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University of Alberta

Sensory Control of Upper Limb Movements

by

David Frederic Collins 

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Ph.D.

Division of Neuroscience

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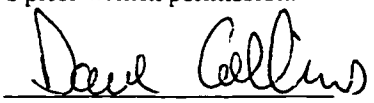

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, the thesis entitled Sensory Control of Upper Limb Movements submitted by David F. Collins in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Abstract

This thesis comprises five projects focussing on sensory feedback and upper limb movements. The first goal was to record forelimb afferent activity in freely moving cats (Chapter 2). The limited data showed firing rates similar to hindlimb units. The remaining projects explored sensorimotor control in humans. The first two investigated the conscious perception of signals involved in kinesthesia. The experiments in Chapter 3 demonstrate the kinesthetic importance of cutaneous receptors on the hand dorsum. Selective stimulation of these receptors evoked illusory finger movements in 71% of the subjects. Chapter 4 describes the first experiments to investigate the perception of muscle receptor signals during movements. Subjects rated the amplitude of experimentally-induced muscle twitches during various tasks. Ratings were significantly attenuated before, during and after wrist movements. The final two projects investigated afferent contributions to grasp movements. Chapter 5 shows the importance of the afferent "contact signal" to the generation of EMG activity. Subjects were requested to grasp, lift and replace a target object. EMG activity was compared between trials in which the target was present and those in which it was unexpectedly absent. Contact-dependent changes in EMG activity were identified during the first 100 ms after contact in 40/46 muscles. Local anesthesia often reduced, but did not always abolish, these contact-dependent responses. The final project (Chapter 6) investigated task-dependent gating of proprioceptive reflex pathways to hand muscles. Index finger flexion significantly attenuated stretch reflex amplitudes, compared to static trials. Some of the attenuation was alleviated when movements involved grasping and lifting a weight compared to simply moving the index finger to touch the thumb. Together these experiments

demonstrate the attenuation of afferent signals through both spinal and supraspinal pathways during upper limb movements. The attenuation arose from central and peripheral sources and was dependent on task. Cutaneous receptors on the hand dorsum were shown to be important in kinesthesia and in the gating of ascending pathways from muscle receptors. Also, the importance of the afferent signals evoked by contact with the target object during grasp was demonstrated. These experiments highlight the task-dependence of transmission through somatosensory pathways and identify several roles for afferent feedback in the control of hand movements.

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1.0 General Introduction

How do we move? Certainly, this question has fascinated, and frustrated, inquisitive minds since the days of Aristotle. Today, vast amounts of information have accumulated on this topic. Most, if not all, of the anatomical pieces of the puzzle have been identified. However, our understanding of the underlying physiological processes and their interactions is still in relative infancy. The goal of this thesis is to build on what is known about the afferent control of movement and provide unique insights into this aspect of the neural control of hand movements. It is hoped this work may contribute to the formulation of new and more general ideas regarding the sensory control of movement.

Each time a movement is made the central nervous system receives a massive barrage of feedback from receptors located in the moving body segments. It has been estimated that during an imposed movement of the cat hindlimb ensemble input from muscle spindles may exceed 0.2 million impulses each second (imp/s) (Prochazka, 1996). During human grasp, inputs from cutaneous receptors in one hand may reach twice this value. Despite, and perhaps in part because of, the volume and complexity of this feedback its role in the control of movement is still unclear.

This introductory chapter reviews our current knowledge regarding afferent feedback from the upper limb. Due to the wealth of literature in this area, the material covered will be limited to that pertaining to sensory feedback from the upper limbs of conscious mammals. Data from reduced or anesthetized preparations will be discussed only as required. A review of the "motor" side of the nervous system and its role in the control of the upper limb is also beyond the scope of this review. The review is further limited to roles for feedback from mechanosensitive receptors. Potential roles of peripheral thermo- and nocisensitive receptors will not be reviewed. Finally, attempts will be made to avoid unnecessary repetition of details presented in the introductions in Chapters 4-6.

Much of the groundwork in this field has involved investigations of receptor morphology and activity patterns during movements. This material is reviewed in section 1.1. As this body of knowledge developed, researchers began investigating the neural routes taken by these signals. A synopsis of this work is reviewed in section 1.2. Presently there is a strong framework upon which to base ideas regarding how peripheral feedback integrates with descending motor commands to culminate in the vast repertoire of movements we are able to perform. Current ideas regarding roles for afferent feedback, particularly as they pertain to hand movements, are reviewed in section 1.3. Section 1.4 outlines the specific objectives of the research projects presented in the subsequent chapters.

1.1 Peripheral Receptors and Activity Patterns During Movement

A clear understanding of the various types of peripheral receptors and the nature of the signals they provide is prerequisite to formulating ideas regarding their role in movement control. The following sections outline the structure of the different mammalian peripheral mechanosensitive receptors and describe what is known of their activity during movements of the upper limb. More detailed information on the peripheral receptors can be found in several reviews (Matthews, 1972; Gladden, 1992; Prochazka, 1996)

1.1.1 Muscle Receptors

Two types of large, specialized receptors have been identified in mammalian muscle, the muscle spindle and the Golgi Tendon Organ (GTO). Theories regarding the extent to which they contribute to the control of movement have waxed and waned over the last century. Arguably, they have never been attributed a greater role in motor control than in current thinking.

Muscle Spindle Receptors

The muscle spindle is by far the most complex and intensely studied of the peripheral receptors. First discovered in the mid-eighteen hundreds, muscle spindles were thought of as "special sense organs entrusted with some peculiar sensorial function" before the turn of that century (Ruffini, 1898). Muscle spindle discharge encodes muscle length and its rate of change. For an extensive review of the muscle spindle see the review by Hulliger (1984).

The structure of this receptor is variable. A "typical" receptor comprises 5–10 intrafusal muscle fibres (0.5–10 mm long) which lie in parallel with, and attach to, the extrafusal muscle fibres. The intrafusal fibres have been subdivided into bag_1 (1/spindle), bag_2 (1/spindle) and chain fibres (3–5/spindle) based on histochemical and electrophysiological measurements (Boyd, 1981). The central half of the spindle is encapsulated and contains two types of sensory ending (Ruffini, 1898). The annulospiral primary ending innervates the central portion of all three types of intrafusal fibre. These give rise to one or two, fast-conducting (65–120 m/s), type Ia afferent fibres per spindle (Boyd, 1981). The secondary ending is a flower spray type ending which innervates bag_2 and chain fibres. There are between 1–10 of these endings per muscle spindle, each of which gives rise to slower conducting (45 m/s) type II afferents (Boyd, 1981).

The spindle is the only somatosensory receptor under direct efferent control. Though this motor innervation was suspected from outset (Ruffini, 1898), conclusive evidence was relatively slow in coming (Matthews, 1933). Two classes of motor innervation have presently been identified. The fusimotor neurons (or γ-motoneurons) supply only the intrafusal fibres thereby allowing the CNS to adjust the sensitivity of the receptor via contractions of the intrafusal muscle fibres separately from the extrafusal fibres. Less frequently intrafusal fibres are also innervated by a β-skeletomotor fibre which sends branches to extra- and intrafusal fibres, thereby evoking an obligatory contraction of both types of muscle fibre. Both γ- and β-motoneurons have been further subdivided into dynamic (which innervate bag1 fibres) and static (Murthy, 1983) (innervating bag2 and chain).

During locomotion muscle spindle primary afferents in the hindlimb of freely moving cats fire between 50-200 imp/s (Loeb & Duysens, 1979; Prochazka *et al.*, 1977) and impulse rates can reach over 600 imp/s during imposed movements (Prochazka *et al.*, 1989). Discharges from suspected Ia afferents from the monkey forelimb have complex discharge patterns, typically firing at rates between 50-60 imp/s with the maximum published rates reaching approximately 130 imp/s during an imposed ramp and hold stretch (Schieber & Thach, 1985). In contrast, Ia discharge rates during voluntary human hand movements are relatively low, rarely exceeding 30 imp/s (Al-Falahe *et al.*, 1990). Responses recorded during slips of an object held between the index finger and thumb reached peaks of approximately 20 imp/s and did not begin until after the onset of compensatory grip force adjustments (Hager-Ross & Johansson, 1996). The highest published firing rate from a human primary ending is approximately 110 imp/s, briefly reached at the termination of a pulling load delivered tangentially to an object held between the index finger and thumb (Macefield & Johansson, 1996). It is still unclear whether the discrepancies between the low firing rates reported in humans and the higher rates in animals are a real species difference. Technical constraints of human microneurography restrict the range of movement velocities which can be studied (Prochazka, 1996). When these velocities are matched between the human and monkey data the differences in firing rates are much reduced (Prochazka, 1996). Also, the laboratory setting may cause the animals to become aroused which could result in unnaturally high firing rates (Prochazka, 1996). Interspecies differences in tendon compliance have also been suggested as a reason for the discrepancies between the human and animal data (Herbert & Gandevia, 1995). However, these discrepancies may reflect a real difference between spindles in the forelimb and the hindlimb. This is an issue we attempted to resolve in our laboratory by recording forelimb afferents in freely moving cats. The results are presented in Chapter 2.

Golgi Tendon Organs

The GTO is located at the musculo-tendinous junction (Golgi, 1903, in Jami, 1992). Originally thought to signal muscle force, the effective stimulus is now known to be active muscle contraction (Houk & Henneman, 1967). For an extensive review of the GTO see the review article by Jami (1992).

A single GTO is an elongated fascicle of collagen bundles (length 0.1–1.5 mm, diameter 30–220 μm) attached at one end to the individual tendons of 10–20 extrafusal muscle fibres; the other end is in continuity with the whole muscle tendon or aponeurosis. In this way each receptor is situated in series with a group of muscle fibres (which load the GTO) and in parallel with a larger number of fibres (which tend to unload the GTO). The receptor is enclosed in a lamellar capsule and gives rise to a single Ib afferent fibre. Conduction velocities for these afferents fall in the 60–110 m/s range which overlaps Ia conduction velocities, though more Ia afferents are generally found in the high velocity range (Hunt, 1954). Interestingly, GTOs are often absent in the intrinsic muscles of the hand (Devanandan *et al.*, 1983).

GTOs are highly sensitive to contraction of in-series muscle fibres. An individual receptor can monitor the activity of a single motor unit (Houk & Henneman, 1967). During normal locomotion GTOs in the hindlimb of freely moving cats fire between 0–150 imp/s with peak firing rates of over 400 imp/s observed during imposed stretches (Appenteng & Prochazka, 1984). These firing rates contrast with the relatively low peak firing rates of between 30 imp/s in the human arm during a mild contraction (Vallbo, 1974) to approximately 60 imp/s at high contraction forces (Macefield & Johansson, 1996). This discrepancy may be accounted for by the species, limb, task or tendon compliance differences discussed above for the similar discrepancies in the muscle spindle data. Our attempts to resolve this issue are presented in Chapter 2.

During imposed sinusoidal finger movements Ib afferents in human finger extensors showed no modulation with length changes. During voluntary reproduction of the same movements firing rates were maximal during muscle shortening (Al-Falahe *et al.*, 1990). Most Ibs are inactive in silent muscle and begin firing with EMG activity

(Edin & Vallbo, 1990; Al-Falahe *et al.*, 1990). GTO discharges often display staircase type changes in firing during smooth changes in force (Vallbo, 1974; Appenteng & Prochazka, 1984; Macefield & Johansson, 1996). It is thought that this is due to the additional recruitment or derecruitment of motor units in series with the receptor or unloading of the receptor by contraction of fibres in parallel (Vallbo, 1974). Such non-linearities in firing are smoothed out in ensemble averages (Prochazka, 1986).

1.1.2 Cutaneous Receptors

Four types of receptor have been identified in mammalian glabrous (non-hairy) skin. These four morphologically distinct receptors can also be identified based on differences in their adaptation to sustained stimuli and receptive field sizes (Westling, 1986). This has led to the development of a classification system whereby receptors are identified as being either slowly adapting (SA) or rapidly adapting (RA) type I (small receptive field) or type II (large receptive field) receptors (Westling, 1986). This nomenclature has been adopted throughout this thesis. All the cutaneous receptors have afferent fibres with conduction velocities in the range of 35-80 m/s (Johansson & Vallbo, 1983).

Merkel cells (SAI) and Meissner corpuscles (FAI) are located in the skin's epidermal layer, within a few hundred microns of the body surface and have small receptive fields (typically <10 mm^2) (Johansson, 1978). Merkel cells are located at the base of epidermal infoldings and adapt slowly to externally applied stimuli. Their afferent innervation arises from a disc below the cell and a single axon supplies several cells resulting in multiple receptive fields per afferent. Meissner corpuscles are located at the tip of dermal protrusions and they exhibit rapid adaptation to stimuli. Each corpuscle is innervated by two to nine afferent fibres each of which may innervate more than one corpuscle. Receptor densities are highest in the distal skin, with the digit tips containing 70 and 140 receptors/cm^2 for Merkel cells and Meissner corpuscles, respectively (Johansson, 1996).

The encapsulated Ruffini endings (SAII) and Pacinian corpuscles (FAII) are located within the deeper, dermal, layer of the skin. These receptors have large receptive fields (<25 cm^2) despite their typical 1:1 fibre-to-receptor ratio. Ruffini ending afferents terminate on collagen fibres which are fused with the dermal collagen. Receptive fields are often ill defined and oriented longitudinally in the limb. The Pacinian corpuslce is the largest of the cutaneous receptors (length 1–4 mm, diameter 0.5–1mm) and exhibits rapid adaptation to external stimuli. Innervation densities are typically lower and more uniform than for the receptors located in the more superficial layers (Johansson, 1996).

The hairy skin contains an additional type of receptor associated with guard hairs. These receptors are rapidly adapting and have large receptive fields (Munger & Martin, 1988). The role of these receptors in the control of movement has not been explored.

Two studies have examined the activity of cutaneous receptors in the human glabrous skin during natural hand movements. All type II units and 2/3 of type I units were activated by human voluntary movements (Hulliger *et al.*, 1979). Firing rates decreased as movement speed increased from 1-5 Hz. Eighty-seven percent of FA units responded during both flexion and extension. In contrast, 50% of SA units had unidirectional firing. Only type SAII units displayed tonic firing in the relaxed hand. A static response to joint position was observed in 81% of SAII units and 17% of SAI units. The authors estimated that FAII units were most responsive to movements and FAI units were the least responsive and that SAII units provided the best signals from which to determine movement direction (Hulliger *et al.*, 1979). This conclusion regarding SAII activity was also reached by Burke et al. (1988). They observed that most SA units were activated by movement, 2/3 of these with a directional specificity. However, the rest fired at extremes of both flexion and extension (Burke *et al.*, 1988). Many of the FA units were highly sensitive to small movements and though they lacked directional and angular specificity they may serve as peripheral timing markers (Hulliger *et al.*, 1979; Burke *et al.*, 1988).

Recent attention has focused on receptors located in the hairy skin on the dorsum of the hand (Edin, 1992; Edin & Abbs, 1991). SA units discharged during flexion and reduced firing during extension. Many of these units were responsive to movement at

only one joint, others were activated by movement at two or more joints. Some of the units exhibited complex firing patterns which may be accounted for by the uneven skin strain patterns observed during finger movements (video of skin strain patterns: B.B.Edin, personnel communication). SAII units were as sensitive to metacarpophalangeal joint movement as were muscle spindle primary endings (Grill & Hallett, 1995; Edin, 1992). In contrast to signals from joint and spindle receptors, cutaneous receptor activity is not altered between active and passive movements and may therefore provide a less ambiguous signal about joint position.

Cutaneous activity during human grasping movements has been well documented (Westling & Johansson, 1987; Johansson & Westling, 1991). Distinct bursts of activity are observed at each phase transition. Upon contact with the target object responses are seen in SAI and FAII units, but the most consistent signals are from FAI units. It has been estimated that at low grip forces approximately 300 FAI and 150 SAI units are engaged at each digit and when the object is lifted off or contacts the table 500 FAII units in each digit may become active (Westling & Johansson, 1987). Afferent discharges during slips of an object held in the fingers include brief bursts of activity from FA and SAI units (Westling & Johansson, 1987; Johansson & Westling, 1987; Macefield *et al.*, 1996). Tactile receptors in the digits also provide feedback about the frictional characteristics of a held object (Johansson & Westling, 1987; Edin, 1992; Johansson & Westling, 1987). Stronger responses are seen in FAI units as the surface becomes more slippery (Johansson & Westling, 1987; Edin, 1992) and this is not dependent on surface texture (Cadoret & Smith, 1996).

1.1.3 Joint Receptors

Despite our understanding of the morphology of the receptors located in the joints, relatively little is known of their functional significance. Four classes of joint receptors have been identified which bear a morphological resemblance to some of the receptors located in the skin and tendons.

The Ruffini endings are thinly encapsulated globular corpuscles usually found in groups of 2–6, all of which share one myelinated axon. They adapt slowly and have a low threshold to mechanical stimuli. These receptors may account for much of the joint receptor activity throughout the mid-range of joint motion. The conically shaped Pacinian corpuslces are thickly encapsulated, show rapid adaptation and have a low threshold to mechanical stress. These receptors become active during acceleration and deceleration of the joint. The GTO-like endings are the largest of the articular receptors. They are thinly encapsulated and fusiform in shape. These endings are slowly adapting, have a high threshold and are inactive in the immobile joint. Free nerve endings are widely distributed throughout most articular tissues. They become active when subjected to abnormal mechanical stress or chemical agents and are believed to function in a nociceptive role.

There are relatively few published reports of joint afferent activity in freely moving mammals. This may be due in part to difficulties in receptor identification. Acute afferent recordings from the cat knee (Burgess & Clark, 1969; Clark & Burgess, 1975; Ferrell, 1980), elbow (Millar, 1975) and wrist (Tracey, 1979) indicate that most receptors fire at or near the extremes of joint rotation. After removal of the popliteus muscle, to remove most muscle spindle inputs, Ferrell (1980) found 18% of the remaining afferents discharged in the mid-range of joint rotation and increased activity toward one extreme. Thirty-three percent of joint receptors recorded from the human median and ulnar nerves had background discharge which did not change until the joint was placed in hyperflexion or hyperextension (Burke *et al.*, 1988). Half of the articular receptors in these nerves discharged bi-directionally (Burke *et al.*, 1988). Many joint receptors in the superficial radial nerve fired at both extremes of movement (Edin, 1990).

Joint receptor activity depends on the forces applied to the joint. Background firing increases with actively or passively applied force (Grigg & Greenspan, 1977). Tonic muscular contraction increases the angular range over which receptors respond to passive movement (Grigg & Greenspan, 1977). During active thumb movements joint afferents in that digit responded in extension; during passive movements the same receptors were active in flexion (Edin, 1990). It has been suggested that this contraction

dependent firing may represent a type efferent of control over the receptor activity similar to the fusimotor control of the muscle spindle (Grigg & Greenspan, 1977).

1.2 Neural Pathways for Afferent Signals

As well as an understanding of receptor structure and activity, functional interpretations must also be based on knowledge of the neural pathways followed by the afferent signals. The following sections describe the segmental (1.2.1) and supraspinal (1.2.2) somatosensory pathways of the upper limb.

1.2.1 Segmental Pathways

Afferent information reaches the spinal cord from the periphery through the dorsal roots. The site of termination in the cord is dependent on the fibre diameter; large afferents enter more medially and descend deeper into the gray matter before making synapses. Therefore, lamina I and the dorsal aspect of lamina II receive input from the smallest myelinated fibres arising from mechanosensitive receptors located in the skin (Brown, 1981). Laminae II-VI receive the fibres of intermediate diameter and the large, group I, muscle afferents terminate in lamina V and deeper (Brown, 1981).

Ia afferents enter the spinal cord and bifurcate into ascending and descending branches which travel in the dorsal columns (Brown, 1981). These axons send off several collaterals which descend into the dorsal horn (laminae VI, VII and IX). These terminations exert two major segmental effects on spinal motoneurons. 1. Monosynaptic and polysynaptic excitation to homonymous and heteronymous motoneurons. These connections are quite widespread in both the cat (Fritz *et al.*, 1989) and baboon forelimb (Clough & Sheridan, 1968). Interestingly, in the baboon forelimb heteronymous EPSPs can be considerably larger than homonymous EPSPs (Baldiserra *et al.*, 1981). 2. Disynaptic inhibition of antagonist motoneurons. This "reciprocal inhibition" is mediated via the Ia inhibitory interneuron located in laminae VII (Jankowska & Lindstrom, 1972). This interneuron receives extensive convergence from descending tracts, other afferent

sources, Renshaw cells and Ia inhibitory interneurons of antagonist muscles. Most of these inputs also send excitatory collaterals to agonist α- and γ-motoneurons. This results in simultaneous α-γ coactivation and reciprocal inhibition of antagonists.

The termination patterns of Group II spindle afferents tend to be more variable. Upon reaching the spinal cord they bifurcate and send collaterals to laminae IV–VII and IX (Brown, 1981). Group II afferents mediate disynaptic excitation of flexors (via interneurons located in ventral laminae VII) and trisynaptic inhibition of extensors (Lundberg *et al.*, 1987).

Afferents from GTOs tend to have a relatively restricted pattern of termination. The main area of termination is in laminae V-VII (Brown, 1981). These inputs are classically thought disynaptically to inhibit homonymous and synergistic motoneurons and di- or trisynaptically to excite antagonistic motoneurons (Laporte & Lloyd, 1952). However, evidence has accumulated that during locomotion in the cat hindlimb this inhibition switches to excitation (Conway *et al.*, 1987; Pearson & Collins, 1993). Like Ia inhibitory interneurons, interneurons interposed in Ib pathways receive extensive convergence from several descending and peripheral sources. Feedback from cutaneous afferents tends to facilitate both the excitatory and inhibitory effects of Ib afferents and this facilitation appears to be stronger in the forelimb than the hindlimb (Illert *et al.*, 1976).

Reflex pathways from joint afferents have primarily been studied in the cat knee joint. Inflammation of that joint, known to selectively excite Ruffini endings, characteristically evokes excitation of extensor and inhibition of flexor α-motoneurons. Joint afferents may exert their reflex effects on α-motoneurons via their interactions with pathways from other afferent populations and have more direct influence on the γ-motoneuron system (Johansson *et al.*, 1991). Joint afferent input influences activity in γ-motoneurons more frequently than α-motoneurons when electrical (Eccles & Lundberg, 1959; Johansson *et al.*, 1986), mechanical (He *et al.*, 1988) or traction force (Johansson *et al.*, 1990) type stimuli are applied to knee joint receptors. Responses in α-motoneurons were only observed with high intensity stimuli which may have recruited some nociceptive receptors (Solomonow *et al.*, 1987).

Unlike hindlimb afferents, forelimb afferents can also exert segmental effects via terminations on propriospinal neurons located in the C3-C4 spinal cord segments. This system has been well described in the cat (Illert *et al.*, 1977; Illert & Tanaka, 1978; Petterson, 1990). There is indirect evidence to support its presence in man (Pierrot-Deseilligny, 1996), though attempts to obtain direct evidence in the monkey have been unsuccessful (Maier *et al.*, 1998). These propriospinal neurons receive direct projections from cortico-, rubro-, reticulo-, and tectospinal fibres and low threshold cutaneous and muscle afferents (Illert *et al.*, 1978). They also receive di-synaptic inhibition from supraspinal and peripheral sources (Alstermark *et al.*, 1984; Illert *et al.*, 1978). The feedback inhibition from forelimb afferents is facilitated by corticospinal inputs. After bifurcation the descending axonal branch projects to motoneurons and Ia inhibitory interneurons in the forelimb segments. A single propriospinal neuron may project to many motor nuclei, even those acting at several joints (Alstermark *et al.*, 1990). This descending branch also excites long propriospinal cells which project to lumbar segments (Alstermark *et al.*, 1987). The ascending collateral projects to the lateral reticular nucleus (Illert & Lundberg, 1978) and may provide a type of efference copy (Pierrot-Deseilligny, 1996). Behavioral experiments have revealed that this system is involved in production of coordinated synergies which underlie reaching movements (Illert *et al.*, 1977; Illert & Tanaka, 1978; Petterson, 1990).

