurophysiol.* **84**, 698-709.

Nardone, A. & Schieppati, M. (1998). Medium-latency response to muscle stretch in human lower limb: estimation of conduction velocity of group II fibres and central delay. *Neuroscience Letters* **249**, 29-32.

Nori, S., Soo, K. C., Green, R. F., Strong, E. W., & Miodownik, S. (1997). Utilization of intraoperative electroneurography to understand the innervation of the trapezius muscle. *Muscle and Nerve* **20**, 279-285.

O'Sullivan, M. C., Eyre, J. A., & Miller, S. (1991). Radiation of phasic stretch reflex in biceps brachii to muscles of the arm in man and its restriction during development. *J Physiol (Lond)* **439**, 529-543.

O'Sullivan, M. C., Twomy, L., & Allison, G. (1998). Altered abdominal muscle recruitment in patients with chronic back pain following a specific exercise intervention. *Journal of sports and physical therapy* **27**, 114-124.

Paine, R. M. & Voight, M. (1993). The role of the scapula. *J Orthop. Sports Phys. Ther.* **18**, 386-391.

Palmer, E. & Ashby, P. (1992). Evidence that a long latency stretch reflex in humans is transcortical. *J Physiol (Lond)* **449**, 429-440.

Pauvert, V., Pierrot-Deseilligny, E., & Rothwell, J. C. (1998). Role of spinal premotoneurones in mediating corticospinal input to forearm motoneurones in man. *J Physiol (Lond)* **508 (1)**, 301-312.

Pearson, A. (1938). The spinal accessory nerve in human embryos. *J Comp Neurol* **68 (2)**, 243-266.

Peat, M. (1986). Functional anatomy of the shoulder complex. *Physical Therapy* **66**, 1855-1865.

Petersen, N., Christensen, L. O., Morita, H., Sinkjaer, T., & Nielsen, J. (1998). Evidence that a transcortical pathway contributes to stretch reflexes in the tibialis anterior muscle in man. *J Physiol (Lond)* **512 (1)**, 267-276.

Peterson, E. H. (1989). Motor pool organisation of vertibrate axial muscles. *American Zoologist* **29**, 123-137.

Petrera, J. E. & Trojaborg, W. (1984). Conduction studies of the long thoracic nerve in serratus anterior palsy of different etiology. *Neurology* **34**, 1033-1037.

Pierrot-Deseilligny, E. (1996). Transmission of the cortical command for human voluntary movement through cervical propriospinal premotoneurons. *Progress In Neurobiology* **48**, 489-517.

Pierrot-Deseilligny, E. & Mazevet, D. (2000). The monosynaptic reflex: a tool to investigate motor control in humans. Interest and limits. *Neurophysiologie Clinique* **30**, 67-80.

Pink, M. (2000). Scapulohumeral Rhythm. Singer, K. p 381-386. Perth Australia, University of Western Australia. IFOMT 2000.

Pratt, C. A., Chanaud, C. M., & Loeb, G. E. (1991). Functionally complex muscles of the cat hindlimb. IV. Intramuscular distribution of movement command signals and cutaneous reflexes in broad, bifunctional thigh muscles. *Exp Brain Res* **85**, 281-299.

Pratt, C. A. & Loeb, G. E. (1991). Functionally complex muscles of the cat hindlimb. I. Patterns of activation across sartorius. *Exp Brain Res* **85**, 243-256.

Priori, A., Berardelli, A., Inghilleri, M., Cruccu, G., Zaccagnini, M., & Manfredi, M. (1991). Electrical and magnetic stimulation of the accessory nerve at the base of the skull. *Muscle and Nerve* **14 (5)**, 477-488.

Ratto, S., Reni, L., Abbruzzese, G., Abbruzzese, M., & Favale, E. (1986). Facilitation and inhibition of synaptic transmission in the spinal cord: an electroneurographic study in humans. *Exp Brain Res* **64**, 411-420.

Richmond, F. J., Liinamaa, T. A., Keane, J., & Thomson, D. B. (1999). Morphometry, histochemistry, and innervation of cervical shoulder muscles in the cat. *J Morphol.* **239**, 255-269.