1.2.2 Supraspinal Pathways

This section outlines the ascending pathways for afferent information with particular attention on pathways to the somatosensory cortex and cerebellum, two areas prominent in theories regarding the control of movement.

The main route for somatosensory inputs to the cerebral cortex is the dorsal column-medial lemniscal pathway (Norton, 1969). The dorsal columns contain first and second order neurons, propriospinal axons and some descending axons. The ascending fibres are somatotopically organized; afferent information from the leg travels in the fasciculus gracilus and from the arm, more laterally, in the fasciculus cuneatus. These

tracts terminate in their respective dorsal column nuclei. From there fibres maintain their somatotopic organization and travel in the medial lemniscus, decussate in the medulla, and terminate in the ventroposterior lateral (VPL) nucleus of the thalamus (Norton, 1969).

Apart from the dorsal column system the main ascending tracts arise from cells in specific laminae. The spinothalamic tract arises from neurons in the dorsal and intermediate laminae of the spinal cord whose axons cross at the segmental level and ascend in the contralateral ventrolateral funiculus. In the cervical cord cells of origin reside in laminae I and IV–VI. This pathway transmits intense mechanical or painful heat stimuli (from lamina I), light tactile and intense noxious stimuli and also inputs from muscle and joint afferents. Ascending fibres pass through the medulla and pons dorsal to the lemniscal fibres, send collaterals to the reticular formation, and terminate in VPL of the thalamus.

Most lemniscal fibres terminate in the caudal portion of the VPL in the thalamus. Spinothalamic fibres generally terminate at the border of VPL and VL. Generally cells in the thalamus are responsive to only one modality. Cells in the rostral and caudal portions of the VPL receive inputs from deep receptors (joint and muscle). The central portion receives cutaneous inputs. The somatotopic organization of inputs to the VPL ensures that these cells are generally responsive to one modality from a specific part of the body.

After the thalamus neurons project through the internal capsule to the primary somatosensory cortex (S1). This region comprises four cytoarchitectonic zones (from rostral to caudal: 3a, 3b, 1 and 2). Throughout S1 cells are organized in vertical columns with similar receptive fields and modality specificity. Each cytoarchitectonic zone contains a complete topographic representation of the contralateral half of the body, with the head lateral and foot medial (Kaas *et al.*, 1979). The largest cortical areas are devoted to the hand and perioral region reflecting the density of the peripheral innervation (Penfield & Rasmussen, 1950). Areas 3b and 1 receive primarily tactile inputs while areas 3a and 2 receive primarily proprioceptive inputs (Iwamura *et al.*, 1985). One exception is the hand region of area 2 which receives primarily tactile inputs (Iwamura *et al.*, 1985). Of the four cytoarchitectonic zones area 3b contains the smallest receptive

fields and is the only one with receptive fields segregated into those with inputs from either rapidly or slowly adapting cutaneous receptors (Sur *et al.*, 1984). Cells in area 3b exhibit relatively simple responses to external stimuli and response complexity generally increases in a rostro-caudal gradient with the most complex responses recorded most caudally in area 2 (Chapman *et al.*, 1996).

Afferent signals from the forelimb reach the cerebellum via two major tracts. Muscle and cutaneous input ascends ipsilaterally in the cuneocerebellar tract and terminates in the external and main cuneate dorsal column nuclei, respectively (Oscarson, 1965). This tract has a hindlimb analogue in the dorsal spinocerebellar tract. Most cuneocerebellar tract fibres terminate in the ipsilateral cerebellar cortex though some travel to the VPL of the contralateral thalamus. Inputs from flexor reflex type afferents cross the midline to ascend in the rostral spinocerebellar tract. The hindlimb analogue of this tract is the ventral spinocerebellar tract. Cells in the rostral spinocerebellar tract generally have wide receptive fields with extensive convergence between muscle and cutaneous afferents. This tract receives input from several descending systems and collaterals from many of the inputs to α-motoneurons.

1.3 Roles for Afferent Signals During Upper Limb Movement

Over the years a sound understanding of the sensory receptors and their neural pathways has developed. This has lead to ideas regarding the functional roles for afferent feedback during arm movements. The following two sections discuss these roles as they pertain to grasping and kinesthesia. The final section reviews the literature on the gating of ascending pathways.

1.3.1 Grasp

During human grasp, distinct activity patterns are observed in tactile afferents upon contact with the target object (see section 1.1.2). Once contact has been established grip force (perpendicular to the object surface), and load force (parallel to the object

surface), increase in parallel until the load force overcomes the weight of the object and it is lifted from the surface (Westling & Johansson, 1984; Johansson & Westling, 1984). This parallel increase in forces is delayed during digital anesthesia, suggesting that it is initiated by the tactile afferent activity (Johansson & Westling, 1984; Westling & Johansson, 1984). The specific contribution made by the afferent contact signal to subsequent EMG activity has been studied in our laboratory and is the topic of Chapter 5. Afferent feedback also provides information about the frictional characteristics of the object surface. This information is used to ensure that an adequate "safety margin" is maintained between grip force and load force to prevent unwanted slips (Westling & Johansson, 1984; Johansson & Westling, 1984). Unanticipated changes in the frictional characteristics at individual digit tips reveal that the regulation of grip force is adjusted separately for each digit (Edin, 1992).

A similar reliance on afferent feedback underlies the termination of grip forces at the end of grasp. When subjects replace an object on a table without the aid of vision changes in EMG activity appeared to be triggered by the afferent signals indicating that contact had been made (Johansson & Westling, 1988a). This reliance on the afferent signal became more clear in trials in which the height of the table was unexpectedly raised or lowered. After table contact was established EMG activity decreased 60-70 ms and 40-50 ms in the intrinsic and extrinsic hand muscles, respectively (Johansson & Westling, 1988a). During trials in which the support surface was within the subjects view, release of the muscle command appeared to be more anticipatory, though clear triggered responses were also observed (Johansson & Westling, 1988a).

The role of afferent feedback in compensating for unexpected slips of a held object has also been extensively studied. Experimentally induced slips evoke bursts of EMG activity at latencies of 35–40 ms in proximal muscles and 55–65 ms in distal muscles (Johansson & Westling, 1988b). Compensatory increases in grip force are observed at latencies of 60–90 ms (Cole & Abbs, 1988). The amplitude of grip force adjustment was scaled to the load application (Cole & Abbs, 1988; Johansson *et al.*, 1992a) and the latency decreased as the rate of load force increased (Johansson *et al.*, 1992b). These adjustments are believed to be dependent on characteristic bursts in

cutaneous afferents as they were usually, but not always, abolished during anesthesia of the involved digits (Cole & Abbs, 1988; Johansson *et al.*, 1992c). In a recent series of experiments 20% of the SA units and 50% of the FAIs responded to slips at latencies suitable to initiate the compensatory responses (Macefield *et al.*, 1996). In contrast, afferent responses recorded from joint, spindle and GTO afferents occurred after the grip force adjustments, clearly too late to be involved (Macefield & Johansson, 1996). Cutaneous receptors remote to the digits can also contribute to grip force adjustments (Hager-Ross & Johansson, 1996). This may account for the fact that grip adjustments were not always abolished in the studies using digital anesthesia (Cole & Abbs, 1988; Johansson *et al.*, 1992c). These slip adjustments can be mimicked by electrical stimulation of finger tips (Johansson & Westling, 1987). Interestingly, only very weak, single pulse and unanticipated stimuli were effective (Johansson & Westling, 1987).

Less attention has been paid to potential roles for inputs from muscle receptors in the regulation of human grasp. Several studies have examined the excitability of stretch reflexes in hand and arm muscles between tasks in which subjects were required to maintain position versus maintain force. In all cases reflexes were larger for the maintain position task than for maintenance of force (Akazawa *et al.*, 1983; Doemges & Rack, 1992a; Doemges & Rack, 1992b; Kanosue *et al.*, 1983). The excitability of reflex pathways mediated by muscle spindle afferents has also been tested prior to the onset of a grasping movement (Cole & Abbs, 1987). Small amplitude stretches were delivered to the thumb from 0-125 ms before movement onset. Response amplitudes decreased in three of the four muscles studied as loads were delivered closer to the onset of the movement. The authors concluded that afferent input prior to grasp onset initiated appropriate kinematic changes in the trajectory of the tip of the index finger to result in successful completion of the task (Cole & Abbs, 1987). Proprioceptive feedback has also been shown to be involved in triggering hand opening during a throwing task (Cordo *et al.*, 1994). A recent study has shown that stretch reflexes are also attenuated during thumb movements, compared to stationary control trials (Wallace & Miles, 1998). However, the increased amplitude of stretch reflexes when subjects held their hand next to a glass, compared to control trials (Traub *et al.*, 1980), suggests that the gain of these

pathways may be increased during functional grasp tasks. We have performed a series of experiments comparing stretch reflex amplitudes in three hand muscles during grasping tasks to those from stationary trials. These experiments are described in Chapter 6.

1.3.2. Kinesthesia

Kinesthesia describes our ability to determine the position and movements of our body segments without the aid of visual feedback. Kinesthetic signals may arise from corollary discharges of the descending command to move (Helmholtz, 1867; Sperry, 1950) or peripheral feedback from the moving segments (Sherrington, 1900). The following section describes the evidence which has mounted to support the latter source.

During the 1950s and 1960s a major kinesthetic role was assigned to receptors located in the joints, primarily based on studies suggesting that their firing profiles were ideal to signal joint position (Boyd & Roberts, 1953). Subsequently, joint receptors fell out of favor when it was found that only a few joint receptors fire over the full range of motion (Burgess & Clark, 1969; Ferrell, 1980). Since then, the evidence has mounted to support the theory that muscle spindles play a dominant role in our kinesthetic sensibility. The main impetus for this shift in thinking was the finding that vibration, which selectively excites the primary ending of the muscle spindle, can create powerful illusions of movement (Goodwin *et al.*, 1972; Eklund, 1972). Subsequent experiments supported this idea. The velocity of illusory movements increases with increasing vibration frequency (Goodwin *et al.*, 1972; Roll *et al.*, 1989; Roll & Vedel, 1982). The effect can be very powerful resulting in illusions of impossible positions (Craske, 1977). Vibration of the biceps tendon (to mimic elbow extension) while the finger is touching the nose results in the illusion that the nose elongates (Lackner, 1988). Vibration of the arm in the dark results in the illusion of movement of a light held in the hand (Dizio *et al.*, 1993). Vibration of one limb during bilateral matching tasks results in errors in position consistent with the spindle feedback from the vibrated limb (Capaday & Cooke, 1981; Gilhodes *et al.*, 1986). However, microstimulation of single muscle spindle afferent fibres does not or rarely evokes illusions of movement (Macefield *et al.*, 1990), a fact thought to indicate that spatial summation of spindle input is required in order to be perceived.

Several studies have taken advantage of an anatomical peculiarity whereby flexion of the middle finger accompanied by extension of the surrounding ones disengages the muscular insertions distal to the proximal interphalangeal joint of digit III. In this way contributions from muscle receptors can be isolated from cutaneous and joint afferents (Clark *et al.*, 1989; Ferrell *et al.*, 1987; Gandevia *et al.*, 1983; Gandevia & McCloskey, 1976; Gilhodes *et al.*, 1986; Hall & McCloskey, 1983). These studies suggested a dominant role for spindle inputs and a less important or facilitatory role for receptors located in joints and skin.

Investigations of the kinesthetic properties of muscle receptors have often overshadowed potential roles for cutaneous receptors. However, several lines of evidence indicate that cutaneous receptors may be just as important. Their impulses reach the sensori-motor cortex at short latencies (Mountcastle, 1957), similar to the group I afferents (Oscarson & Rosen, 1963). Also, the activity patterns of some cutaneous receptors are sufficient to provide detailed proprioceptive information about joint position and movement (Edin & Abbs, 1991; Edin, 1992) which may be just as reliable as that from muscle spindles (Grill & Hallett, 1995). However, the fact that cutaneous receptors provide signals which are appropriate to mediate kinesthetic sensations does not indicate that they are used by the CNS in this way. Two studies have investigated illusory movements evoked by stimulation of non-muscle afferents. Stimulation of digital nerves produced an illusory twisting or oscillation of the fingers (Gandevia, 1985). In contrast, stimulation of the superficial radial nerve created an illusion of "smooth flexion, akin to a grasp" (Gandevia, 1995). However both these nerves contain joint and cutaneous afferents. Study of illusory movements arising from solely cutaneous inputs has been conducted in two laboratories. Edin (Edin & Johansson, 1995) was able to evoke illusory finger movements by physically stretching the skin around the index finger metacarpophalangeal joint. However, there remained some question as to the selectivity of the stimulation and the resultant illusory movements were poorly quantified. In our laboratory, we independently developed a skin stretch technique and an electrical stimulation technique to recruit ensembles of cutaneous afferents and accurately

quantified the resulting illusory movements. The results of this work are presented in Chapter 3.

Microstimulation of single cutaneous afferents creates tactile sensations consistent with the receptor type stimulated. Stimulation of FAI units resulted in sensations of tap, flutter or vibration. FAII unit stimulation evoked sensations of tickle or vibration. Local pressure or indentation was perceived upon stimulation of SAI units. No tactile perceptions were evoked when SAII units were stimulated; however, movement illusions were sometimes evoked (Macefield *et al.*, 1990; Ochoa & Torebjork, 1983; Schady & Torebjork, 1983; Vallbo, 1981).

1.3.3. Gating of Ascending Signals

The previous section revealed the importance of ascending afferent signals to our kinesthetic sensibility. Studies of how these signals are gated en route to the cerebral cortex have attempted to shed some further light on the function of this afferent input. Considering the roles ascribed to ascending afferent signals, one might expect that transmission to the cortex is retained or even augmented during movement. However, it is becoming clear that this is not the case.

The transmission of cutaneous inputs to the cortex is suppressed during movement in cats (Ghez & Pisa, 1972) monkeys (Chapman *et al.*, 1988; Jiang *et al.*, 1990b) and humans (Angel & Malenka, 1982; Coquery, 1978; Rushton *et al.*, 1981). This is evident in recordings of single cells (Chapman *et al.*, 1988; Jiang *et al.*, 1990a), ensemble neuronal discharges (Ghez & Pisa, 1972; Chapman *et al.*, 1988), evoked potentials (Rushton *et al.*, 1981) and subjective reports (Angel & Malenka, 1982). The characteristics and sources of this suppression have been examined in some detail.

Active finger movement attenuates the amplitude of cutaneous somatosensory evoked potentials (SEPs) in humans to about 50% of those recorded during stationary controls. This attenuation increases with increasing movement velocity (Angel & Malenka, 1982) and is specific to the finger being moved. It is largest when the stimulus is delivered to the moving finger and is reduced when stationary fingers adjacent to the

moving finger are stimulated (Tapia *et al.*, 1987). No attenuation is observed when digits further away on the ipsilateral hand or digits on the contralateral side are stimulated (Tapia *et al.*, 1987; Rushton *et al.*, 1981).

Experiments in monkeys trained to perform voluntary elbow flexion movements recorded from medial lemniscus, VPL and S1 reveal that the signal gets increasingly attenuated as it ascends the dorsal column medial lemniscal pathway, beginning at the dorsal column nuclei, through the thalamus to become most attenuated at S1 (Chapman *et al.*, 1996).

There is clear evidence that both central and peripheral sources contribute to the attenuation. However, the extent of each contribution during natural movements is still a matter of debate. Evidence for a central origin comes from several sources. Volleys recorded at the medial lemniscus in monkeys are larger during passive movements than during comparable active movements, suggesting an increased attenuation at the dorsal column nuclei associated with the central command to move (Chapman *et al.*, 1988). In humans, differences between active and passive movements are less clear. The observation that the attenuation begins before movement onset provides strong evidence for a central origin as this occurs before peripheral sources can contribute (Coquery, 1978; Dyhre-Poulsen, 1975; Starr & Cohen, 1985). In monkeys the time course of attenuation is similar from the dorsal column nuclei to the S1 beginning about 60–80 ms before movement onset (Chapman *et al.*, 1988). The motor cortex may be a major source of the attenuation since intracortical microstimulation within area 4 diminishes the amplitude of S1 cortical SEPs (Jiang *et al.*, 1990a).

There is also clear evidence that peripheral sources contribute. In humans (Rushton *et al.*, 1981; Jones *et al.*, 1989; Huttunen & Homberg, 1991; Milne *et al.*, 1988) and monkeys (Chapman *et al.*, 1988) passive movements decrease the amplitude of response in S1 to the same extent as active movements. The attenuation during passive movements provides strong evidence for a peripheral contribution. Further, perceived intensity of stimuli delivered to the index finger is reduced by non-noxious stimulation of the ipsilateral thumb or little finger (Milne *et al.*, 1988). Detection thresholds are also increased during stimulation of adjacent areas of skin (Ferrington *et al.*, 1977; Martin *et*

al., 1985). The contribution from muscle contraction is unclear. During a tonic voluntary contraction in humans SEPs were not suppressed (Dimitrov *et al.*, 1989), however in a different study the conscious perception of the stimuli was (Milne *et al.*, 1988). During the dynamic phase of an isometric contraction in monkeys equally powerful suppression of responses in single cells in areas 1 and 3a was observed (Jiang *et al.*, 1990b). The attenuation is also independent of movement direction. It was just as powerful during flexion as during extension of the elbow as recorded from SEPs and single units in areas 3b and 1 (Jiang *et al.*, 1990b; Jiang *et al.*, 1991).

Several studies have investigated whether the amount of attenuation is dependent on the relevancy of the stimulus to the task. During a vibrotactile discrimination task cells in S1 were more responsive to stimuli during the task (when they were relevant) than when the same stimuli were delivered outside the task (Hyvarinen *et al.*, 1980). A similar dependence on stimulus relevance was shown when cells in areas 3b and 1 showed larger responses when the fingers were scanned over embossed letters when the animals were attending to them than when they were not (Hsiao *et al.*, 1993). These two studies used stimuli that were passively applied to the immobile hand. The gating of behaviorally relevant inputs has also been studied during movement. A proportion of the neurons in area 1 failed to discharge during the movement when the input was no longer behaviorally relevant (Ageranioti-Belanger & Chapman, 1992; Chapman & Ageranioti-Belanger, 1991).

There is also some evidence that further processing occurs after the signals reach S1. Cells in area 3b generally discharged when their receptive field was stimulated regardless of the relevance of the stimuli. However, the frequency of responses to relevant inputs increased and to irrelevant ones decreased as cells were located in regions progressively more caudal in S1 (Chapman *et al.*, 1996). Results suggest that even behaviorally relevant inputs are gated during movements but to a lesser extent than irrelevant inputs. Also, there is a further processing in the cortex with relevant input being passed on and irrelevant ones not.

Several studies have investigated the gating of SEPs arising from muscle receptors from the hand during movement in humans (Abbruzzese *et al.*, 1981; Cheron &

Borenstein, 1987; Huttunen & Homberg, 1991; Jones *et al.*, 1989; Tapia *et al.*, 1987). SEPs were attenuated to the same extent during active and passive movements of the fingers (Abbruzzese *et al.*, 1981; Huttunen & Homberg, 1991; Jones *et al.*, 1989). Ischaemic blockade of the group I afferents from the hand eliminated the attenuation in one study suggesting an important contribution from peripheral sources (Abbruzzese *et al.*, 1981). However, another study showed attenuation at the onset of active but not passive movement, before afferent feedback could contribute, suggesting a contribution from descending sources (Jones *et al.*, 1989). The similar attenuation observed during passive and exploratory movements suggested that the modification of SEPs is not dependent on the importance of proprioceptive feedback to the task (Huttunen & Homberg, 1991). However, SEPs from median nerve stimulation were attenuated by simple hand movements but during passive tactile stimulation a negative wave appeared at 28 ms which became most pronounced during active exploratory movements (Knecht *et al.*, 1993). A similar task dependent gating has been recently documented during tracking movements with the feet suggesting that the cortex does alter the gating according to proprioceptive requirements (Staines *et al.*, 1997). Further evidence for a central contribution was provided in this study as SEPs were depressed 100 ms prior to the onset of plantarflexion. Similar to the gating of cutaneous SEPs, SEPs from muscle inputs are also dependent on the area stimulated. SEPs from median nerve stimulation were most attenuated during movement of the thumb and were not affected by movement of the little finger. Opposite effects were observed for ulnar nerve SEPs (Tapia *et al.*, 1987).

The movement-induced attenuation of the ability to detect cutaneous stimuli and of the amplitude of SEPs from both muscle and cutaneous receptors has been established. However, the corresponding studies investigating the subjective intensity of inputs from muscle receptors during movement have not been conducted. The relationship between evoked potentials and conscious perception is unclear. Attenuation of SEPs does not necessarily indicate a similar gating of the conscious perception of the stimuli. We have completed the first series of experiments investigating our ability to detect inputs from muscle receptors during movements. These are described in Chapter 4.

In hindsight, considering the immense amount of afferent activity generated during movement, and the fact that under static conditions a single action potential from the periphery can reach consciousness, it is not surprising that the CNS limits the amount of information reaching higher centres during movement. This gating appears to permit the CNS to attend to the relevant ascending signals and occurs at every level along the ascending pathway. The extent to which central and peripheral sources contribute to this gating is still under investigation and probably depends on the task.

1.4 Thesis Objectives

The main objective of this thesis was to investigate how sensory information is utilized by the CNS in the neural control of the upper limb. Sites used for recording EMG activity from the various muscles of the upper limb are shown in Figure 1-1. The five projects that were conducted are described in Chapters 2-6. The specific objectives for each project are outlined below.

Chapter 2. The first objective was to develop a technique to obtain stable afferent recordings from forelimb afferents in freely moving cats and use it to characterize the activity patterns during various unrestrained movements including reaching and manipulative tasks. These would be the first such recordings in any species. The results would help resolve issues regarding species differences in afferent firing rates and the fusimotor control of spindle sensitivity.

Chapter 3. In this study we quantified illusory movements evoked by selective stimulation of ensembles of cutaneous receptors on the dorsum of the hand. The effect of different patterns of stimulation on the illusory movements was examined. Also, these illusory movements were compared to those evoked by vibration in an attempt to compare the relative kinesthetic roles of cutaneous and muscle spindle input. The objective of these experiments was to provide evidence for an important role for skin receptors in kinesthesia.

Chapter 4. In this study we compared the ability to detect signals from muscle receptors during various tasks. The objective was to describe, for the first time, how our ability to consciously perceive these signals is altered by movement.

Chapter 5. These experiments investigated the role of afferent feedback during human grasp. The objective was to identify the contribution of the afferent "contact signal" to the generation of subsequent EMG activity and determine to what extent this was dependent on cutaneous receptors in the digits.

Chapter 6. These experiments investigated the excitability of stretch reflexes during grasping movements. The objectives were to determine whether these reflexes are attenuated during index finger flexion, compared to stationary controls, and to identify whether the movement-induced attenuation was task-dependent.

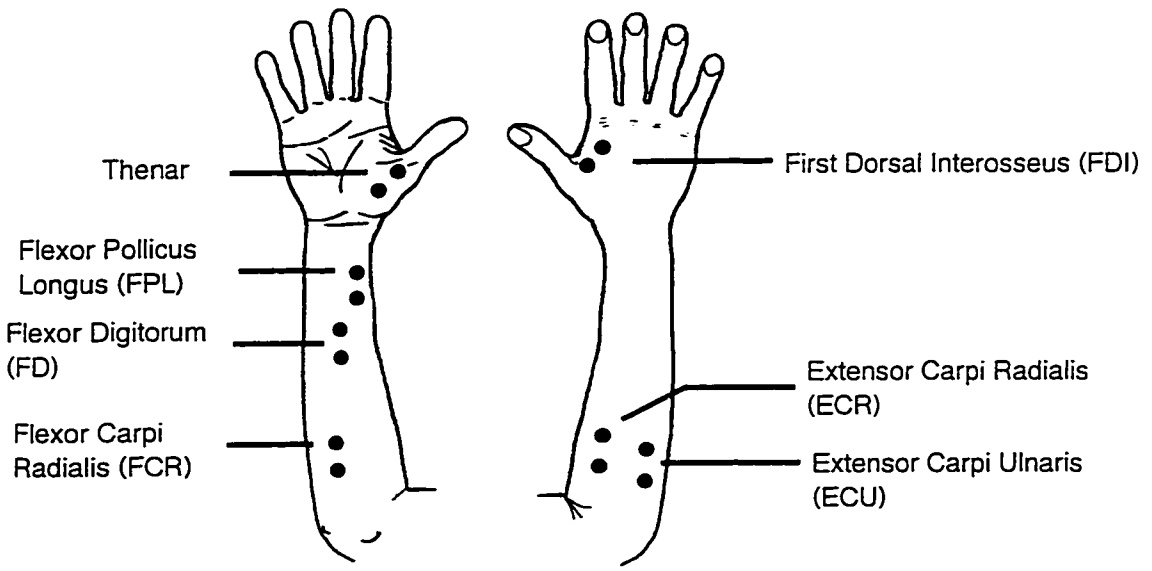

Figure 1-1. Placement sites for surface electrodes used for EMG recording.

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2.0 Forelimb Proprioceptors Recorded During Voluntary Movements in Cats*

2.1 Introduction

Most of our knowledge regarding proprioceptive activity in freely moving cats comes from recordings from hindlimb afferents. Currently, little is known about this activity in the forelimbs. One might speculate that this could be extrapolated from existing hindlimb data. Indeed, assuming similarities in receptor morphology and sensitivity, this may be true for receptors not under efferent control. However, there are several reasons to suspect that this extrapolation is less secure for the muscle spindle receptor; 1. The forelimb performs reaching and manipulative tasks requiring more supraspinal control than hindlimb movements (Pettersson, 1990), 2. Supraspinal sites branch more extensively to cervical regions (Kuypers & Martin, 1982), 3. Presumed spindle afferents in arm and hand muscles of monkeys generally had more complex firing characteristics than cat hindlimb spindles (Schieber & Thach, 1985), 4. There may be differences in spindle receptor morphology, as demonstrated between hindlimb and neck musculature (Dutia, 1991). A knowledge of spindle receptor firing patterns from the cat forelimb may also shed some light on the differences in firing rates in humans (peak approx. 85 imp/s) compared to cats (peak approx. 600 imp/s). We have therefore been developing a technique to obtain forelimb afferent recordings in awake cats.

Initially, we intended to implant electrodes into the cervical dorsal root ganglia, along similar lines to the lumbar hindlimb recordings (Prochazka et al., 1977). However, the lateral location of the ganglia and the large range of motion between the cervical vertebrae thwarted our attempts to obtain stable afferent recordings. Therefore, we modified the technique so as to record from the primary afferent fibres as they ascend the dorsal columns.

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* A version of this chapter has been published. Collins, Prochazka, Gorassini 1995. Alpha and Gamma Motor Systems, Eds. Taylor, A., Gladden, M.H., and Durbaba, R.: 586-588, New York, N.Y. Plenum. Approximately 70% of the work for this project was conducted by author DC.

2.2 Methods

Prior to implantation a flexible microwire loop was fabricated and attached to a cable of Cooner wires (AS632). During the surgical procedure the dorsal aspect of one side of vertebrae C2-C3 was exposed. The exposed C3 lamina was removed to provide access to the dorsal columns. Initial dissections revealed that the movement between the vertebrae and the spinal cord was the least at C2-3. The Cooner wire-microwire loop junction was anchored to the caudal aspect of C2 using dental acrylic and cyano-acrylate (Figure 2-1). The cable was led subcutaneously to a dental acrylic headpiece. The 25 mm loop was led down, and sutured to, the exposed dura at the rostral end of C3. Its flexibility allowed movement between vertebrae and spinal cord without dislodging the 6 microwire electrodes. The electrodes (17-μm diameter nickel-chrome, 8-12 mm long from point of suture to deinsulated, bevelled tip) were implanted into the fasciculus cuneatus region through a slit cut in the dura. Cats recovered over a 24 hour period. Length data were obtained via an external mercury-in-rubber length gauge mounted across the appropriate joint. EMG data were obtained via needle electrodes inserted into the receptor bearing muscle through a patch of skin anaesthetised with lidocaine cream.

Data collection sessions were videotaped and the three channels of telemetered data (EMG, length and afferent activity) were stored in frequency-modulated form on the stereo audio channels. Subsequent data analysis were performed by replaying the data and digitizing the relevant segments with a CED 1401 (Cambridge Electronic Design) interface and a microcomputer running customized software. EMG signals were rectified and filtered before digitization.

2.3 Results

Data have been obtained from forelimb and neck afferents in 3 cats. These recordings depend on a balance between a migration of the electrode tip to favourable positions near afferent axons and the maintenance of those positions long enough for data collection and unit identification. So far we have obtained periodic, stable recordings for

up to 6 weeks. In one case the same slowly-adapting skin receptor was recorded for over 3 weeks. It was located over the dorsal ridge of the scapula and was highly sensitive to skin stretch along a medial-lateral axis. Peak firing rates reached 500 imp/s with dynamic indices up to 200 imp/s. Over 3-4 consecutive stretches the dynamic indices dropped to about 50 imp/s, indicating a decline of the phasic component of response (see Figure 2-2).

Data has also been obtained from a Golgi tendon organ in the long head of triceps brachii, identified by suxamethonium and twitch tests. Peak firing rates during imposed ramp and hold stretches reached 150 imp/s. An average of 15 step cycles revealed that the receptor was active during the stance phase of locomotion with maximal discharge of 125 imp/s around foot contact, declining steadily to near zero around lift off (see Figure 2-3). This pattern was similar to that of tendon organs of the hindlimb, though more recordings are needed before firm conclusions can be drawn.

Some data have also been obtained from two units presumed to be of muscle spindle origin. One recording, from a receptor located in a flexor/adductor of the lateral toe and suspected to be a Ia afferent, had peak firing rates of 250 imp/s and a dynamic index of 150 imp/s during imposed ramp and hold stretches (see Figure 2-4). The second, from a receptor in the neck musculature which we suspect was a b2c or a group II afferent, was very length-sensitive and had relatively small dynamic components of response. This unit fired at rates up to 140 imp/s during sinusoidal imposed movements (see Figure 2-5).

2.4 Conclusions

We have developed a viable technique to obtain stable afferent recordings from cat forelimb via microelectrodes implanted into the cervical dorsal columns. Preliminary data reveal receptor firing rates similar to those in the cat hindlimb. In the future we intend to investigate the fusimotor control of the muscle spindle during movements such as reaching and manipulative tasks. We also intend to contribute to a further characterization of the activity of neck proprioceptors.

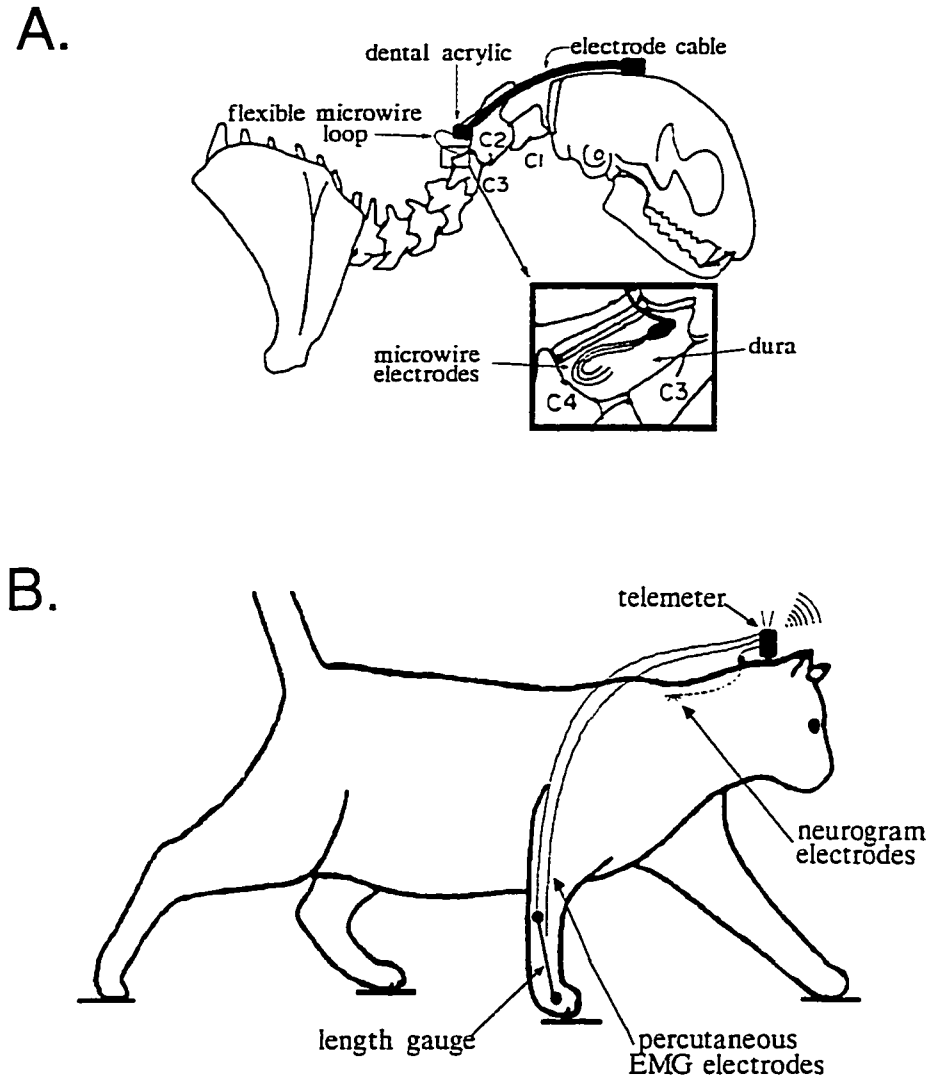

Figure 2-1. Diagram of the experimental paradigm.
A. Cat skeleton (adapted from Dutia, 1991) depicting method used for neurogram implant. B. Radio telemetry technique used for data acquisition.

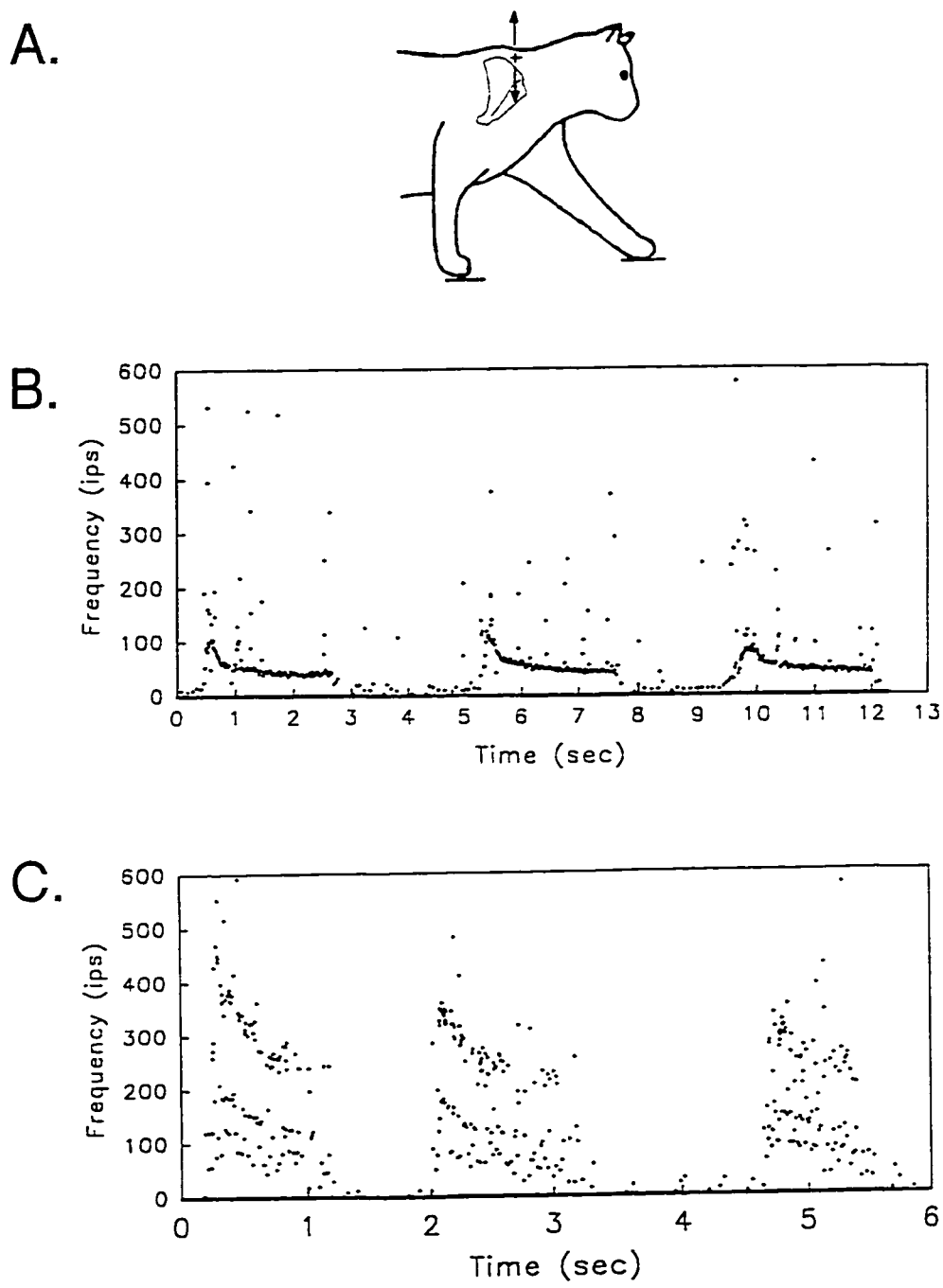

Figure 2-2. Activity of a slowly adapting cutaneous receptor.
A. Diagram showing receptor location and the direction of highest sensitivity to applied skin stretch. B. Receptor activity during pinch at receptor site. C. Receptor activity during skin stretch applied along the axis of highest receptor sensitivity as shown in A.

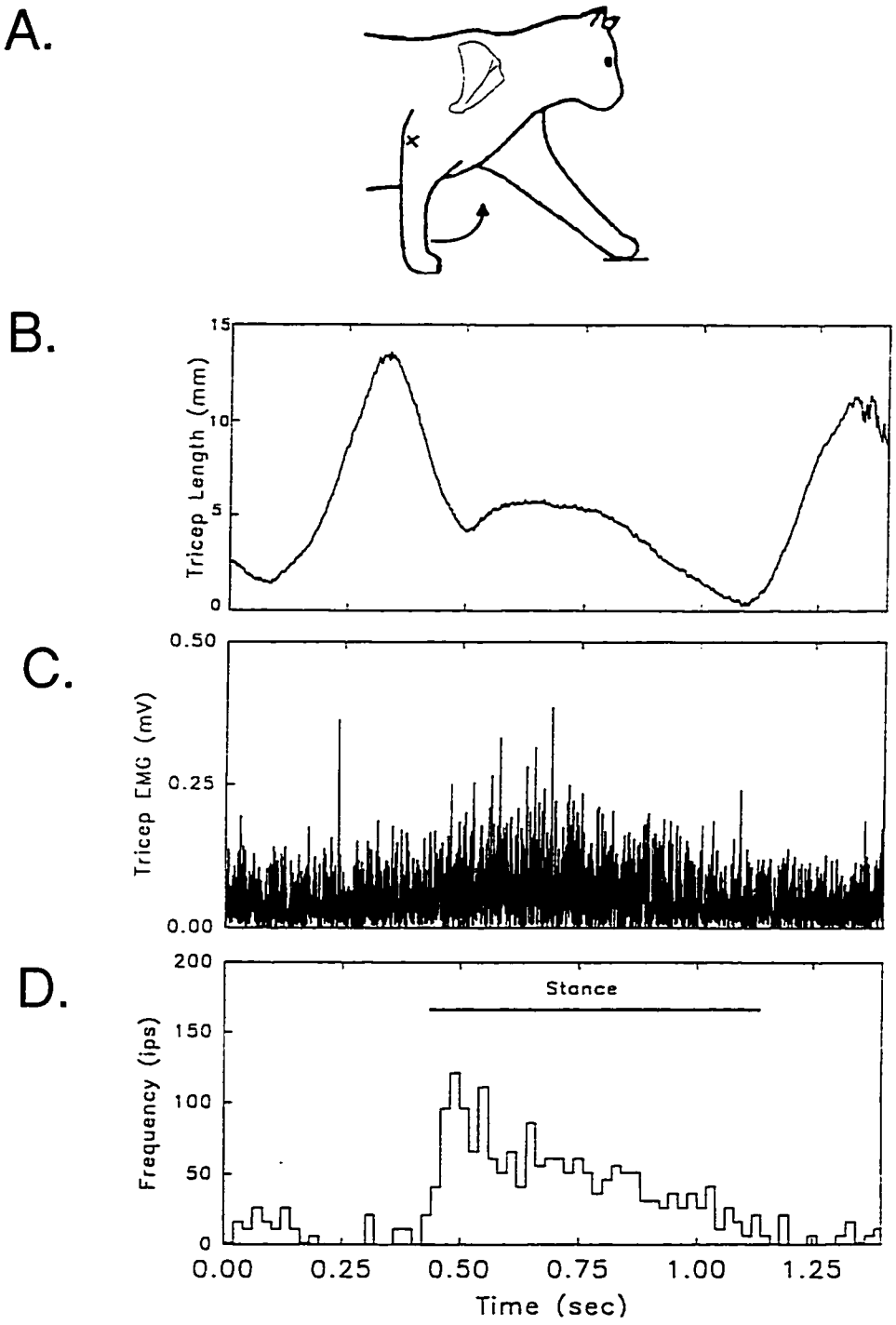

Figure 2-3. Mean activity of an identified Golgi tendon organ.
Data were averaged over 15 cycles of locomotion. A. Diagram showing receptor location in the long head of the triceps and the movement direction to best recruit the receptor. B. Mean length changes in the host muscle. C. Mean EMG activity recorded from the host muscle. D. Mean receptor activity averaged over one cycle of locomotion (20 ms bins).

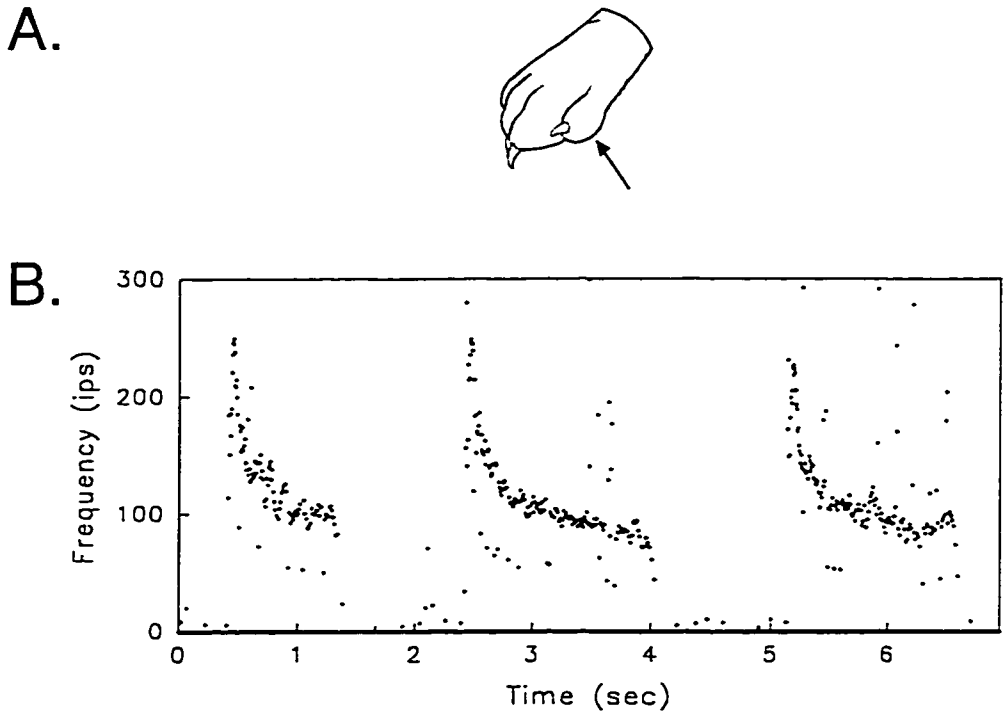

Figure 2-4. Activity of a suspected Ia afferent.
The receptor was located in a flexor/abductor of the lateral toe. A. Diagram showing the movement direction which evoked the highest firing rates in response to imposed ramp and hold stretches. B. Receptor activity during an imposed ramp and hold stretch along preferred direction as in A.

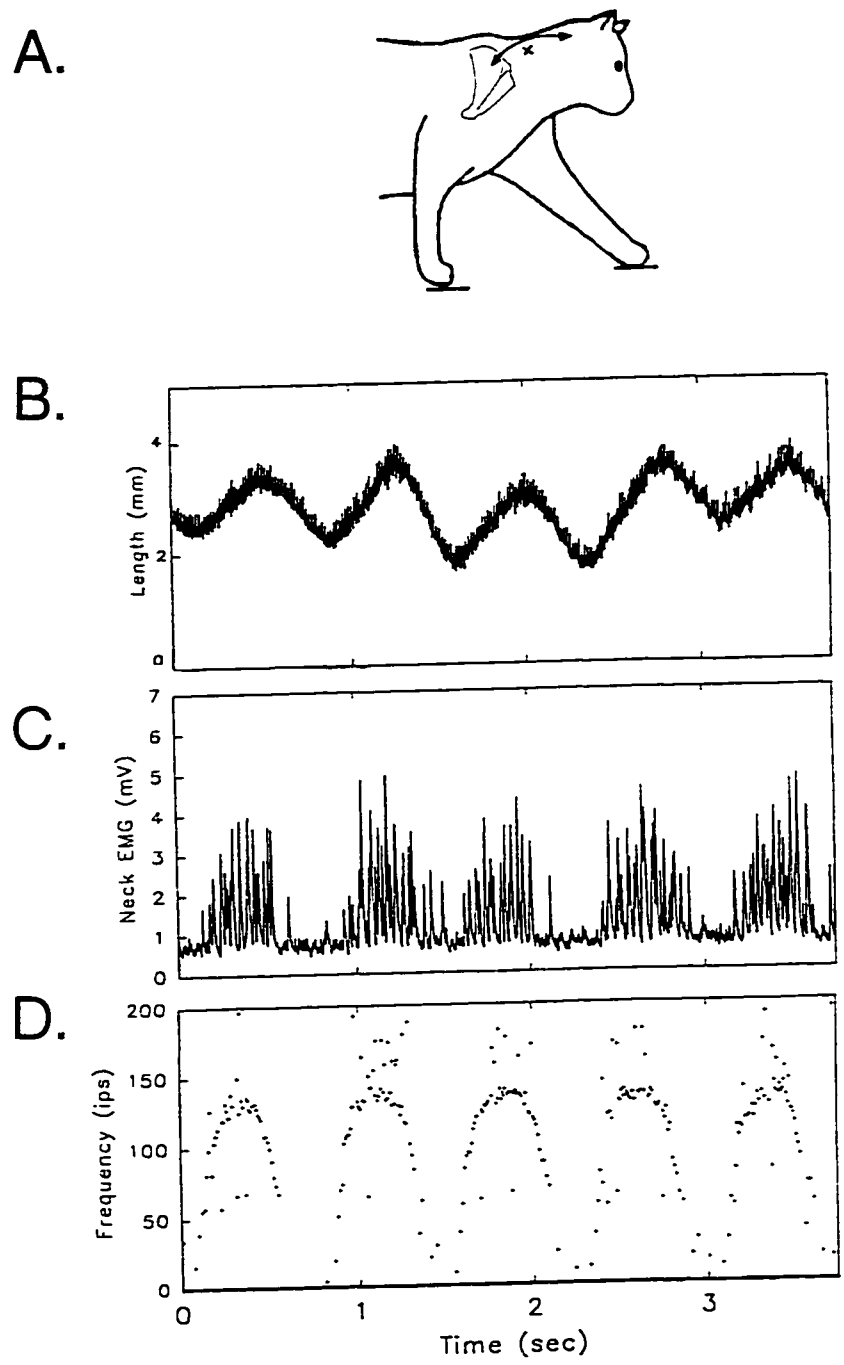

Figure 2-5. Activity of a suspected spindle afferent.
A. Diagram showing receptor location in the musculature between the scapula and the base of the skull and the movement that evoked the highest firing rates in response to imposed ramp and hold stretches. B. Length changes measured between the scapula and the base of the skull during sinusoidal imposed movements. C. EMG activity recorded from the neck musculature during the imposed movements. D. Receptor activity during the imposed movements.