Ridding, M. C. & Rothwell, J. C. (1999). Afferent input and cortical organisation: a study with magnetic stimulation. *Exp Brain Res* **126**, 536-544.

Ritz, L. A., Bailey, S. M., Carter, R. L., Sparkes, M. L., Masson, R. L., & Rhoton, E. L. (1991). Crossed and uncrossed projections to cat sacrocaudal spinal cord: II. Axons from muscle spindle primary endings. *J Comp Neurol.* **304**, 316-329.

Roman-Liu, D., Tokarski, T., & Kaminska, J. (2001). Assessment of the musculoskeletal load of the trapezius and deltoid muscles during hand activity. *Int. J Occup. Saf Ergon.* **7**, 179-193.

Rose, P. K. & Richmond, F. J. (1981). White-matter dendrites in the upper cervical spinal cord of the adult cat: a light and electron microscopic study. *J Comp Neurol.* **199**, 191-203.

Rothwell, J. (1994). *Control of human voluntary movement*, 2nd ed. London. Chapman & Hall.

Schieppati, M. & Nardone, A. (1997). Medium-latency stretch reflexes of foot and leg muscles analysed by cooling the lower limb in standing humans. *J Physiol (Lond)* **503 (3)**, 691-698.

Schnoz, M., Laubli, T., & Krueger, H. (2000). Co-activity of the trapezius and upper arm muscles with finger tapping at different rates and trunk postures. *Eur. J Appl. Physiol* **83**, 207-214.

Schomburg, E. D. (1990). Spinal sensorimotor systems and their supraspinal control. *Neuroscience Research* **7**, 265-340.

Sears, T. A. & Stagg, D. (1976). Short-term synchronization of intercostal motoneurone activity. *J Physiol (Lond)* **263**, 357-381.

Shefner, J. M. (2001). Motor unit number estimation in human neurological diseases and animal models. *Clinical Neurophysiology.* **112**, 955-964.

Shimizu, T., Shimada, H., & Shirakura, K. (1993). Scapulohumeral reflex (Shimizu). Its clinical significance and testing maneuver. *Spine* **18**, 2182-2190.

Simonetta-Moreau, M., Marque, P., Marchand-Pauvert, V., & Pierrot-Deseilligny, E. (1999). The pattern of excitation of human lower limb motoneurones by probable group II muscle afferents. *J Physiol (Lond)* **517 (1)**, 287-300.

Sjogaard, G., Lundberg, U., & Kadefors, R. (2000). The role of muscle activity and mental load in the development of pain and degenerative processes at the muscle cell level during computer work [editorial]. *Eur. J Appl. Physiol* **83**, 99-105.

Soo, K. C., Hamlyn, P. J., Pegington, J., & Westbury, G. (1986). Anatomy of the accessory nerve and its cervical contributions in the neck. *Head Neck Surg.* **9**, 111-115.

Soo, K. C., Strong, E. W., Spiro, R. H., Shah, J. P., Nori, S., & Green, R. F. (1993). Innervation of the trapezius muscle by the intra-operative measurement of motor action potentials. *Head & Neck* **15**, 216-221.

Sporrong, H., Palmerud, G., & Herberts, P. (1995). Influences of handgrip on shoulder muscle activity. *Eur. J Appl. Physiol* **71**, 485-492.

Stacey, R. J., O'Leary, S. T., & Hamlyn, P. J. (1996). An anomaly in the nerve supply of the trapezius muscle. *Clin. Anat.* **9**, 414-416.

Svensson, P., Miles, T. S., Graven-Nielsen, T., & Arendt-Nielsen, L. (2000). Modulation of stretch-evoked reflexes in single motor units in human masseter muscle by experimental pain. *Exp Brain Res* **132**, 65-71.

Tantisira, B., Alstermark, B., Isa, T., Kummel, H., & Pinter, M. (1996). Motoneuronal projection pattern of single C3-C4 propriospinal neurones. *Can. J Physiol Pharmacol.* **74**, 518-530.