2.5 References

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3.0 Movement Illusions Evoked by Ensemble Cutaneous Input from the Dorsum of the Human Hand*

3.1 Introduction

The study of human kinaesthetic sensibility has had a long and interesting history. Sherrington (1900) suggested a kinaesthetic role for "sense organs in muscles, tendons and joints". A rival theory which gained popularity suggested that "corollary discharge" (Sperry, 1950) or "efference copy" (von Holst, 1954) of the descending command dominated kinaesthesia. The notion of centrally generated kinaesthetic signals had its roots in Helmholtz's (1925) "sensation of innervation" which derived from studies of eye movements. The 1950s and 1960s saw a renewed interest in receptors located in the joints, primarily due to studies suggesting that their firing profiles were ideal to signal joint position (Boyd & Roberts, 1953). However, subsequently it was found that in fact few joint receptors fire over the full range of motion (Burgess & Clark, 1969; Ferrell, 1980). Attention quickly shifted back to the muscle receptors with the demonstration that excitation of muscle spindles by vibration induced illusory movements consistent with lengthening of the vibrated muscle (Eklund, 1972; Goodwin, McCloskey & Matthews, 1972). This finding has been corroborated many times since and it is now widely accepted that muscle spindles play an important role in kinaesthesia (Lackner & Levine, 1979; Roll & Vedel, 1982). Numerous reviews have been written on the topic (McCloskey, 1978; Matthews, 1982; Gandevia, 1995b).

In contrast to muscle and joint receptors, cutaneous receptors have rarely been accorded a significant role in kinaesthesia, though the issue has been discussed for over a century (McCloskey, 1978). The question now is, to what extent does the central nervous system (CNS) extract proprioceptive and kinaesthetic information from the responses of

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* This chapter has been published. Collins and Prochazka 1996. J.Physiol. 496:857-871. Approximately 85% of the work for this project was conducted by author DC.

cutaneous receptors to skin deformations accompanying movement. The terms proprioception and kinaesthesia are sometimes used synonymously, but proprioception has a more general connotation, encompassing all movement sensation, whether consciously perceived or not. Direct evidence that some cutaneous receptors can generate signals of a proprioceptive nature came from human neurographic recordings from receptors in the glabrous skin of the hand (Knibestöl & Vallbo, 1970; Hulliger, Nordh, Thelin & Vallbo, 1979). However the response characteristics of these afferents during movements suggested that they could play only a small or facilitatory role in kinaesthesia (Hulliger et al. 1979; Burke, Gandevia & Macefield, 1988). In contrast, recent studies have indicated that receptors located in the hairy skin on the dorsum of the hand, particularly slowly adapting type II (SAII) receptors, provide ideal signals from which to derive finger movements (Edin & Abbs, 1991; Edin, 1992; Grill & Hallett, 1995). There is also some evidence from animal studies that cutaneous signals are appropriate for proprioception (Appenteng, Lund & Seguin, 1982).

The fact that certain receptors generate signals from which kinaesthetic information can be derived does not of itself show that the CNS uses the signals in this way. However, indirect evidence for a kinaesthetic role for skin input came from studies in which finger movements were still detected after contributions from receptors in joint and muscle were removed either experimentally (Moberg, 1983; Ferrell, Gandevia & McCloskey, 1987; Clark, Grigg & Chapin, 1989) or as a result of reconstructive surgery (Moberg, 1972; but cf. McCloskey, 1978; McCloskey, Cross, Honner & Potter, 1983). Microstimulation of presumed single cutaneous afferents has only on rare occasions resulted in kinesthetic illusions (Torebjörk & Ochoa, 1980; Vallbo, 1981; Torebjörk, Vallbo & Ochoa, 1987; Macefield, Gandevia & Burke, 1990). Torebjörk et al. (1987) concluded that spatial summation of input from SAII receptors may be required for conscious perception of their input. It should be noted that stimulation of presumed single muscle spindle afferents, the afferents most often implicated as the source of kinaesthetic information, has also rarely resulted in perception of movement (Macefield et al. 1990).

In two recent studies, selective stimulation to recruit ensembles of skin afferents was attempted. Gandevia (1995a) reported briefly on the use of electrical stimulation to

excite a population of non-muscle afferents in the human superficial radial nerve. Edin & Johansson (1995) stretched the dorsal and palmar skin of the index finger in human subjects. In both cases illusions of finger movement were evoked. Indeed the results suggested that in certain circumstances, skin input may have precedence over the other proprioceptive modalities in the perception of movement and control of motor behavior. Our study used elements of both of these recent investigations. However, we adopted a more quantitative approach, both in relation to the selective activation of afferents and in comparing the relative importance of cutaneous and non-cutaneous input in kinaesthesia. In all, we used three techniques to excite ensembles of afferents of the hand. Cutaneous input was evoked either by electrical stimulation delivered through an array of electrodes on the dorsum of the hand and fingers or by accurately controlled skin stretch. Muscle receptor input was evoked by vibration (Eklund, 1972; Goodwin et al. 1972), so that the kinaesthetic action of muscle and skin input could be compared. Part of this work has been reported elsewhere (Collins & Prochazka, 1995).

3.2 METHODS

Three sets of related experiments are described in this paper. The nineteen subjects (9 female, 10 male; aged 15 to 48 years old) had no history of neurological, allergic or skeleto-motor disorders and they were naive to the research hypotheses. Experiments were performed in accordance with the Declaration of Helsinki and were approved by the University of Alberta Hospitals ethical committee. All subjects gave their informed written consent to the procedures. Subjects were seated with their arms resting comfortably on a narrow table in front of them with their hands hanging relaxed over the edge. A screen blocked the subject's vision of sites distal to the mid-forearm. Stimuli were applied to the right hand and perceived movements were matched with the left hand. Subjects were told that the purpose of the experiment was to investigate the way people perceive sensations from the hands. They were asked to describe any sensations such as touch, pressure, movement, vibration and warmth associated with the

stimuli. Movement was not emphasized. Experimental protocols are summarized in Table 3-1.

3.2.1 EXPERIMENT 1

The main aim was to characterize illusory movements evoked by electrical stimulation of the skin. A secondary aim was to characterize illusory movements evoked by mechanical stretching of the skin or vibration-elicited activity of muscle spindles. Seven subjects took part.

Electrical Stimulation. Twelve pairs of 1 cm diameter brass electrodes with 0.63 mm thick conductive gel were stuck to the skin, in each case the anode being 1 cm distal to the cathode. Electrode pairs were located in three rows over the proximal inter-phalangeal (PIP), the metacarpo-phalangeal (MCP) joints and the dorsum of the hand (pairs 1-12 in Figure 3-1A). A custom-built stimulator delivered independent, interleaved trains of 80 μs pulses through each electrode pair. Two personal computers with Cambridge Electronic Design 1401 interfaces were used to frequency-modulate the pulse trains of all electrode pairs in phase at 0.3 Hz. Electrode pairs 1-8 were modulated through 5-650 Hz. Pairs 9-12 were modulated through 5-325 Hz, to mimic firing associated with smaller amounts of skin stretch. Perceptual threshold (PT) was determined separately for each electrode pair using a graded 300 Hz pulse train. Then with all 12 electrode pairs active, pulse amplitudes were individually increased to levels somewhat below those which subjects considered uncomfortable. If the stimulation caused overt muscle twitches the trial was discontinued. Stimulation was delivered in 3-6 blocks of 15-75 consecutive cycles.

Skin Stretch. Loops of thread about 4 mm in diameter soaked in cyano-acrylate glue were stuck to the skin at 5-7 locations proximal and distal to the index finger MCP joint (see Figure 3-1B). The threads were tied to elastic bands which were fixed to stretch bars held by the experimenter on either side of the MCP joint. Movements of the stretch bars away from each other stretched the skin over the MCP joint in an even and balanced

manner (see Figure 3-1B). Thicker pairs of elastic bands (ca. 60 N/m compliance) were used at the two locations on either side of the MCP joints and thinner bands (approximately 20 N/m compliance) were used at the more proximal sites to provide a graded skin stretch centered over the MCP joint. The stretch was delivered manually in a quasi-sinusoidal fashion at about 0.3 Hz so that the strain of the skin was similar to that seen during finger flexion of about 45° from neutral. Each subject received a block of 10-25 consecutive stretches. Stretch was applied so as to minimize movement of the hand or fingers, which was examined in video films (see below).

Vibration. Small-amplitude 100 Hz vibration was applied to tendons in the dorsum of the hand. The 10mm diameter tip of the custom-built vibrator was applied to sites that were the most effective in creating illusions of index finger flexion. Typically this was just proximal and slightly medial to the index finger MCP joint, over the tendons of the extensor indicis and extensor digitorum muscles (between electrodes 11 and 12 in Figure 3-1A). The vibrator was turned on and off at about 0.3 Hz. Each subject received a block of trials of 10-25 consecutive cycles of stimulation. If the vibration evoked overt reflex-mediated muscle twitches, the trial was discontinued.

3.2.2 EXPERIMENT 2

Experiment 1 was repeated using more controlled stimuli to allow comparisons of the relative strengths of the effects produced by the three stimulus modalities. Stimuli were delivered in equal blocks of trials and at three intensities chosen to encompass the presumed physiological range for each modality. We also examined the effects on illusory movement of the spatial pattern of electrical stimulation and skin stretch. Two spatial patterns were used for each modality, one to mimic flexion of all the fingers and the other flexion of the index finger only. Eleven subjects participated. Each experimental session was conducted in three randomized blocks of trials, each involving a given stimulus modality. Matching movements of the left index finger were monitored with a silastic length gauge attached across the MCP joint. These data along with the

time course of electrical, stretch and vibratory stimuli were sampled and stored using a CED 1401 interface and computer system running custom software.

Electrical Stimulation. Twelve electrode pairs were stuck to the dorsum of the hand in three rows, the most distal row spanning the MCP joints of each finger (5-16 in Figure 3-1A). Two spatial patterns of stimulation were used. Spatial pattern 1: frequency-modulated stimulation (0.3 Hz) was delivered in-phase through all 12 electrode pairs to elicit illusions of rhythmical flexion of all the fingers. Spatial pattern 2: frequency-modulated stimulation (0.3 Hz) was applied in-phase through electrode pairs 8 and 10-16 (Figure 3-1A) to elicit illusions of movement of the index finger only. Table 3-2 shows the three frequency ranges used (low, medium and high) and their allocations to different electrode pairs. We used a video, kindly supplied by Dr. B.B. Edin showing skin strain at a matrix of points on the dorsum of the hand as a guide in selecting the range of stimulus frequencies at the different electrodes. We wanted to ensure that our highest stimulation rates matched or exceeded natural firing in the fastest possible finger movements. In freely-moving cats, skin afferents can fire in excess of 700 /s (Trend, 1987; personal observations). We therefore selected 5-700 /s for our largest frequency range, a maximum well above that of skin afferents recorded neurographically during slow finger movements (Edin & Abbs, 1991) or during skin stretch corresponding to fast finger movements (Edin, 1992). Each combination of stimulus pattern and intensity was delivered in 2-4 successive trials of 15 consecutive cycles of stimulation. The presentation order of the 6 combinations within a block was randomized across subjects.

Skin Stretch: The skin stretch apparatus was attached to the skin at 10-11 sites on the dorsum of the hand (Figure 3-1C) using pieces of adhesive tape (about 12 x 16 mm). Two spatial patterns of manually-applied skin stretch were used. Spatial pattern 1: the stretch was bi-directional away from the MCP joints, using all the pieces of adhesive tape, to mimic skin stretch associated with movement of all the fingers. Spatial pattern 2: stretch was applied through 4-5 pieces of tape on either side of the index finger MCP joint, to mimic skin stretch associated with movement of the index finger only. For each

pattern the skin was stretched by amounts intended to mimic small, medium and large flexions of the MCP joints. The corresponding skin strains were estimated to be in the range 2 - 8 % (see Experiment 3 Results). Each combination of spatial pattern and intensity was delivered in 2-4 successive trials of 10-15 consecutive cycles. The presentation order of the 6 combinations within a block was randomized across subjects. A length gauge was used to monitor the time course of the movements of the proximal stretch bar.

Vibration: The optimal stimulation sites to evoke illusions of index finger flexion were determined as in experiment 1. The vibrator was then clamped in place with a retort stand and turned on and off at approximately 0.3 Hz. Vibration at 70, 100 and 130 Hz was delivered in randomized blocks of 2-4 successive trials, each consisting of 10-15 consecutive cycles of stimulation.

3.2.3 EXPERIMENT 3

The skin stretch trials in experiments 1 and 2, while often successful in producing movement illusions, involved manual stretching that was variable and difficult to quantify. Moreover, we found that it was difficult to stretch the skin without moving the fingers albeit very slightly. Our aims were to: a) apply accurately controlled skin stretch, b) quantify the magnitude and time course of the stretch, c) minimize and quantify joint movements evoked by the stretch and d) establish the subjects' ability to detect comparable joint movements. Six subjects participated, 5 of whom had taken part in experiment 1 or 2. The sixth subject had been involved in pilot studies prior to experiments 1 and 2. Subjects were chosen on the basis that in previous skin stretch trials, 3 had reported illusory movements (subjects S6, S17, S19 in Table 3-3) and 3 had not (S2, S5, S8).

Subjects were told that the experiment was a continuation of the study on the perception of sensations from the hands, but they were not informed that skin stretch or finger movement trials were involved. They were told that if they perceived any

sensations they should respond as in experiments 1 and 2. Skin stretch and joint movements were each delivered at three amplitudes. All trials of one amplitude were delivered within a single block of approximately 80 consecutive cycles. Blocks were alternated between skin stretch and finger movement and presentation order of the small, medium and large amplitudes was randomized across subjects.

Skin stretch was applied via two pieces of adhesive tape (circa 12 x 16 mm) stuck to the skin just proximal and distal to the index finger MCP joint (Figure 3-2A). During skin stretch trials threads attached to the tape were connected via pulleys to a feedback-controlled electromagnetic length servo which provided 0.3 Hz sinusoidal stretches of different amplitudes. To minimize actual joint movement caused by the applied skin stretch, the fingers of the right hand were suspended from above by threads stuck to the fingernails with cyano-acrylate glue (Figure 3-2B). The pulleys were carefully positioned so that the skin stretch was well balanced and produced minimal movements of the finger. Despite these precautions, minute joint movements were usually observed. They were measured from video films as described below and compared to the perceptual thresholds determined as follows. The suspension thread attached to the nail of the index finger was connected to the servo motor to permit application of precisely-controlled 0.3 Hz sinusoidal movements at the MCP joint. Care was taken to ensure that subjects were unaware of whether skin stretch or real finger movements were involved in a trial. Three movement amplitudes were applied that encompassed the detection threshold.

3.2.4 Data Collection and Statistical Analysis

All sessions were videotaped (Sony Video Camera, Panasonic OmniMovie HQ). Subjects matched with their left index finger the magnitude and time course of illusory movements of the right index finger. Images were digitized post-hoc (Video Blaster/ Video Kit 1.20) and movements of ink dots or self-adhesive dots on the medial side of the left and right index fingers were quantified using image analysis software (SigmaScan/Image 1.20.09). In experiment 3 a Sharp Viewcam was used for close-up videotaping of the dots, giving a spatial resolution of 80 μm, as determined by filming

movements of a linear servo motor. For a dot located at the distal inter-phalangeal (DIP) joint, this is equivalent to rotation of the MCP joint of 0.1^0 or less. Skin strain was calculated from digitized, close-up images of a 12x12 mm grid (2 mm between lines) stamped on the skin over the right index finger MCP joint. Between 12 and 24 measurements were made from each of the stretched and unstretched grid images for each calculation.

To evaluate the relative strengths of each technique in evoking illusory movements the 10 largest movements at the index finger MCP joint, regardless of spatial pattern or intensity of the stimulus or the resultant movement direction, were averaged together for each subject in experiments 1 and 2 (see Table 3-3). In cases where fewer than 10 illusory movements were recorded, all the available movements were used for the mean. These data were tested using the ANOVA analyses described below. The relative strengths of the techniques in producing illusions were also tested using McNemar's test to make pairwise comparisons between the proportions of subjects who perceived illusory movements for each technique. Within a subject the direction of the perceived movement was consistent, i.e. movements contributing to the means for a given subject were always of the same direction. Tests for a significant effect of spatial pattern and/or intensity of stimulation on movement magnitudes were conducted on the mean movement amplitudes for each combination of pattern and intensity for subjects in experiment 2 who reported illusory movements. Statistical tests across subjects were conducted using one and two-way repeated measures analysis of variance (ANOVA) followed by the Student-Newman-Keuls post-hoc multiple comparisons test to identify significant differences. When the data was found not to be normally distributed and/or of equal variance analyses were conducted using Friedman's ANOVA on ranks followed by Wilcoxon signed rank (Bonferroni) or Student's *t* (when pair-wise comparisons were normally distributed) tests. Comparison of illusory movement magnitudes between techniques within a subject were conducted using Student's *t*-tests or Mann Whitney U tests (when tests for normality or equal variance failed) on the data in Table 3-3. Statistical significance was accepted when $P<0.05$.

3.3 RESULTS

The main aim of this study was to evoke illusory movements by activating predominantly skin receptors or predominantly muscle receptors and compare the strengths of the illusions. Electrical stimulation and skin stretch were used to excite skin receptors and vibration was used to excite muscle receptors in experiments 1 and 2. We first present the characteristics and relative strengths of the movement illusions evoked by each technique using data from all the subjects in experiments 1 and 2. Next we describe the relationship between the spatial pattern and intensity of stimulation on the illusory movements as examined in experiment 2. Finally, the results of experiment 3, which focused on the skin stretch technique, are described.

3.3.1 MOVEMENT CHARACTERISTICS AND RELATIVE STRENGTHS (EXPERIMENTS 1 AND 2)

In this section we describe, first qualitatively and then quantitatively, the illusory movements evoked by each technique. It should be noted that all illusions involved the perception of smooth movements, temporally linked to the cyclical application of the stimuli (with one exception: see Electrical Stimulation below). First we will concentrate on movements of the index fingers. Movements of the other fingers are described in section 2 below. Mean movement magnitudes used for this analysis, along with movement direction and the number of movements comprising each mean are given in Table 3-3. Subject numbers in Table 3-3 reflect the chronological order of participation in the study and are subsequently used in the text to identify subjects.

Electrical Stimulation. Sinusoidal variations in stimulus frequency were delivered through an array of electrodes stuck to the dorsum of the right hand. One subject's data (S5) are omitted from this section as the stimulus could not be applied without an accompanying motor response. Average stimulus intensity across the remaining 17 subjects was 1.34 ± 0.13 times perceptual threshold (mean $\pm$ 1 S.D.).

Electrical stimulation evoked illusory movements in 6/17 subjects (35%, Figure 3-3A). McNemar's test identified that this proportion was not significantly different than that for the skin stretch technique (P=0.289) but was significantly smaller than that for vibration (P=0.012). As we posited, the most common illusory movement (5/6 subjects) was flexion at the index finger MCP joint as stimulus frequency increased (see Table 3-3). An example of this is shown in the raw data in Figure 3-4A for three cycles of stimulation through the whole electrode array over the low frequency range ("all low" stimulus combination in Table 3-2). These data are from subject S14 who perceived movement during all three stimuli. Subject S3 perceived a slight extension of the MCP joint during increasing stimulus frequency, but found the movement direction "difficult to determine". Movement characteristics within a subject were consistent within an experimental session. Perceived flexion of the PIP and DIP joints generally matched that of the MCP joint, but occasionally a large illusory flexion at the PIP joint was accompanied by a small illusory movement at the MCP joint (example subject S6). One subject (S10) reported a paradoxical sense of position change without a sense of movement: in several trials the perception was of a static flexion of all the fingers as if in a grasp throughout several cycles of stimulation. Four subjects (S9, S13, S14, S16) occasionally felt "as though their fingers should be moving" but knew that they were not.

The magnitude of the illusory movements at the MCP joint evoked by electrical stimulation was generally small. Mean amplitude across the six subjects who clearly perceived movement during electrical stimulation was $11.3^0 \pm 16.6^0$ (range 1.0^0-44.8^0), see Table 3-3. Five of these six subjects perceived movements smaller than 10^0 during electrical stimulation (see Figure 3-3B). ANOVA analysis identified no significant difference between electrical stimulation and skin stretch (P=0.052) but electrical stimulation was significantly less effective than vibration in evoking illusory movements (P=0.009). Of the three subjects who perceived illusory movements with both electrical stimulation and vibration, significantly larger illusory movements were evoked by electrical stimulation in one subject (S2) and by vibration in the other two (S10, S14).

Electrical stimulation also evoked tactile illusions of a non-kinaesthetic nature. All subjects perceived "pins and needles" sensations under the stimulating electrodes.

Pressure was the next most frequently reported tactile sensation. Descriptions also included a squeezing of the fingers "like a firm hand-shake", a pushing down on the dorsum of the hand, rubbing, brushing or scraping across the skin, touch, tapping, flutter, warmth, cold and occasional numbness. A sensation of skin tightening was also frequently reported yet this was not always associated with sensations of movement. Three subjects described some of the sensations as being similar to those evoked by actual skin stretch.

Skin Stretch Threads stuck to the dorsum of the hand were used to manually stretch areas of skin over the MCP joints and hand. This was effective in creating the illusion of movement in 10/18 (56%) of subjects tested in experiments 1 and 2 (see Figure 3-3). This proportion was not significantly different than that for electrical stimulation (P=0.289) or vibration (P=0.07). Raw data for three cycles of small-amplitude skin stretch across the whole hand are shown in Figure 3-4B for subject S14 who perceived illusory movement from all three types of stimuli. This subject reported illusions of finger flexion consistent with our hypothesis. However, most subjects (7/10) perceived extension of the MCP during periods of skin stretch. As with electrical stimulation, responses tended to be variable between subjects, though relatively stable for a given subject. Movements during illusory MCP joint extension were usually restricted to that joint, though some subjects reported concomitant flexion or extension of the more distal joints. The three subjects who perceived MCP flexion consistently reported concomitant flexion at the PIP joint. In one case a slight abduction of the MCP joint was perceived.

Illusory movement amplitudes evoked by the skin stretch tended to be intermediate between those evoked by electrical stimulation and vibration. Mean movement amplitude across the 10 subjects who perceived movements was $13.8^0 \pm 9.7^0$ (range 3.7^0-31.4^0) as shown in Table 3-3. Movement amplitudes were categorized as small (0^0-9^0), medium (10^0-19^0) and large (20^0+) and are displayed graphically in Figure 3-3B. ANOVA analyses identified no significant difference between skin stretch and electrical stimulation (P=0.052) and a significantly smaller effect of the skin stretch when compared to vibratory-evoked illusions (P=0.02). Of the seven subjects who perceived

illusory movements with both skin stretch and vibration, significantly larger illusory movements were evoked by skin stretch in three subjects (S10, S14, S17) and by vibration in two subjects (S13, S15). Movement magnitudes were not significantly different in the other two (S1, S4).

Close inspection of the filmed sessions revealed some trials in which very small amplitude "real" movements of the fingers were generated by the skin stretch. In about half of the cases these movements were so small that their direction could not be reliably discerned from the video images. In the remainder, small flexion, extension or lateral movements of the finger were distinguished during skin stretch. It should be noted that such movements were present both when illusory movements were reported and when they were not. Furthermore, the amplitudes of the "real" movements were always much smaller than those of the corresponding illusory movements (i.e. contralateral matching movements).

Vibration Vibration was applied to the finger extensor tendons on the dorsum of the hand just proximal to the index finger MCP joint. In two subjects (S3, S6) this consistently caused reflexive movements of the fingers and so their data were discarded. Vibration evoked illusory movements in 14/16 subjects (88%), which, as mentioned previously, was a significantly greater proportion than for electrical stimulation but not for skin stretch (see Figure 3-3A). Responses to vibration were the most consistent within and between subjects. All but one of the subjects (S1) reported flexion of the MCP joint during extensor tendon vibration. This is to be expected, given that extensor muscle spindles increase their firing during passive flexion movements (Al-Falahe, Nagaoka & Vallbo, 1990). An example of illusory movements evoked by vibration is shown in Figure 3-4C: subject S14, 3 cycles of vibration at 70 Hz. Perceived flexion of the MCP joint was generally accompanied by perceived flexion of the two more distal joints.

As well as evoking illusory movements in the largest number of subjects, vibration evoked illusory movements tended to be of larger amplitude than did the other two techniques as shown in Figure 3-3B. ANOVA analyses revealed that vibration was significantly more effective than either of the other two techniques at evoking illusory

movements (see above). Mean amplitude across the 14 subjects who perceived movements was $16.7^0 \pm 9.8^0$ (range 6.2^0-38.9^0), see Table 3-3. However, as indicated above, when illusory movements were evoked by skin stimulation and vibration within subject analysis revealed that larger movements were evoked by skin stimulation in three subjects, by vibration in two subjects and movement magnitudes were not significantly different in the other two.

Efficacy of the Cutaneous Stimuli Electrical stimulation and skin stretch both evoked illusory movements but the difference in their efficacy was not statistically significant (see above). It should be noted that nearly three quarters of the subjects (12/17: 71%) responded to at least one of the cutaneous stimuli and about a quarter (4/17: 24%) responded to both (see Figure 3-3A).

3.3.2 DEPENDENCE OF MOVEMENT ILLUSIONS ON STIMULUS LEVEL AND PATTERN (EXPERIMENT 2):

In experiment 2 all stimuli were delivered at three intensities, to cover the range which evoked maximal illusory movements for each subject. As well, two patterns of electrical and skin stretch stimulation were used, one to mimic flexion of all the fingers and the other flexion of the index finger only.

The size of illusory movements of the index finger MCP joint reported by subjects was not significantly correlated with stimulus amplitude (electrical pulse frequency range, skin strain amplitude or vibration frequency) for any of the modalities studied ($P>0.05$). Similarly, the spatial pattern of electrical and skin stretch stimulation had no statistically significant effect on the magnitude of the illusory movement at the index finger MCP joint ($P>0.05$). However, inspection of the video-taped sessions revealed that in some cases the pattern of stimulation appeared to have an effect on illusory movement of the other fingers.

Electrical stimulation was only effective at evoking illusory movements in 3/11 subjects in experiment 2. Two spatial patterns of stimulation were used: the first to evoke illusions in all the fingers and the second to evoke illusions in the index finger only. In

either case the 3 responding subjects felt most movement in the index finger, as judged from the contralateral matching movements, but smaller movements of the other fingers were also perceived. There were cases where the illusory movements corresponded to the spatial pattern of stimulation (i.e. all fingers or index finger only), but generally the contralateral matching movements were surprisingly similar for the two spatial patterns.

Illusory movements of the index finger MCP joint were not significantly different for the two spatial patterns of skin stretch, though illusory movements of the other fingers did show some correlation. This was most pronounced in subject S17, so a second length gauge was fitted across the MCP joint of his third finger to record this effect (Figure 3-5). Figure 3-5A depicts the contralateral matching movements when medium amplitude skin stretch was applied over all the MCP joints and the dorsum of the test hand. The subject perceived that all the joints of all the fingers flexed as if in a grasping movement. When medium amplitude skin stretch was applied only around the index finger the resultant illusory movement was localized to flexion of the joints of that finger and to a lesser extent of the adjacent finger (see Figure 3-5B). Similar but less extreme dependence on stimulus pattern was observed in other subjects.

Vibration was applied at points which best evoked illusions of index finger flexion. However, some subjects perceived movements of the adjacent middle finger. The lack of a significant effect of vibration frequency on the resultant illusory movements is contrary to previous results (Roll & Vedel, 1982) and may be due to a lack of precise control over the pressure of application of the vibration in our trials.

3.3.3 ACCURATELY CONTROLLED SKIN STRETCH (EXPERIMENT 3)

Actual Movement Detection and Matching: In most cases it was difficult to impose skin stretch without causing concomitant small movements of the finger. To determine if these real movements could be detected by the subjects we purposely applied similar movements through a thread stuck to the subject's fingernail, using a linear electromagnetic servo as described in Methods. Subjects were requested to match 0.3 Hz

sinusoidal movements of the right index finger MCP joint of three amplitudes. The mean amplitudes of these imposed movements across all 6 subjects and the attempts to match them are shown graphically in Figure 3-6A. The mean amplitude of the small movement was $0.21^0 \pm 0.03^0$ (range = 0.18^0-0.25^0) and this was below the detection threshold of all the subjects. The amplitude of the medium sized movement was increased until the subject first sensed the movement. Mean amplitude of these movements, averaged across the 6 subjects, was $0.41^0 \pm 0.13^0$ (range = 0.29^0-0.64^0). The highest detection threshold was seen in the oldest subject, in accord with recent reports of reductions in kinaesthetic sensitivity with age (Gilsing, Van Den Bosch, Lee, Ashton-Miller, Alexander, Schultz & Ericson, 1995). Five of the six subjects overestimated this movement amplitude when trying to match it with movements of the contralateral index finger, though the differences were not statistically significant (P=0.052). Mean amplitude of the matching movements of the left index finger MCP joint was $2.71^0 \pm 2.20^0$ (range = 0.30^0-6.06^0). All subjects detected the large amplitude movements ($2.77^0 \pm 0.80^0$, range = 1.24^0-3.51^0). This amplitude of movement was significantly overestimated by all subjects (P=0.008). Mean matching movements of the left index finger MCP joint for these large movements was $7.25^0 \pm 3.14^0$ (range = 3.27^0-11.28^0). Across all subjects the small, medium and large movements of the right index finger had mean peak movement velocities at the MCP joint of 0.4, 0.8 and 2.6 ^{0}/sec, respectively.

With few exceptions subjects were accurate at matching the direction of the movement and were able to identify that the movement was restricted to the index finger MCP joint. However, there were cases, especially for the movements just above detection threshold, where matching movements occasionally drifted out of phase with the actual movement. Subjects would then comment that they knew that the finger was moving but had difficulty identifying the direction or matching the amplitude. Such difficulty in determining the direction of movements close to detection threshold has been reported previously (Hall & McCloskey, 1983). Also, the matching movements of two subjects included some movement at the PIP joint and one of these subjects occasionally reported a scissoring movement at the MCP joints of the first two fingers.

Skin Stretch: The skin over the right index finger MCP joint was stretched at three amplitudes. The results of these trials were consistent with those obtained from the same subjects in earlier experiments: illusory movements were only evoked in the three subjects who had previously reported them. Also, even though the characteristics of the illusory movements were quite different between these three subjects, within a subject, movement characteristics were consistent with those perceived in the earlier experiments. One subject reported large flexions of the MCP and PIP joints of the index finger. Another reported extension at these two joints of the index finger with occasional similar movements of the next finger. The third subject reported a slight flexion and abduction at the index finger MCP joint. All illusory movements smoothly followed the cyclical application of the stretch, beginning during periods of skin stretch and returning to the rest position when the stretch was not applied.

The amplitude of the illusory movements, averaged across the 3 subjects who perceived them, tended to become progressively larger as the amplitude of the stretch increased (see Figure 3-6B). However, this tendency failed to reach statistical significance (P=0.08).

The amplitude of the skin stretch was calculated for each skin stretch trial from digitized images of the grid patterns stamped over the MCP joint. The skin stretch amplitudes, expressed as a percent of unstretched values and averaged across the six subjects were 2.2 $\pm$1.8%, 4.9 $\pm$4.4% and 7.7 $\pm$5.4%, for the small, medium and large stretch trials, respectively. These means were significantly different across all six subjects (P=0.003) and no significant differences were identified in the amplitude of skin stretch between the three subjects who perceived movements and the three who did not (P=0.995).

In many trials the skin stretch generated measurable movements of the index finger. These "real" movements (mean=$0.20^0 \pm 0.09^0$) were measured in 4/6 trials in which subjects perceived illusory movements and in 10/12 trials in which illusory movements were not perceived. In all cases these "real" movements were below the movement detection threshold determined for a subject. In two trials illusory movements were

reported when actual movements of the MCP joint were absent or immeasurably small (< 0.1^0).

3.4 DISCUSSION

In this study we tested the hypothesis that ensemble cutaneous inputs from the human hand can produce sensations of joint movement. Cutaneous activity was evoked either by electrical stimulation through arrays of skin electrodes or by stretching of the skin. In the majority of subjects (71%) movement illusions were evoked by one or other of these stimuli. We also evoked illusory movements of the fingers by muscle vibration. Vibration applied laterally to the tendon, which excites predominantly muscle spindle afferents (Roll, Vedel & Ribot, 1989), tended to be more reliable (88%) and effective in evoking movement illusions than the skin stimulation when all three types of stimulation were applied over their estimated physiological range. The results were therefore consistent with the prevailing view that cutaneous input contributes to human kinaesthesia, but perhaps to a lesser extent than muscle afferent input.

During the preparation of our manuscript, and after our study was complete, Edin & Johansson (1995) published the results of a study in which skin stretch was found to evoke sensations of movement. These investigators were "unable to elicit movement illusions when skin deformations were applied to a sentient index finger". This was attributed to the fact that the skin deformations, which were applied by manipulation of the subjects' skin with the experimenters' own fingertips, were accompanied by "substantial squeezing forces" that the subjects could feel. These sensations apparently masked any underlying joint movement illusions. An ingenious experiment was devised to overcome this problem. Localized skin anesthesia was used to block the pressure sensations at the points of manipulation, while preserving sensation in adjacent areas of skin being stretched. Illusions of movement were then easy to elicit. Our technique differed from that of Edin & Johansson (1995) in that skin stretch was applied through threads stuck to the skin, avoiding squeezing of underlying tissues and other conflicting

sensations. Under these conditions, movement illusions were evoked in the sentient index finger. Furthermore, we were at pains to monitor the small joint movements produced by skin stretching and to compare these to joint movement thresholds for conscious perception. In experiment 3, we verified that real joint movements were below perceptual threshold ($0.41° \pm 0.13°$) when bi-directional, balanced stretches were applied to the skin, the hand being stabilized by suspending all the fingers from a static frame. Our study provides verification that cutaneous sensory activity, rather than the accompanying joint movements or pressure on deep tissues, can be shown to be responsible for sensations of movement in this type of experiment. The conclusion is strengthened by the demonstration of kinaesthetic illusions with electrical stimulation of ensembles of skin afferents.

3.4.1 Electrical Stimulation: Experiments 1 and 2

The notion of electrically stimulating cutaneous afferents through an array of small surface electrodes arose from a computer animation of strain patterns across the dorsal surface of the hand during individual finger movements (Edin, B.B., personal communication). We reasoned that if skin afferents contributed to kinaesthesia, it should be possible to evoke illusions of movement by independently stimulating groups of them electrically to mimic their ensemble firing patterns. The stimulation we used was highly localized and too weak to activate either joint afferents (which are mostly high-threshold nerve fibres located away from the chosen stimulation sites) or muscle afferents or efferents (as indicated by the higher stimulus strengths required to elicit visible muscle contractions). Illusions of movement were indeed evoked by electrical stimulation in experiments 1 and 2, but only in 6/17 (35%) subjects. If the 3 subjects who felt "as though their fingers should be moving" but knew that they were not (S9, S13 and S16) are included as experiencing movement-related illusions, the overall success rate was still only 9/17 (53%), significantly below that of muscle vibration (88%).

The electrical pulse trains were delivered over three frequency ranges and in two spatial patterns intended to mimic flexion of all the fingers versus flexion of the index

finger alone. There were cases in which illusory finger movements conformed to the spatial and temporal parameters of the stimuli. However, in several subjects the perceived finger movements were always essentially the same, regardless of the frequency range or spatial pattern of electrical stimulation applied.

An inherent disadvantage of the electrical stimulation technique is that it is not specific to receptors excited by finger movements. Our subjects often reported tactile sensations including scratching, touch, flutter and pressure, all of which are remarkably similar to the sensations described by subjects during microstimulation of single cutaneous afferents (Torebjörk et al. 1987). These different and in some cases conflicting sensations may have masked illusions of movement in some of our subjects. If stimulus pulse parameters or patterns could be found that selectively activated the "right" skin receptors, this might evoke more reliable and graded kinaesthetic illusions.

3.4.2 Skin Stretch: Experiments 1, 2 and 3.

Skin stretch produced illusions of movement in 11/19 (58%) subjects. The spatial pattern of skin stretch more clearly influenced the illusory movements than was the case with electrical stimulation (see Figure 3-5). Skin stretch adjacent to the index finger tended to produce illusory movements localized to that finger and stretch adjacent to other fingers generally produced illusory movements in those fingers. In some subjects the amplitude of skin stretch was also reflected in the amplitude of the illusory movements. However, this effect was not statistically significant when tested across subjects. This may be due to differences in optimal stimulus intensities between subjects or the small sample size in experiment 3. Initially we applied the skin stretch manually (experiments 1 and 2), but we found that it occasionally caused small accompanying joint rotation. Experiment 3 was therefore conducted to validate the findings of experiments 1 and 2. In all cases in which illusory movements were reported in experiment 3, "real" movements of the fingers were below perceptual threshold or were undetectable ($<0.1^0$ at the MCP joint). An unexpected outcome was that in 7/11 subjects skin stretch evoked illusions of movement in the opposite direction to that predicted (i.e. stretching the dorsal

skin over the MCP joint caused perceptions of extension, whereas in "real" movements this area of skin stretches during flexion). We offer four possible explanations for this. 1. Close inspection of the video-taped sessions in experiments 1 and 2 revealed that there may have been small "real" extension movements in some of the trials. Though reported illusory movements were always of a much larger magnitude than any of these observed "real" movements, perception of the latter via muscle and joint receptors may have been "amplified" by cutaneous facilitation (Hulliger et al. 1979; Burke et al. 1988). However, this explanation seems unlikely in light of the very large difference between the illusory movements evoked in experiment 3 and the accompanying "real" movements, which were either below detection threshold or undetectable. 2. Similarly, we noticed in the "real" movement matching trials of experiment 3, when movements were close to perceptual threshold, some subjects detected movement but were unreliable in matching direction, as has been reported previously (Hall & McCloskey 1983). The incorrect assignment of direction in skin stretch trials, especially those in which illusory movements were very small, may therefore reflect this low threshold of detection and higher threshold for directional resolution. 3. Our technique of stretching the skin over the MCP joint via threads stuck to the skin produced local compression or bunching of the skin close to the attachment points, along the line of pull. Responses of skin receptors in this locally distorted area may provide enough conflicting input to contaminate illusions evoked by the stretched portion of skin (as pointed out by Edin & Johansson, 1995). 4. Finally, our skin stretch stimulation elicited input from only a limited area of the dorsum of the hand, especially in experiment 3. A more physiological stimulus that would include the palmar glabrous skin and a larger area of dorsal hairy skin might have improved directional resolution. The palmar glabrous skin was included in the study of Edin and Johansson (1995) and may account for the higher success rate (5/5 subjects perceived movement) and less ambiguous directional perceptions (all movements were in the hypothesized direction) in that study. Explanations 3 and 4 also suggest that in our study we may have underestimated the potency of skin-evoked kinaesthetic input, particularly when compared to that evoked by vibration. It should be noted that in the ten subjects in whom illusory movements were evoked by both skin stimulation and

vibration, the size of the illusions was larger for skin input in four subjects, for muscle input in four subjects and was not significantly different in the other two. This suggests that when skin input does take part in kinaesthesia, it may be just as effective as muscle input.

In experiments 2 and 3 the skin stretch was applied at three different amplitudes to mimic skin stretch amplitudes generated by small, medium and large flexions of the MCP joint. The actual applied skin strain over the MCP joint, averaged across all subjects in experiment 3, ranged from 2.2%-7.7% of unstretched values for the small to large amplitude stretches, respectively. Edin (1992) reported that the maximal skin strain measured 2-3 cm proximal to the MCP joint during rotation of that joint from fully extended to fully flexed is 10-15%. The firing of slowly adapting type I and SAII receptors begins to saturate above approximately 10% skin strain (Edin 1992).

3.4.3 Vibration: Experiment 1 and 2

ANOVA analysis revealed that vibration was significantly more effective at evoking illusory movements than electrical stimulation or skin stretch (see Figure 3-3). Also, the illusory movements were more consistent within and between subjects. At face value, this supports the view that muscle spindles produce more powerful kinaesthetic effects than cutaneous receptors. However, there are some problems in drawing physiological conclusions from the relative efficacy of the three stimulus modalities in our study. The first and most obvious difficulty is alluded to above. None of the artificial stimuli could have produced completely "natural" firing patterns in the targeted sensory afferents. Thus although the electrical, stretch and vibratory stimuli were chosen to activate receptors over their estimated physiological range, the spatial and modality-specific recruitment of receptors and the firing elicited in them could only have been a crude approximation of that in natural movements. Second, it is very difficult to estimate the relative proportion of the "appropriate" afferents recruited by the artificial stimuli. As mentioned above the skin stretch, and also the electrical stimulation, were limited to only a portion of the dorsal aspect of the hand. Reciprocal signals from the palmar glabrous skin were not

included. Similarly, although the vibration may have excited a good proportion of the index finger extensor spindles, it certainly excited additional receptors as well, notably skin receptors under the probe, and it did not elicit the reciprocal reductions in firing of finger flexor spindles that would normally occur during flexion movements (Al-Falahe et al. 1990).

While acknowledging the above problems of interpretation, we were nonetheless struck by the ease with which we could elicit kinaesthetic sensations with vibration and the relative difficulty we had in eliciting comparable kinaesthetic sensations with predominantly skin input, even when this was quite intense. This is certainly consistent with the many indirect pieces of evidence that muscle and joint receptors are more crucial than skin receptors in kinaesthesia and position sense (Refschauge, Chan, Taylor & McCloskey, 1995). In contrast, Edin & Johansson (1995) concluded that skin stretch took precedence over joint rotation, at least in the conscious appreciation of certain manual manipulations of skin and joints, when these elicited conflicting signals from skin and muscle receptors. The problem with these latter results is that local anaesthesia probably abolished input from the joint undergoing "real" rotation and muscle receptor input was modulated in an unknown way by these movements and by local pressure on the underlying tendons and ligaments from the experimenters' fingers.

3.4.4 Conclusion

Our study confirms that input to the central nervous system from ensembles of skin receptors contributes to the conscious perception of movement. The data left us with the impression that in the human hand, activity in muscle afferents dominates over skin input in eliciting sensations of movement, but because the adequacy of the stimuli in eliciting firing patterns similar to those associated with "real" joint movement may have varied from one technique to another and for other reasons discussed above, this issue remains open. Similarly, care should be taken in extending these results to kinaesthesia at other joints of the body: skin receptors in the forearm, and indeed most of the hairy skin in the rest of the body, may differ substantially from those of the dorsum of the hand (Vallbo,

Olausson, Wessberg & Kakuda, 1995). Further study is therefore required to elucidate the kinaesthetic role of cutaneous input at other joints in the body and the relative importance and interactions of the different sensory modalities in kinaesthesia

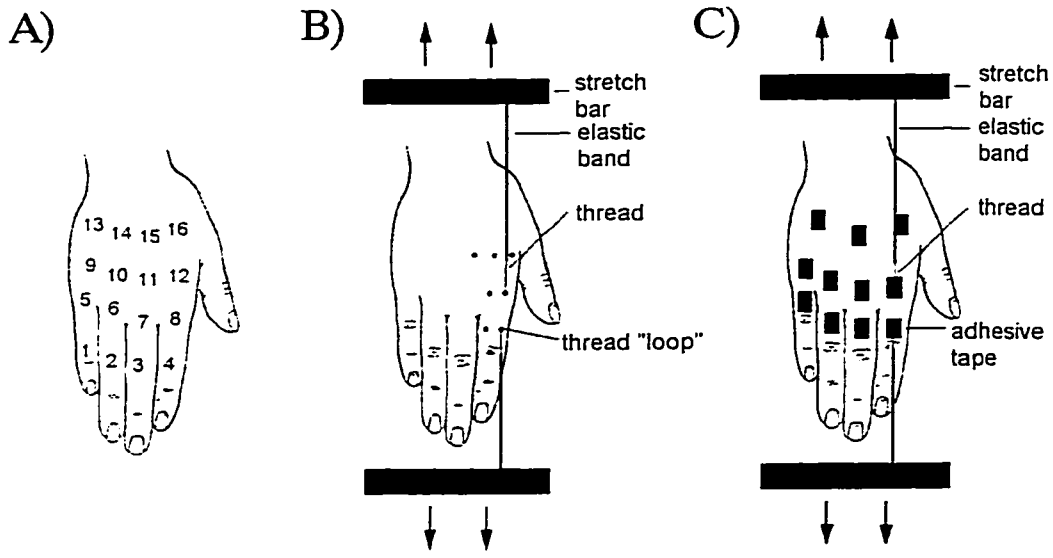

Figure 3-1. Diagram of the experimental hand for experiments 1 and 2.
A, electrode placements for the electrical stimulation. Each number represents an electrode pair. Numbers are consistent with those in the text and in Table 3-2. For each pair, cathode was just proximal to the number and anode was just distal (5 mm separation). Experiment 1: electrode pairs 1-12, experiment 2: pairs 5-16. B, schematic of the skin stretch technique used in experiment 1. Each dot represents a site at which the looped end of a short thread was stuck to the skin. Elastic bands were attached to each thread, shown twice only for clarity. Elastic bands were clamped to the stretch bars and the skin was stretched when the bars were moved away from each other. C, schematic of the skin stretch technique used in experiment 2. Filled squares represent patches of adhesive tape securing threads to skin.