Taylor, J. L., Fogel, W., Day, B. L., & Rothwell, J. C. (1995). Ipsilateral cortical stimulation inhibited the long-latency response to stretch in the long finger flexors in humans. *J Physiol (Lond)* **488 (3)**, 821-831.

Turker, K. S. (1993). Electromyography: some methodological problems and issues. *Physical Therapy* **73**, 698-710.

Turker, K. S. & Miles, T. S. (1990). Cross-talk from other muscles can contaminate EMG signals in reflex studies of the human leg. *Neuroscience Letters* **111**, 164-169.

Uysal, H., Mogyoros, I., & Burke, D. (1999). Reproducibility of tendon jerk reflexes during a voluntary contraction. *Clinical Neurophysiology* **110**, 1481-1487.

Van Boxtel, A. (1986). Differential effects of low-frequency depression, vibration- induced inhibition, and posttetanic potentiation on H-reflexes and tendon jerks in the human soleus muscle. *J Neurophysiol.* **55**, 551-568.

Vanner, S. J. & Rose, P. K. (1984). Dendritic distribution of motoneurons innervating the three heads of the trapezius muscle in the cat. *J Comp Neurol.* **226**, 96-110.

Wada, N. & Kanda, K. (2001). Neuronal pathways from group-I and -II muscle afferents innervating hindlimb muscles to motoneurons innervating trunk muscles in low-spinal cats. *Exp Brain Res* **136**, 263-268.

Wadsworth, D. J. & Bullock-Saxton, J. E. (1997). Recruitment patterns of the scapular rotator muscles in freestyle swimmers with subacromial impingement. *Int. J Sports Med.* **18**, 618-624.

Waersted, M., Eken, T., & Westgaard, R. H. (1996). Activity of single motor units in attention-demanding tasks: firing pattern in the human trapezius muscle. *Eur. J Appl. Physiol Occup. Physiol* **72**, 323-329.

Wang, K., Svensson, P., & Arendt-Nielsen, L. (1999). Modulation of exteroceptive suppression periods in human jaw-closing muscles by local and remote experimental muscle pain. *Pain* **82**, 253-262.

Warner, J. J., Micheli, L. J., Arslanian, L. E., Kennedy, J., & Kennedy, R. (1992). Scapulothoracic motion in normal shoulders and shoulders with glenohumeral instability and impingement syndrome. A study using Moire topographic analysis. *Clinical Orthopaedics and Related Research* **285**, 191-199.

Watson, C. J. & Schenkmann, M. (1995). Physical therapy management of isolated serratus anterior muscle paralysis. *Physical Therapy* **75**, 194-202.

Westgaard, R. H. & De Luca, C. J. (2001). Motor control of low-threshold motor units in the human trapezius muscle. *J Neurophysiol.* **85**, 1777-1781.

Wickham, J. B. & Brown, J. M. (1998). Muscles within muscles: the neuromotor control of intra-muscular segments. *European Journal of Applied Physiology and Occupational Physiology* **78**, 219-225.

Williams, G. R., Jr., Shakil, M., Klimkiewicz, J., & Iannotti, J. P. (1999). Anatomy of the scapulothoracic articulation. *Clinical Orthopaedics and Related Research* **359**, 237-246.

Williams, P., Warwick, R., Dyson, M., & Bannister, L. (1989). Myology. In *Gray's Anatomy*, eds. Williams, P., Warwick, R., Dyson, M., & Bannister, L., London. Churchill Livingstone. pp. 545-660.

Winter, D., Fuglevand, A., & Archer, S.E. (1994). Crosstalk in surface electromyography: Theoretical and practical estimates. *J. Electromyogr. Kinesiol.* **4(1),** 15-26.

Wohlert, A. B. (1996). Reflex responses of lip muscles in young and older women. *J Speech Hear. Res* **39**, 578-589.

Zedka, M., Kumar, S., & Narayan, Y. (1998). Electromyographic response of the trunk muscles to postural perturbation in sitting subjects. *J. Electromyogr. Kinesiol.* **8**, 3-10.