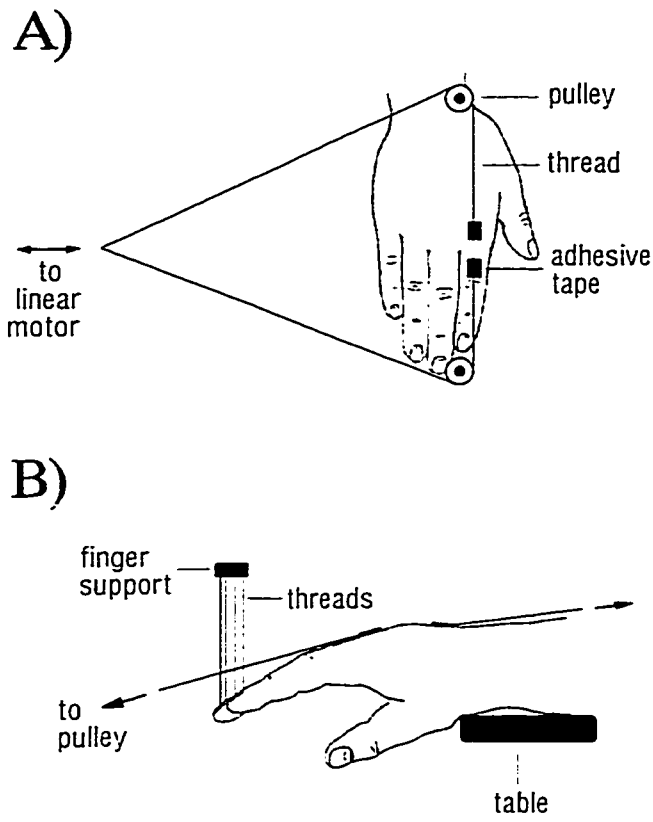

Figure 3-2. Diagram of the skin stretch technique used in experiment 3.
A, top view showing the threads attached to skin by patches of adhesive tape (filled squares). Each thread was connected via a pulley to the shaft of a linear servo motor. This provided precise, equal and opposite sinusoidal stretches to the skin. B, side view showing the position of the experimental hand and other threads supporting the fingers from above (adapted from Vallbo et al. 1995).

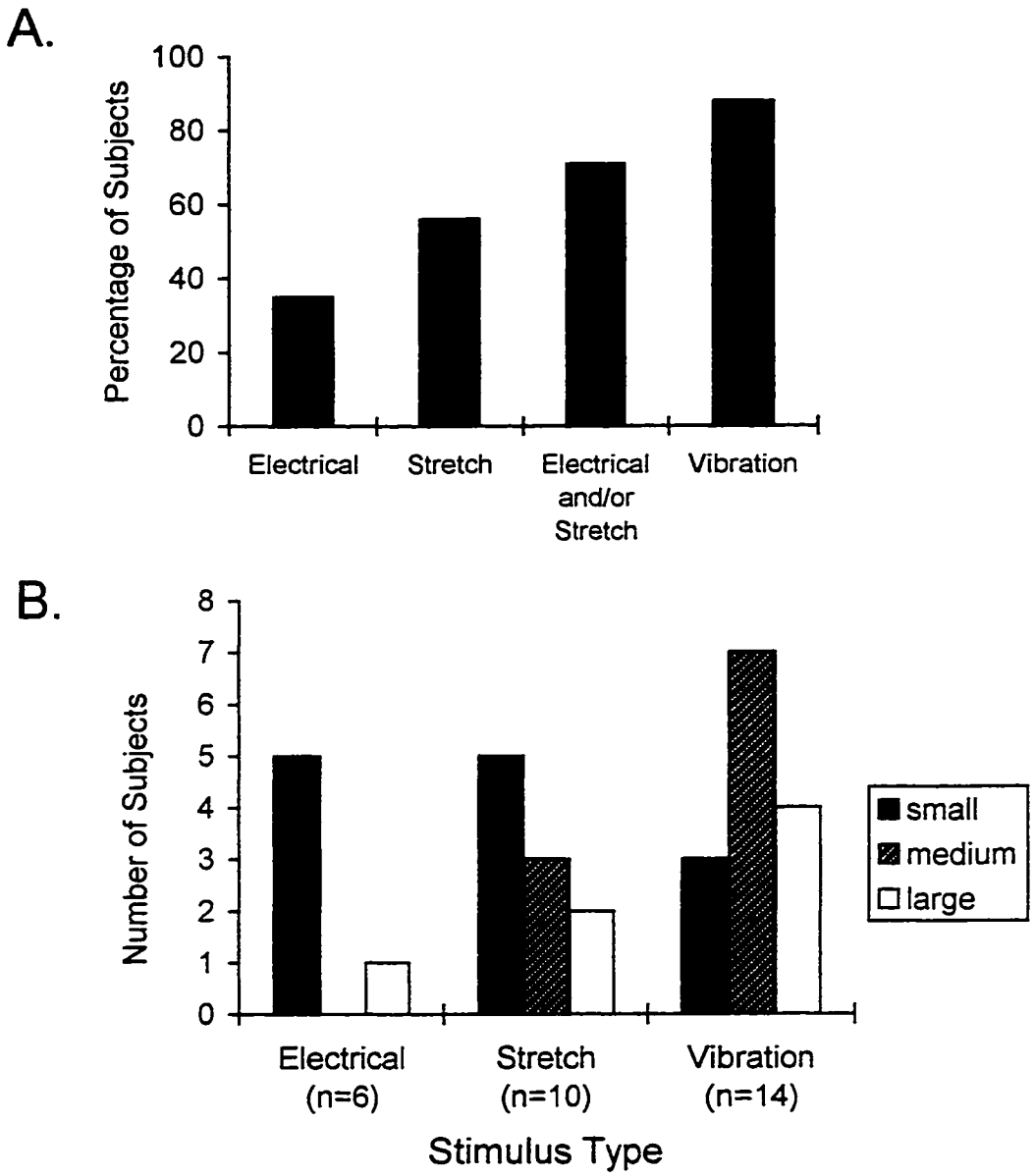

Figure 3-3. Results summary for experiments 1 and 2.
A, percentage of subjects who perceived illusory movements of the fingers for each type of stimulation. B, number of subjects who perceived small (0^0-9^0), medium (10^0-19^0) and large(20^0+) illusory movements evoked by each technique.

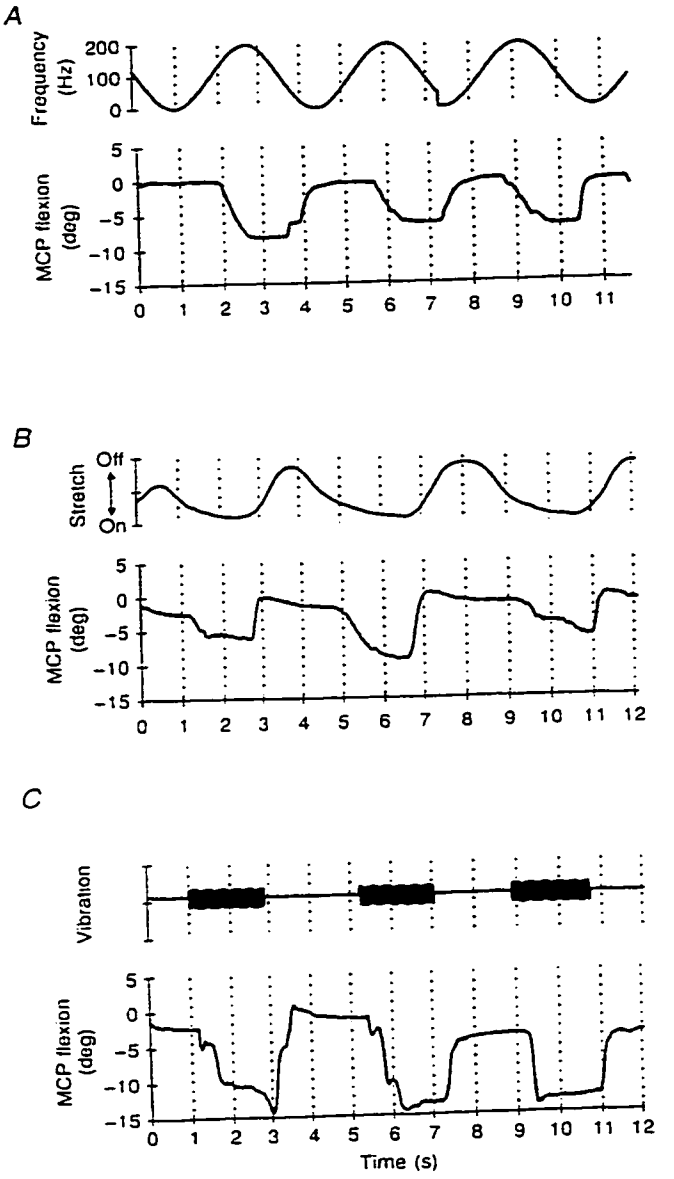

Figure 3-4. Illusory movements evoked by all three techniques in a single subject. These raw data show three cycles of each type of stimulation for subject S14. A, illusory movements of the index finger evoked by electrical stimulation through the full electrode array over the low frequency range. Top trace: time course of stimulus frequency; bottom trace: movements of the left index finger matching the perceived illusory movement. Stimulus frequencies shown are for electrode pairs over the MCP joints (pairs 5-8 in Table 3-2). B, illusory movements of the index finger evoked by small-amplitude skin stretch delivered across the whole hand (Figure 3-1C, all patches). Top: time course of the skin stretch; bottom: matched illusory movement. C, illusory movements of the index finger evoked by bursts of 70 Hz vibration. Top: time course of vibration; bottom: matched illusory movement.

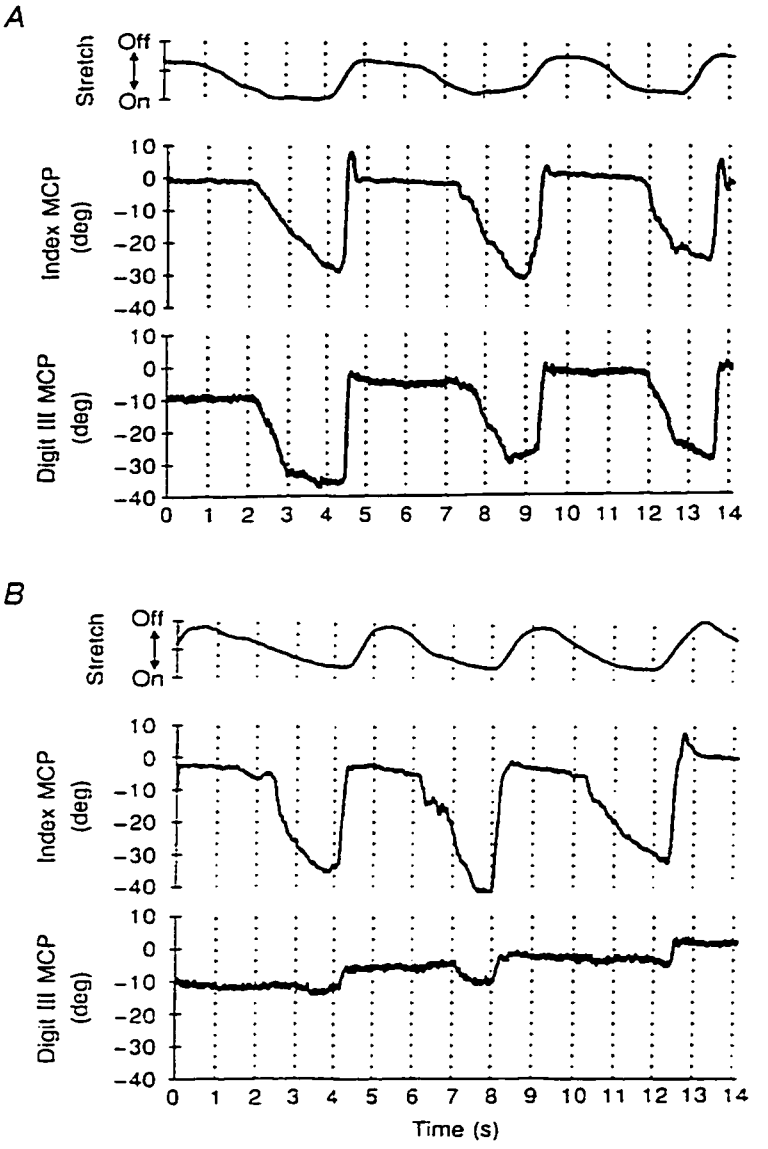

Figure 3-5. Illusory movements evoked by the two spatial patterns of skin stretch. Raw data from subject S17 who had length gauges across both the index finger and digit III MCP joints. A, skin stretch (top trace) and resultant illusory movements of the fingers (lower traces) for medium amplitude skin stretch through all the pieces of adhesive tape in Figure 3-1C. B, skin stretch (top trace) and resultant illusory movements of the fingers (lower traces) for medium amplitude skin stretch through the pieces of adhesive tape over the index finger only.

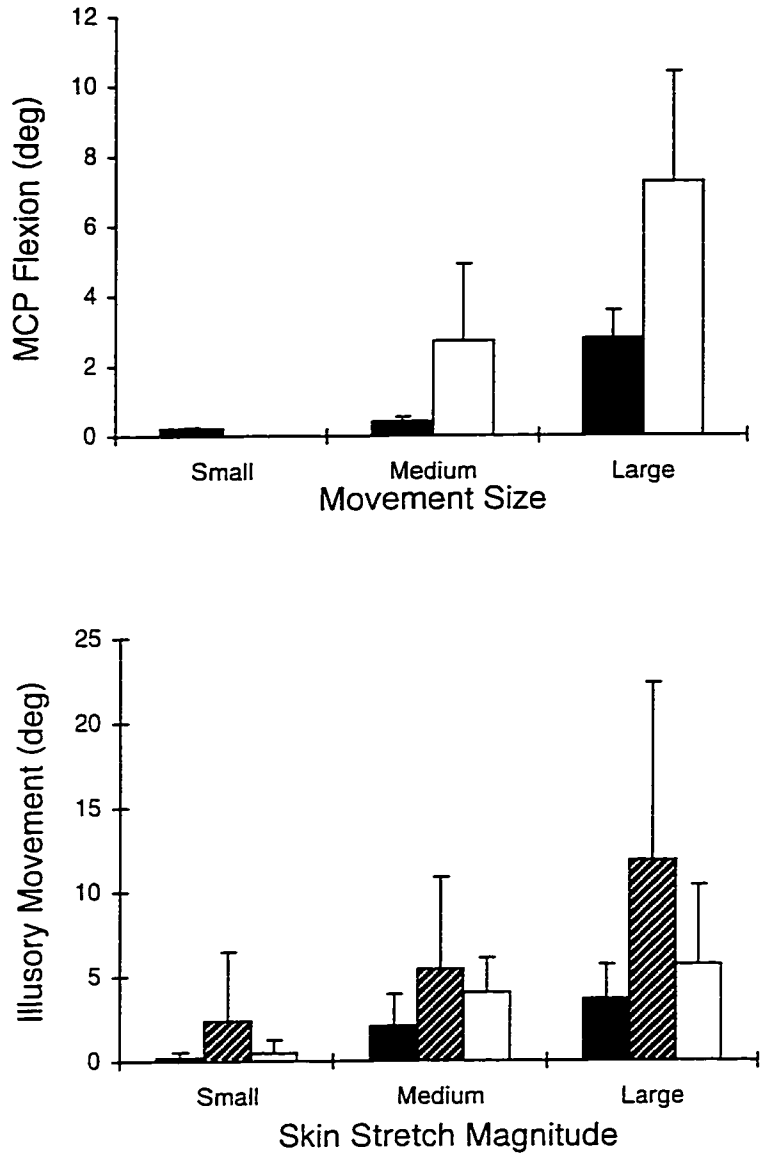

Figure 3-6. Results summary for experiment 3.
A, mean data across the six subjects for movement detection and matching trials. Filled bars: mean amplitude of the actual movement at the right index finger MCP joint. Empty bars: mean amplitude of the movement at the left index finger MCP joint when subjects attempted to match the movement of the right index finger. B, mean amplitudes of illusory movements of the different joints of the index finger evoked by skin stretch over MCP joint of the index finger. Filled bars: MCP joint, hatched bars: PIP joint, empty bars: DIP joint. Mean data from the three subjects who perceived illusory movements for small (2.2% skin strain), medium (4.9% skin strain) and large (7.7% skin strain) amplitudes of skin stretch. Error bars: standard deviations of mean.

Table 3-1. Protocol summaries for the three experiments.
The number of subjects is given in parentheses. n.a., not applicable.

		Experiment 1 (7)	Experiment 2 (11)	Experiment 3 (6)
Elec. Stim.	type	12 pairs, electrodes across PIP, MCP and dorsum of hand	12 pairs, electrodes across MCP and dorsum of hand	n.a.
	parameters	sinusoidal; 5 to 650 Hz & 5-325 Hz	sinusoidal, 3 ranges of stimulus frequencies	n.a.
	pattern	full electrode array	full array and index only	n.a.
Skin Stretch	type	elastics attached at 5-7 small spots on dorsum of index finger MCP joint	elastics attached at 10-11 larger spots on dorsum of hand and across MCP	threads at 2 spots across the index MCP, stretch applied with linear motor
	parameters	medium stretch intensity	3 intensities of stretch	3 intensities of stretch
	pattern	index finger only	all fingers and index only	index MCP only
Vib.	location	dorsum of hand	dorsum of hand	n.a.
	frequency	100 Hz	70, 100, 130 Hz	n.a.
Movement Quantification		calculated from markers on the contralateral index finger on video-tape	calculated from length gauge across contralateral index MCP	calculated from markers on both index fingers on video-tape, movement detection threshold also determined

Table 3-2. Electrical stimulation protocols for experiment 2.
Frequency ranges (Hz) allocated to each electrode pair for each stimulus combination. See Figure 3-1A for electrode locations.

Electrode	Stimulus Combination					
PAIR #	all low	all medium	all high	index low	index medium	index high
5	5-200	5-450	5-700	off	off	off
6	5-200	5-450	5-700	off	off	off
7	5-200	5-450	5-700	off	off	off
8	5-200	5-450	5-700	5-200	5-450	5-700
9	5-150	5-350	5-500	off	off	off
10	5-150	5-350	5-500	5-125	5-250	5-400
11	5-150	5-350	5-500	5-150	5-250	5-500
12	5-150	5-350	5-500	5-175	5-400	5-600
13	5-100	5-250	5-300	5-75	5-200	5-300
14	5-100	5-250	5-300	5-100	5-250	5-350
15	5-100	5-250	5-300	5-125	5-250	5-400
16	5-100	5-250	5-300	5-150	5-350	5-500

Table 3-3. Mean amplitudes of the largest illusory movements produced by each technique for each subject in experiments 1 and 2.

	Electrical Stimulation			Skin Stretch			Vibration		
Subject	Index MCP (degrees±sd)	n	direction	Index MCP (degrees±sd)	n	direction	Index MCP (degrees±sd)	n	direction
Expt 1									
S1	0.00±0.00	10	none	13.6 ± 14.1	2	extension	8.4 ± 4.4	5	extension
S2	44.8 ± 14.9	10	flexion	0.00±0.00	10	none	25.8 ± 8.9	8	flexion
S3	8.6 ± 2.9	10	extension	9.4 ± 5.1	4	extension	n.a.	/	n.a.
S4	0.00±0.00	10	none	12.8 ± 3.5	3	extension	14.9 ± 5.5	5	flexion
S5	n.a.	/	n.a.	0.00±0.00	10	none	38.9 ± 16.3	4	flexion
S6	3.4 ± 3.5	6	flexion	31.4 ± 8.0	10	extension	n.a.	/	n.a.
S7	0.00±0.00	10	none	0.00±0.00	10	none	12.2 ± 6.5	4	flexion
Expt 2									
S8	1.0 ± 0.4	2	flexion	0.00±0.00	10	none	0.00±0.00	10	none
S9	0.00±0.00	10	none	6.4 ± 0.9	2	extension	0.00±0.00	10	none
S10	3.2 ± 0.9	10	flexion	7.5 ± 0.6	10	extension	6.2 ± 0.9	10	flexion
S11	0.00±0.00	10	none	0.00±0.00	10	none	7.1 ± 0.6	10	flexion
S12	0.00±0.00	10	none	0.00±0.00	10	none	11.7 ± 1.7	10	flexion
S13	0.00±0.00	10	none	6.6 ± 4.1	7	extension	12.7 ± 2.1	10	flexion
S14	6.7 ± 1.5	10	flexion	15.9 ± 1.0	10	flexion	10.0 ± 2.5	10	flexion
S15	0.00±0.00	10	none	3.7 ± 1.7	10	flexion	13.2 ± 2.1	10	flexion
S16	0.00±0.00	10	none	0.00±0.00	10	none	28.5 ± 3.9	10	flexion
S17	0.00±0.00	10	none	30.3 ± 1.9	10	flexion	28.7 ± 1.3	10	flexion
S18	0.00±0.00	10	none	0.00±0.00	10	none	15.1 ± 1.9	10	flexion
mean	11.3 ± 16.6	6	flexion	13.8 ± 9.7	10	extension	16.7 ± 9.8	14	flexion

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4.0 Muscular Sense is Attenuated When Humans Move*

4.1 Introduction

Human "muscular sense" refers to our remarkable ability to perceive the position and movement of our body segments without the aid of vision. Nearly a century ago Sherrington believed that this ability, now commonly referred to as kinesthesia, originated primarily from sensory receptors located in skeletal muscle (Sherrington, 1900). These receptors, which also play other important roles in movement control, include the Golgi tendon organ and the muscle spindle. Muscle receptors are still thought to play a crucial, if not dominant role in kinesthesia (Goodwin *et al.* 1972; Gandevia, 1996). Therefore, one might expect that, during movement, the neural pathways mediating muscle receptor signals would remain open to faithfully transmit this information through the central nervous system. However, some previous evidence suggests that this may not be the case. The amplitude of somatosensory evoked potentials (SEPs) recorded through the scalp arising from primarily cutaneous (Abbruzzese *et al.* 1981; Rushton *et al.* 1981) and muscle (Grunewald *et al.* 1984; Staines *et al.* 1997a) receptors is generally smaller during limb movements than in static conditions. While the size of these potentials may not correspond directly to conscious perception, the ability to detect signals from cutaneous receptors is certainly reduced during movement (Angel & Malenka, 1982; Milne *et al.* 1988). Generally, cutaneous input has been equated to "exteroception" (Edin, 1992), that is the signaling of external stimuli applied to the body, though mounting evidence indicates a significant kinesthetic role as well (Edin *et al.* 1995; Collins & Prochazka, 1996).

Muscle receptors play an important role in our conscious perception of movement (Sherrington, 1900; Goodwin et al. 1972; Gandevia, 1996), but there are no published

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* This Chapter has been published. Collins, Cameron, Gillard, Prochazka 1998. J. Physiol. (508):635-643. Approximately 70% of the work for this project was conducted by author DC.

accounts of our ability to detect their signals in different motor tasks and contexts. This represents a significant void in our knowledge regarding how sensory feedback is used to control movement. The present experiments introduce a method to test muscular sense when humans move.

4.2 Methods

Nine subjects (seven male and two female) aged 26-50 participated. All were informed volunteers with no history of neurological or skeleto-motor disease. Experiments were conducted in accordance with the Declaration of Helsinki and the University of Alberta Hospitals Ethical Committee. Subjects were seated comfortably and were informed that the study was designed to investigate the way humans perceive sensations from the arm.

4.2.1 Muscle Stimulation

Muscle receptors were excited by an electrically-induced twitch of the right extensor carpi ulnaris muscle (ECU). The stimulus was delivered using a custom-made, constant-current, stimulator which delivered a single, bi-phasic, 100 μsec pulse. The stimulation site was selected to provide the purest wrist extension, determined by visual inspection of the motor response to a 33 Hz train of suprathreshold stimuli.

It was critical to these experiments that the twitch excite primarily muscle receptors. It is unlikely that the evoked twitch recruited a significant population of joint receptors as these tend to fire at the extremes of joint rotation (Burgess & Clark, 1969) and at high compression forces (Johansson *et al.* 1991). However, it was clear that the electrical stimulation, though producing very small twitches, could excite some skin and hair follicle receptors. Two techniques were used to minimize or abolish this unwanted excitation of cutaneous receptors. 1. In four subjects ECU was stimulated via fine intramuscular electrodes inserted percutaneously (Basmajian, 1974). 2. In five subjects the muscle was stimulated with surface electrodes (ConMed Versa-stim, 5x3.5 cm)

through locally anesthetized skin. Anesthesia was achieved by applying a thick layer of 2.5% lidocaine cream (EMLA) over the extensor surface of the forearm prior to an experimental session. This was covered with an occlusive dressing for 2 hours. The extent of the anesthesia was then tested using Semmes-Weinstein monofilaments (Bell-Krotoski & Tomancik, 1987). A thin layer of cream was left on throughout the experiment. This effectively abolished input from all but the deep pressure receptors for the duration of an experimental session (2-4 hours). Any visible twitch-related skin movement was always well within the anesthetized area.

Twitch amplitude was monitored using one or two 5 g accelerometers (Analog Devices) taped to the skin overlying ECU to measure the evoked movement. Signals were AC coupled (first order filter, corner frequency 0.1 Hz) and low pass filtered (second order filter at 30 Hz). Peak-to-peak amplitudes were calculated over a defined latency after stimulus delivery. During the intramuscular stimulation experiments the electromyographic (EMG) activity associated with the twitch was also recorded using surface electrodes (Jason Electrotrace). The large stimulus artifact during the surface stimulation precluded useful EMG recording during those experiments.

4.2.2 Experimental Protocol

Subjects indicated verbally each time they perceived the muscle twitch. Stimulus intensity was set at a level to evoke a twitch in the stationary arm which subjects could clearly perceive 100% of the time. Twitch amplitude varied between subjects from barely distinguishable to the human eye to clearly discernible, however it rarely resulted in visible wrist movement. During the intramuscular stimulation experiments subjects were asked to report each time they clearly perceived a muscle twitch. For a given task, muscular sense was represented by the number of twitches identified divided by the total number delivered. During the surface stimulation experiments, subjects reported twitch intensity on a subjective scale. Initially, they were presented with a series of twitches delivered at rest and told to "calibrate" the intensity of the twitches as a numerical rating of five. Subjects then reported the twitch intensity in whole numbers relative to this static

rating. Muscular sense was represented by the mean numerical rating during a given task. Twenty twitches were evoked during a block of trials. One to eight blocks of trials were conducted for each task during which twitches were evoked randomly at intervals ranging from 2-10 seconds. Static control values were calculated from blocks (n=2-10) of trials interspersed throughout each experiment during which subjects remained relaxed and stationary. In all trials in which the wrist was stationary, twitches were evoked with the wrist at approximately 180^0.

4.2.3 Tasks

1. Cyclic Wrist Movement

Muscular sense was examined during cyclic wrist movements in seven subjects. During all trials the forearm and hand were restrained to ensure the movement was restricted to the wrist. Subjects were requested to report muscle twitches while making fast (3 Hz) or slow (1 or 1.5 Hz), voluntary flexion-extension movements of the right wrist (45° joint excursion) in time to a metronome. Muscular sense was also examined while subjects remained fully relaxed and movements were driven by a linear servo motor through a similar velocity and range of motion as the fast voluntary movements. In five subjects twitches were evoked 0.5, one or two seconds (3 subjects only) after the abrupt termination of these passive movements.

Muscular sense was examined during the 3 Hz voluntary wrist movements at three twitch amplitudes in five subjects. Stimulus intensity was adjusted to evoke a twitch which stationary subjects rated as approximately 2, 5 or 8, relative to twitches in previous trials. They then rated the twitch during a block of wrist movement trials at each of the three twitch amplitudes. Presentation order of the blocks was randomized across subjects.

2. Reaching

To investigate muscular sense during a more natural movement which may be more reliant on feedback from muscle receptors, subjects (n=8) were requested to reach

out to touch or grasp a target in front of them from a starting position with the arm at rest beside them. Separate blocks of trials were conducted during which subjects performed the self-paced reaching movements with either the stimulated (ipsilateral) or the contralateral arm.

3. Skin Stretch

The potential contribution from signals originating in the periphery was investigated using a skin-stretch technique developed in our laboratory (Collins & Prochazka, 1996). Small pieces of adhesive tape were stuck to the dorsum of the right hand distal and proximal to the metacarpo-phalangeal joints of all the fingers in five subjects. The skin was then cyclically stretched at 3 Hz to evoke discharges from these receptors mimicking those during fast finger movements.

The final two tasks were designed to investigate the potential contribution from central sources. Twitches were evoked when subjects were stationary, thus at a time when there was no movement-evoked re-afference.

4. Counting

For this task, five subjects were requested to continuously count backwards from 100 by threes.

5. Reaction Time

In the final task we investigated the time course of the gating of muscle sensation during the interval just prior to a single flexion-extension movement of the right wrist. Five subjects performed a simple reaction time task whereby two audible tones separated by one second provided the warning signal (WS) and the response signal (RS) to initiate the wrist movement. In approximately 5% of the trials no RS was presented to minimize subject anticipation. In a similar percentage of the trials no stimulus was delivered to minimize anticipation of the twitch. In each subject 120-160 twitches were delivered randomly in the interval between the WS and just after termination of the movement. Combined data from 4-5 blocks of 10 twitches interspersed throughout these trials were

used for the static control. For each subject the data were sorted, post-hoc, into 50 ms bins based on the time of stimulus delivery relative to movement onset (not EMG onset) and averaged.

4.2.4 Data Analysis

Visual inspection of the data collected using the two muscle stimulation techniques showed qualitatively similar results. Therefore, data from trials common to both experiments were combined for statistical analysis. The data were normalized to the appropriate static control trial. Changes in muscular sense were represented by percent changes from the control levels. Statistical tests on combined data were conducted on the normalized values using Friedmans one-way repeated measures on ranks (Friedmans ANOVA) followed by the Student-Newman-Keuls post-hoc multiple comparisons tests to identify significant differences. Statistical analysis for tasks examined in the surface stimulation experiments only (tasks examined in only 5 subjects) and on all accelerometer data were conducted on the raw data using one- or two-way repeated measures analysis of variance (RM ANOVA) followed by post-hoc multiple comparisons tests as above. Pairwise comparisons were made using paired Student's *t* tests or Wilcoxon signed rank tests when tests for normality or equal variance failed. Statistical significance was accepted when $P<0.05$.

4.3 Results

4.3.1 Twitch Amplitude

The amplitude of the evoked twitch was monitored by accelerometers mounted over the muscle belly in all subjects and also by surface EMG recording in four subjects. Examples of the accelerometer signals during single trials are shown in the middle panels of Figures 4-1A and 4-4A during the wrist movement and reaction time tasks, respectively. There were no significant differences across subjects in twitch amplitude

between each movement task and its corresponding control trial as measured by either technique.

4.3.2 Cyclic Wrist Movement

Our first aim was to establish whether human muscular sense is attenuated during simple wrist movements. Figure 4-1A depicts raw data for one subject from the surface stimulation experiments during the fast voluntary and passive movements. Shown are the wrist angle, accelerometer signal and wrist flexor EMG activity. The time of stimulus delivery for both movements is indicated by the large stimulus artifact in the EMG traces. This is followed by the evoked twitch seen in the accelerometer traces and then by a burst of EMG activity (in the voluntary movement trace only). Mean subjective ratings of twitch amplitude for this subject are shown in Figure 4-1B. The wrist movements reduced muscular sense in this subject to 41%, 70% and 68% of control for the fast and slow voluntary movements and the passive movements, respectively. Across all subjects, the fast voluntary movements reduced muscle sense to 37% of control, significantly different from the static control and both other movement conditions (Friedmans ANOVA, Figure 4-1C). However, the reduction (to 60%) during the slow voluntary and the passive movements was not significantly different from control. In contrast, muscular sense was significantly attenuated 0.5, 1 and 2 seconds after the passive movement ended (RM ANOVA).

In general, throughout these experiments the results were consistent within subjects but quite variable between subjects. On only 3 occasions through all the experiments in this study did a subject report a twitch when none was presented.

The effect of movement phase on the gating of ascending muscle afferent signals was investigated using the data from five subjects. Active and passive 3 Hz wrist movement trials were sorted according to the movement phase in which the twitch was delivered. Movements were divided into four phases. Flexion and extension phases were defined as those in which movements were in the appropriate direction and were through the mid-range of joint excursion (approximately $\pm 20^0$ about the mean). The flexed and extended phases included the transitions in movement direction within approximately 15^0

of the corresponding maxima. There were no significant differences between twitch ratings at the different movement phases during either the active or passive movements (RM ANOVA). During active movements mean twitch ratings across subjects (± 1 S.E.M.) were 1.9 ±0.8, 2.0±0.8, 2.4± 0.8, and 2.6±0.9 when the twitch was delivered during the flexion, flexed, extension and extended phases, respectively. Comparable twitch ratings during the passive movements were 2.1± 0.8, 2.8± 0.9, 2.5± 0.9, and 2.7±0.8.

Muscular sense was examined during the fast voluntary wrist movements at three twitch amplitudes. Raw data for one subject are shown in Figure 4-2A. Across all subjects twitch perception was reduced to 65%, 51% and 58% of the stationary control for the small, medium and large amplitude twitches, respectively (Figure 4-2B). Statistical analysis (2-way RM ANOVA) identified a significant main effect of task and no significant interaction between task and amplitude. Multiple comparisons tests showed that the difference between tasks (i.e. static versus movement) was significant at all three twitch amplitudes.

4.3.3 Reaching

Reaching with the arm being stimulated totally abolished the perception of muscle twitches in one subject (Ipsi. Reach in Figure 4-3A) and reduced twitch perception to 40% of control values across all subjects, which represented a significant attenuation from both control and contralateral reaching values (Friedmans ANOVA, Figure 4-3B). The contralateral reaching task (Contra. Reach in Figure 4-3) reduced twitch perception to 13% of control in the subject in Figure 4-3A. However, in five of the other seven subjects twitch perception remained within 5% of the static control value and muscular sense was not significantly attenuated from control during this task (Figure 4-3B).

4.3.4 Skin Stretch

Cyclical stretching of the skin on the dorsum of the hand reduced the ratings of twitch perception to 19% of control in the subject in Figure 4-3A. Muscular sense was significantly reduced to 58% of control across all subjects (paired *t* test, Figure 4-3B).

4.3.5 Counting

To test whether the attenuation of twitch perception was a non-specific attentional mechanism, we asked subjects to count backwards in threes from 100. Against expectations, this did not result in significant reductions in perceptual ratings. Thus in Figure 4-3A, the mean rating was reduced to 94% of the corresponding static control in one subject, but across subjects muscular sense was not significantly reduced from control (Wilcoxon signed rank test, Figure 4-3B).

4.3.6 Reaction Time

Raw data from a typical reaction time trial are presented in Figure 4-4A. Shown are the wrist angle, accelerometer signal and the wrist flexor EMG. During this trial the muscle twitch was delivered 116 ms (at the time labeled SA in EMG trace) prior to wrist movement.

Attenuation of muscle sense prior to movement was seen in all five subjects. Mean twitch ratings for one subject are shown in Figure 4-4B. Statistical analysis across all subjects showed that the attenuation was significant throughout the preparation to move (RM ANOVA, Figure 4-4C). Over the six bins during the interval up to 100 ms before movement onset muscular sense was reduced on average to 72% of control. Each of these bins was significantly attenuated from control but they were not significantly different from each other. Twitch perception then fell to 38% of control 50-99 ms before movement and to 15% during the final 50 ms before movement. Each of these two bins was significantly different from all preceding bins. Twitch perception remained significantly attenuated during and after movement, compared to the static control.

4.4 Discussion

Sensory feedback from receptors located in skeletal muscle has long been thought to underlie our conscious perception of movement (Sherrington, 1900; Goodwin *et al.* 1972; Gandevia, 1996). The present experiments reveal that our ability to detect this feedback is reduced just before, during and after simple hand movements and that the attenuation arises from both peripheral and central sources. The results are consistent with current findings of a general attenuation of sensory feedback during movement (Prochazka, 1989; Brooke *et al.* 1997) and raise questions regarding the role of muscular sense in the control of movement.

Our results were not simply due to differences in the amplitude of the evoked twitch between tasks or signals evoked in non-muscular receptors by the muscle twitches. Two methods were used to monitor the constancy of twitch amplitude. Accelerometers mounted over the muscle belly recorded the mechanical event and, when possible, surface EMG recorded the electrical event. The amplitude of the evoked twitch, as measured by both techniques, was not significantly different between the various movement tasks and the corresponding static control. Two methods were used to avoid or minimize cutaneous receptor excitation. The first method bypassed most of these receptors by stimulating the muscle with percutaneous electrodes. The second method utilized a topical anesthetic cream. The twitches were very small and localized within the muscle belly, so it is unlikely that joint receptors were activated.

Muscular sense was significantly attenuated (to 37% of control) during fast voluntary wrist movements compared to stationary controls (Figure 4-1C). This effect was velocity-dependent as these ratings were significantly lower than those during similar slow movements. Surprisingly, the reduction during fast passive movements (to 60%) was not significantly different from control. Significance may have been attained if more subjects had been tested or if the passive movements involved more than one joint. In contrast, perceptual ratings of twitches evoked 0.5, one and two seconds after the termination of the passive movements were significantly attenuated. The extent of the attenuation was not dependent on the phase of the movement in which the twitch was

evoked during either the fast voluntary or passive movements. The attenuation during the fast voluntary movements was present over a range of twitch amplitudes (Figure 4-2). This shows that the attenuation is not the result of a masking of low intensity stimuli as has been suggested for attenuation of the conscious perception of cutaneous signals (Chapman *et al.* 1987).

The perception of muscle receptor input was attenuated in the simple movements described above. We thought that this may change during skilled tasks more reliant on proprioceptive feedback such as reaching to a target. There is increasing evidence that ascending afferent signals can be selectively gated according to their relevance to the task at hand (Knecht *et al.* 1993; Chapman *et al.* 1996; Staines *et al.* 1997b). Surprisingly, in our experiments muscular sense was still attenuated while subjects reached with the arm being stimulated. Reaching with the contralateral arm did not have this effect suggesting that the attenuation is specific to signals from the moving limb. During preliminary experiments muscular sense remained close to static control values in two subjects during the demanding task of threading a needle.

What is the source of the sensory attenuation we observed? Our results provide evidence that both signals from peripheral receptors excited by the movement itself and central structures can play a role. The attenuation during cyclical stretching of the skin on the dorsum of the hand (Figure 4-3B) indicates a powerful role for cutaneous receptors in gating muscle receptor signals to the brain. Such cutaneous receptors are known to be rhythmically active during movements of the fingers (Edin & Abbs, 1991).

There was also evidence for attenuation of a central origin. Muscular sense was significantly attenuated during active hand movements, compared to that during kinematically-similar passive movements (Figure 4-1). The additional attenuation may reflect centrally mediated effects added to any existing attenuation which may have been laid down from peripheral receptors excited by the movement. Muscular sense was also attenuated throughout the preparation to perform a single flexion-extension movement at the wrist (Figure 4-4). This attenuation, which was evident as long as 350 ms prior to movement onset, occurred before any movement evoked re-afference could have been elicited, though an increase in muscle spindle firing due to preparatory fusimotor set can

not be ruled out. It also seems unlikely that the attenuation was due to a suppression of the memory of twitch perception by the subsequent movement-evoked sensory activity, given the long time course of the effect. The marked increase in the attenuation over the final 100 ms before movement is also likely to have been of central origin. This pattern of premovement gating is reminiscent of that of some spinal reflexes (Pierrot-Deseilligny & Lancert, 1973; Riedo & Ruegg, 1988) and SEPs (Starr & Cohen, 1985; Staines *et al.* 1997a) arising from receptors in the leg and may originate from the motor cortex (Jiang *et al.* 1990).

We do not believe that our finding of a movement-related attenuation of muscle sense is due simply to a non-specific reduction in attention. Firstly, we demonstrated that some of the attenuation can arise from cutaneous feedback not associated with motor preparation. Also, we were unable to demonstrate significant attenuation while subjects counted backwards, a task requiring considerable cognitive attention. During the whole-arm reaching movements, the effect was specific to the arm being moved and was not generalized to both limbs. Further evidence that the attenuation was specific to the performance of movement was the large increase in attenuation over the final 100 ms before movement onset.

Our experiments show that the ability to detect signals from muscle receptors is attenuated during various movement tasks. To what extent does this reflect the normal processing of ascending muscle afferent signals? Admittedly, the afferent volley evoked by our muscle twitch is artificial and unlikely to occur in identical form during natural movements. Recently it has been shown that the ability to detect a small, passively-applied, movement during a voluntary contraction is also attenuated (Wise *et al.* 1998). Though skin sensations were not excluded, these results are consistent with our findings regarding the gating of sensory signals of purely muscle receptor origin. In our experiments, the attenuation was present the first time a twitch was presented during movement and therefore is not the result of a gradually developing active gating of an unwanted signal. Instead, we feel that the results reflect the normal attenuation of anticipated afferent signals. SEP studies have shown that the gating of ascending pathways can be modified according to the relevance of the ascending information

(Knecht *et al.* 1993; Staines *et al.* 1997b). The extent to which such control is exerted over the pathways to the centres of conscious perception is not known.

Previous work has confirmed a major role for muscle receptors in the conscious perception of movement (Goodwin *et al.* 1972; Craske, 1977; McCloskey *et al.* 1983). There is evidence that stationary human subjects may occasionally perceive action potentials from even single muscle receptors in the hand (Macefield *et al.* 1990). However, our results suggest that the ability to perceive these signals is significantly attenuated before, during and after movement. How can we reconcile these findings? First, the sheer magnitude of movement-related sensory input from the periphery should be stressed. During feline locomotion the net input from muscle receptors of a single limb may reach 0.7 million impulses per second (Prochazka & Gorassini, 1997). Under static conditions, this input is far less. Attenuation prior to and during movement may therefore serve to keep the overall input to the central nervous system at manageable levels. In this respect, the control of muscle sense is comparable to the selective gating of ascending cutaneous signals during movement (Angel & Malenka, 1982; Milne *et al.* 1988), which appears to be related to the focusing of attention to relevant inputs (Rushton *et al.* 1981; Chapman *et al.* 1996). The attenuation of muscular sense likely occurs at many levels of the nervous system including the sensory receptors themselves, as a result of control signals emanating from the nervous system.

Our results are consistent with the idea of a general attenuation by spinal and supraspinal mechanisms of peripheral signals during movement (Prochazka, 1989; Brooke *et al.* 1997). In our experiments the attenuation was most evident during large, rapid movements. In tasks requiring fine manipulation involving small, slow movements, muscular sense likely remains closer to static control levels. A technical analogy would be the automatic gain control used in electronic amplifiers to suppress large signals.

We conclude that the conscious perception of signals from muscle receptors is attenuated during movement. This may prevent saturation of the central nervous system by the massive barrage of re-afference generated during movement. The extent to which the nervous system gates the different sensory modalities in the same way, or

differentially, depending on the sensory demands of the task at hand, requires further exploration.

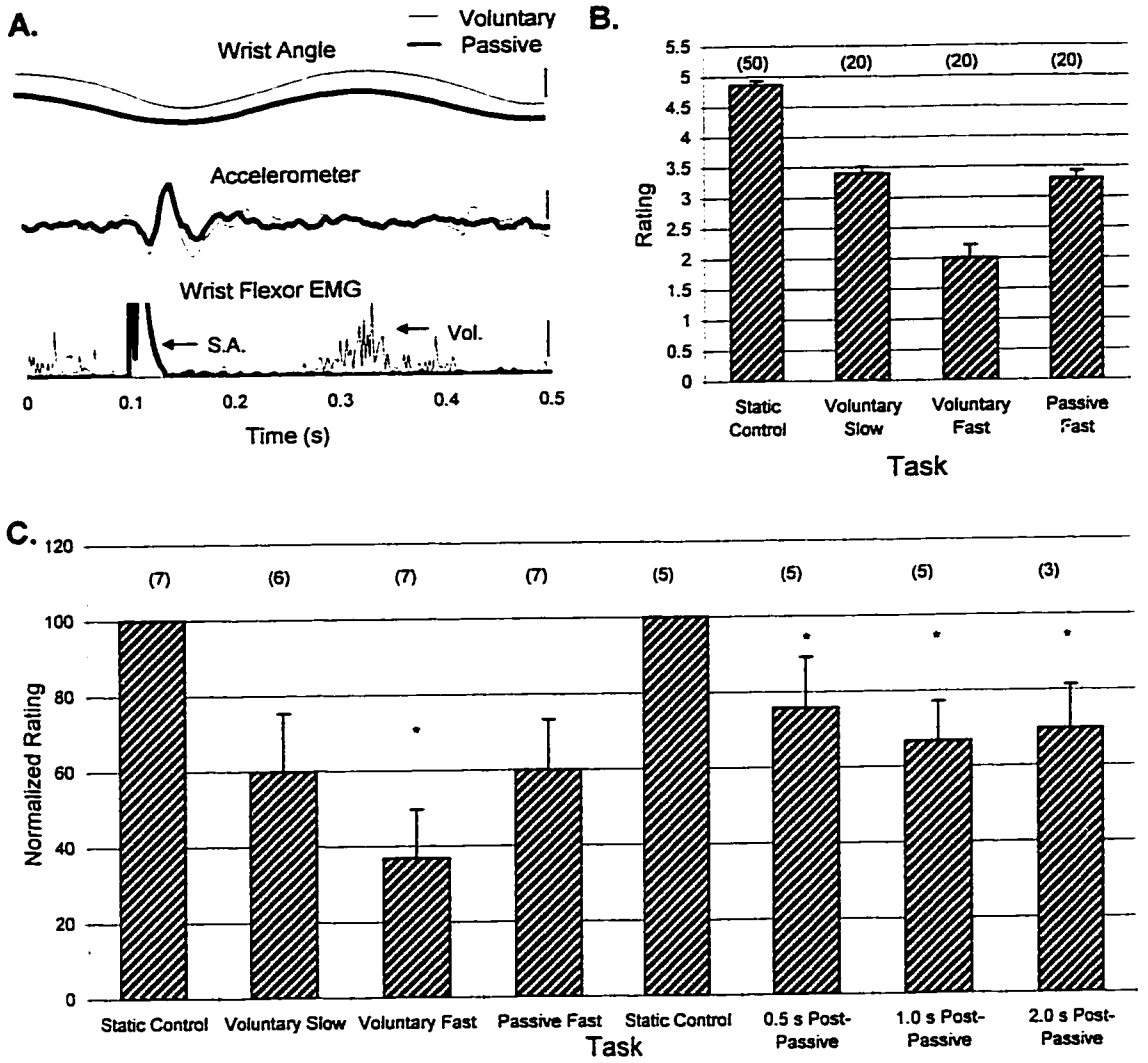

Figure 4-1. Attenuation of muscular sense by wrist movement.
A. Raw data for one subject during fast voluntary (thin line) and passive (thick line) movements. Wrist angle (calibration bar=20^0, flexion downwards), accelerometer signals (approx. calibration 1.2 m/s^2) and wrist flexor EMG (calibration bar=50 μv) are shown in the upper, middle and lower panels, respectively. Stimulus artifact and voluntary EMG activity are denoted by S.A. and Vol., respectively. B. Mean rating of twitch amplitude for the subject in part A. The number of muscle twitches contributing to each mean is given in parentheses. C. Mean ratings across all subjects. The number of subjects contributing to each mean is given in parentheses. Asterisks denote significant differences from control. Error bars depict one standard error about the mean.

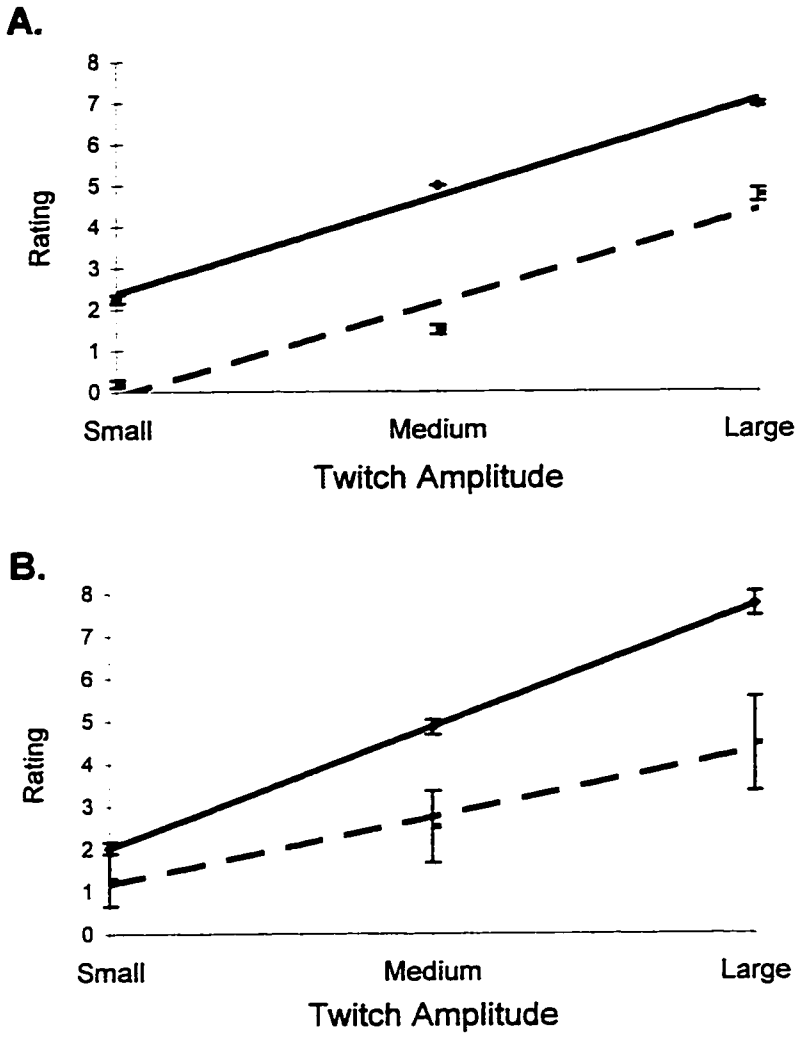

Figure 4-2. Effect of wrist movement on muscular sense at three twitch amplitudes. Mean rating of small, medium and large amplitude twitches for one subject (A) and across all five subjects (B) during 3 Hz voluntary wrist movement (rectangular symbols) and stationary controls (diamond symbols). Dashed and solid lines depict the best-fit lines for the movement and stationary trials, respectively. Error bars depict one standard error about the mean.

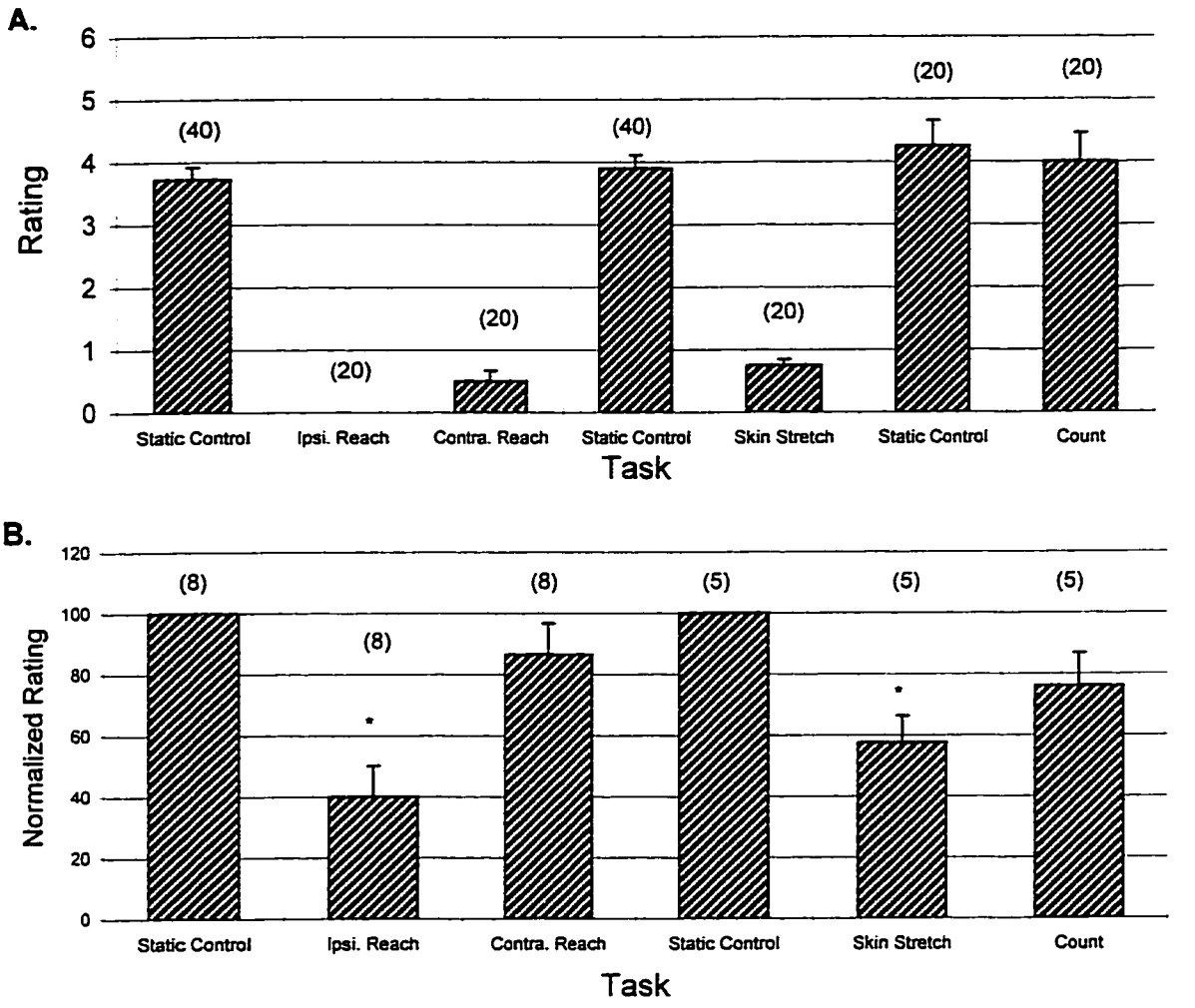

Figure 4-3. Attenuation of muscular sense during other tasks.
A. and B. Mean twitch rating for one subject and across all subjects, respectively. In each graph the appropriate static control rating precedes the corresponding experimental trial. The number of muscle twitches and subjects contributing to each mean is given in parentheses in parts A. and B, respectively. Asterisks denote significant differences from control. Error bars depict one standard error about the mean.

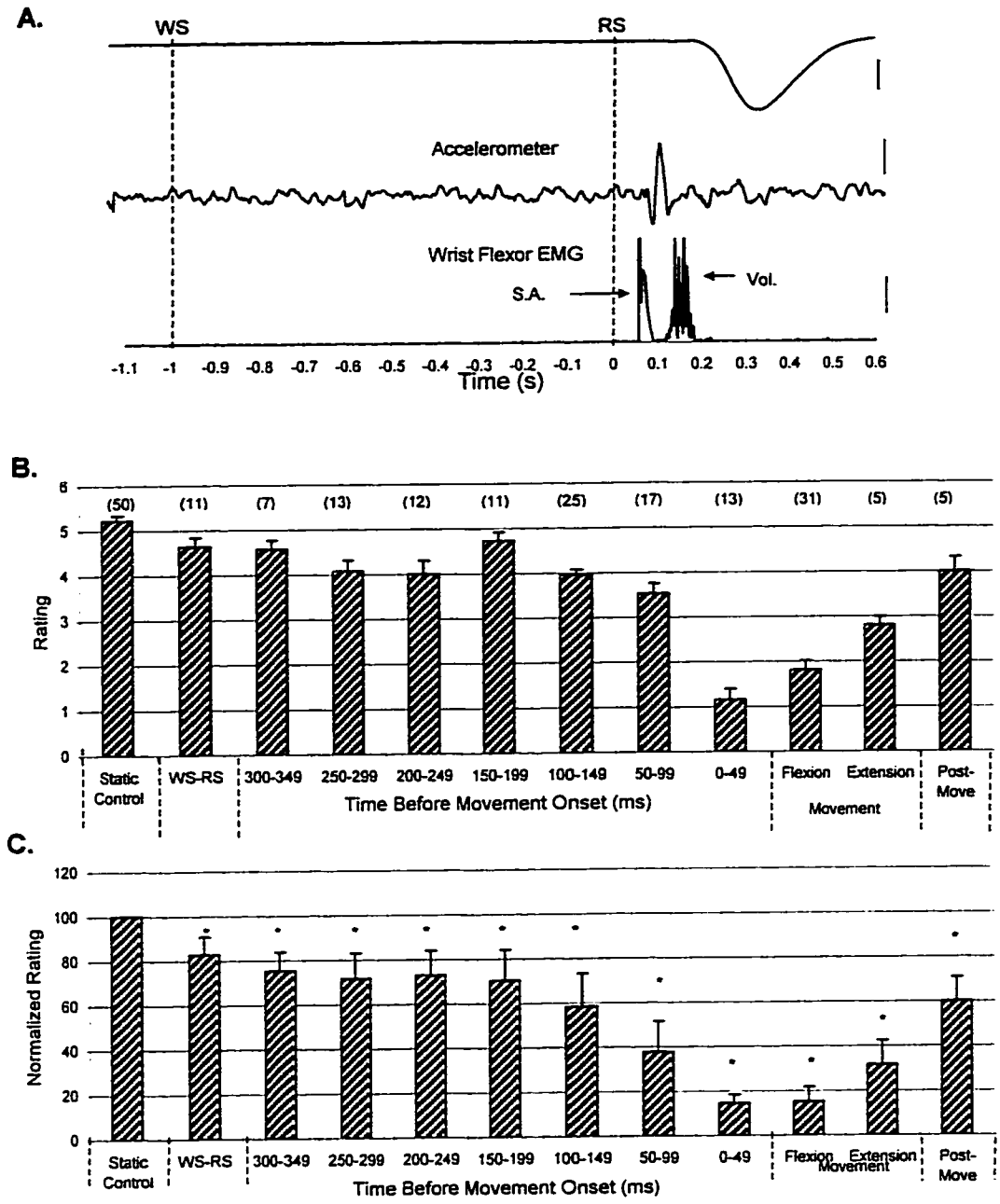

Figure 4-4. Attenuation of muscular sense before movement.
A. Raw data from a typical trial showing wrist angle (calibration bar=20^0, flexion downwards), accelerometer signal (approx. calibration 1.2 m/s^2) and wrist flexor EMG (calibration bar=100 μv) in the top, middle and lower panels, respectively. This trial shows the warning signal (WS) followed 1 second later by the response signal (RS) after which the subject responded with a single flexion-extension movement at the right wrist. Stimulus artifact and voluntary EMG activity are denoted by SA and Vol, respectively. The number of muscle twitches contributing to each mean is given in parentheses. B. Mean rating of twitch amplitude for one subject. C. Mean rating of the twitch amplitude across all subjects. The number of subjects contributing to each mean is shown in parentheses. Asterisks denote significant differences from control. Error bars depict one standard error about the mean.

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5.0 Contact-Evoked Changes in EMG Activity During Human Grasp*

5.1 Introduction

The neural control of hand movements has received increasing attention in recent years. One aspect of this research concerns how sensory feedback modifies the ongoing motor pattern. Since the development of human microneurography (Vallbo and Hagbarth, 1967; Hagbarth and Vallbo, 1967) the nature of the feedback signals has been well documented (Hulliger et al. 1979; Burke et al. 1988; Al-Falahe et al. 1990; Edin and Abbs, 1991; Johansson and Westling, 1991). However, the role of these signals in controlling the grasping of objects is less clear. It has been shown in numerous experiments that sensory feedback is critical in adapting grip forces to sudden slips of an object held between the index finger and thumb (Johansson and Westling, 1984; Johansson and Westling, 1987; Johansson et al. 1992) and while lifting objects with different weights and frictional characteristics (Johansson and Westling, 1984; Westling and Johansson, 1984). In the present study we investigated the contribution of the afferent signal evoked by contact with the grasped object to the modulation of electromyographic (EMG) activity controlling the grasp.

It is well known that immediately after the digits contact the target object during human grasp, grip forces (normal to the object surface) develop in parallel with load forces (tangential to object surface) until sufficient force is developed to lift the object (Johansson and Westling, 1984; Westling and Johansson, 1984). The initial contact with the target object evokes characteristic changes in the activity of cutaneous receptors in the digits (Westling and Johansson, 1987; Johansson and Westling, 1991). Although comparable data for muscle afferents is not available in humans, recordings at footfall during locomotion in cats (Prochazka and Gorassini, 1998) suggests that muscle spindles may also show bursts of activity sufficient to reliably signal contact. It has been shown

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* This chapter has been accepted for publication pending revisions. Collins, Knight, Prochazka. J.Neurophysiol. Approximately 85% of the work for this project was conducted by author DC.

that removal of some of these contact signals by digital anesthesia delays the development of appropriate grip forces (Westling and Johansson, 1984). However, the precise manner in which the signals modify the underlying EMG activity has surprisingly not been as well explored.

Studies of cat locomotion show that some of the EMG activity in early stance arises from afferent input evoked by foot contact (Gorassini et al. 1994). This was revealed by experiments contrasting EMG activity in normal step cycles with those when ground support and thus the sensory burst signaling foot contact, were absent (Gorassini et al. 1994). In the present study we used a similar approach to investigate the role of the sensory contact signal during human grasp. Subjects were requested to grasp, lift and replace an object without the aid of vision. Mean EMG activity from these trials was compared with activity from trials in which the object, and hence the associated contact signal, were unexpectedly absent. We hypothesized that the afferent barrage evoked by contact with the object would initiate increases in EMG activity in the muscles involved in the grasping task beginning at pre-volitional latencies. Portions of these data have been previously published in abstract form (Collins and Prochazka, 1996a).

5.2 Methods

Twelve subjects (9 male, 3 female) aged 22-51 participated. All were informed volunteers and none reported any history of neurological or skeletomotor disease. Experiments were conducted in accordance with the declaration of Helsinki and the University of Alberta Hospitals Ethical Committee. Eight of the subjects were naive to the research hypothesis and the details of the experimental protocol. Two subjects participated in two experimental sessions.

5.2.1 Experimental Protocol

Ten subjects participated in the initial experiments. During all experiments subjects were seated comfortably at a table and were blindfolded or seated behind a

screen to prevent vision of the target object. All movements were made with the right hand. Prior to each trial the right arm and hand rested on the table with index finger and thumb extended in a standardized starting position to adjustable guide-posts on either side of the object (see Figure 5-1A). The guide-post positions were adjusted for the comfort of each subject at the beginning of each session. Subjects were requested to grasp the object between thumb and index finger using a pinch (i.e. precision-type grip), lift it to a height of approximately 5 cm, replace it back on the table and return the fingers to the starting position (object present trials: OP). All movements were self-paced. Before beginning data collection, subjects were allowed sufficient practice to become familiar and comfortable with the grasping task. Rest periods were incorporated to avoid fatigue. Within each session 1-3 blocks of 40-64 trials were collected. After most trials the experimenter replaced the target object to the exact starting position. Randomly interspersed throughout each block were trials (20-33%) in which the object was not replaced by the experimenter and was therefore unexpectedly absent when the subject attempted to grasp it (object absent trials: OA, see Figure 5-1B). Care was taken to ensure that these trials could not be anticipated. Mean EMG activity in OP trials, in which the object and thus the associated sensory contact signals were present, was compared to mean activity in OA trials where these signals were absent.

For the first 5 subjects the target object was a weighted soup can (5 cm diameter, 750 g); for subsequent subjects it was a custom-made rectangular block of stainless steel (3.8x3.8x12 cm high, 500 g). Two thin thermally-molded splints were form-fitted to the dorsal aspect of the right index finger and thumb to reduce movements at the interphalangeal joints (see Figure 5-1). Grip aperture was monitored using a length gauge mounted between the metacarpophalangeal and proximal interphalangeal joints on the index-finger and thumb splints (see Figure 5-1). This gauge was either a mercury-in-rubber length gauge or a strain gauge attached to a thin silastic tube (1mm diameter). The moment of digit contact with the object was monitored in two ways. In the first 5 subjects thin strips of flexible, self-adhesive, conductive material (approximately 5x40 mm) were wrapped around the distal portion of the index finger and thumb that first made contact with the metal object. Upon contact, each digit closed a separate battery circuit and the

resulting signals were recorded. In subsequent subjects two 5 x g accelerometers (Analog Electronics) mounted on the dorsal aspect of the distal part of each splint replaced the conductive strips. The accelerometer signals were band pass filtered (0.1-30 Hz). In the first 9 subjects the duration of the lift of the object from the table was also recorded.

5.2.2 EMG Recording

Surface EMG activity was recorded using self-adhesive, silver/silver-chloride electrodes (2.2 x 3.4 cm, Jason Electrotrace). For each subject, pairs of electrodes were placed over the bellies of 4 of the following muscle groups; first dorsal interrosseus (FDI), flexor pollicus brevis/abductor pollicus brevis (thenar), flexor carpi radialis (FCR), flexor digitorum (FD), extensor carpi radialis (ECR) or extensor carpi ulnaris (ECU). For the intrinsic muscles (FDI and thenar) the electrodes were trimmed to approximately 1.5 cm in diameter. The EMG signals were amplified 1000-3000 times, high pass filtered (10 Hz), full-wave rectified, low pass filtered (300 Hz) and digitized at 500 Hz (see below).

5.2.3 Digital Anesthesia

After initial experiments in 10 subjects the experimental protocol was repeated before and during digital anesthesia of the right index finger and thumb. Four subjects participated in these experiments; 2 of whom had participated in the initial experiments. Four blocks of grasping trials were collected (n=64 trials/block, 25% OA), two before anesthesia and two during the anesthesia. After the first 2 blocks of trials, carbonated Xylocaine (Astra Pharma, product # 173) was injected transcutaneously immediately distal to the metacarpophalangeal joints of the index finger and thumb by an anesthesiologist (co-author BK). The extent of anesthesia was assessed in 3 ways; 1) subjective reports during data collection, 2) standardized tactile perception tests using Semmes-Weinstein monofilaments (Bell-Krotoski and Tomancik, 1987), and 3) comparison of the amplitude of electrically-evoked cutaneous reflexes (see below). Prior to the anesthesia, cutaneous sensibility in all subjects was in the normal range as assessed by monofilament testing (subjects could readily perceive the force applied with the 2.83

monofilament, approximately 0. 8 mN). The extent of the anesthesia was considered sufficient when subjects were unable to detect palpation of the digits by the experimenter and only the largest of the Semmes-Weinstein monofilaments (6.65 monofilament, approximately 2.8 N force) could be detected. Subjects were often unable to detect this monofilament as it indented the skin, but could do so as it was removed. If this extent of anesthesia was not achieved 20-30 minutes post-injection, additional Xylocaine was administered (total amount 2-4 ml/ digit). In 2 subjects, the anesthesia remained complete for the duration of the experiment. The other 2 subjects (S10B and S11 in Table 5-2) reported the return of some cutaneous sensibility during the second block of post-injection trials. Subsequent monofilament and reflex tests confirmed this. For these subjects only data from the first block of post-injection trials were included for analysis of the effect of the digital anesthesia on the contact-evoked responses.

Cutaneous reflexes were evoked by electrical stimulation (3-5 pulses, 300 Hz) of the glabrous skin at the tip of the right index finger and thumb at 3 times perceptual threshold. Three blocks of 100 trials were collected while subjects maintained a moderate pinch grip force. The first block preceded the anesthesia, the second and third occurred during the period of anesthesia, just before and just after the two blocks of grasp trials, respectively.

5.2.4 Reaction Time

A simple reaction time paradigm was used to determine the minimal voluntary reaction time in response to a pulsatile somatosensory stimulus applied to the left index finger. Subjects (n=8) were given a warning signal followed one second later by a response signal to initiate, as quickly as possible, a rapid precision-grip movement using the right hand beginning from the standardized starting position. Both warning and response signals were a mild electric stimulus (single pulse, 1 ms square wave, 1.4 perceptual threshold) delivered to the tip of the contralateral index finger. Contralateral stimulation was used to ensure that changes in EMG activity reflected the voluntary response and not a reflex excitation from the stimulation. Twenty to forty trials were

collected for each subject. To minimize subject anticipation, no response signal was presented in 20% of the trials.

Reaction times were determined by post-hoc analysis of individual reaction time trials from smoothed EMG recordings from FDI. Baseline activity was calculated over the 100 ms immediately prior to the response signal. Onset of voluntary activity was defined as the point at which the EMG activity exceeded 2 standard deviations above this mean for at least 25 ms.

5.2.5 Data Acquisition and Analysis

In order to align all traces to the moment of first contact, or to an estimate of that moment when the object was absent, we derived a trigger pulse from the displacement of the index finger corresponding to close proximity to the object. For each trial, data were stored at least 150 ms before (to a maximum of 1 second) and 250 ms after (maximum 3 seconds) this trigger signal. All data were digitized at 500 Hz (Cambridge Electronic Design 1401 A/D interface using Sigavg 6.0 software) and stored on a personal computer.

Data from the digit contact channels were inspected, post-hoc, to determine the time of first contact in each OP trial. All data from these individual trials were then realigned such that first contact was at time zero. The mean delay from the displacement-derived trigger signal to first contact was calculated and used to align all OA trials.

5.2.6 Statistical Analysis

Contact-Evoked Response Latency

The latency (from contact with the object) at which the mean EMG activity in OP trials became significantly different from that in OA trials was identified for each subject as follows. EMG activity from OP and OA trials was separately averaged over 8 ms bins from time zero (first contact with the object in OP trials) to 98 ms. Student's t-tests (or Mann-Whitney U tests when data were not normally distributed) were used to detect statistically significant differences between corresponding OP and OA bins for individual

subjects. Two-way repeated measures ANOVA tests were used to detect significant differences on mean data across all subjects.

Contact-Evoked Response Magnitude

The magnitude of the contact-evoked responses was expressed as the OP/OA ratio. This ratio was calculated by dividing the mean EMG in the interval 50-100 ms after contact in OP trials by the mean EMG activity over the same interval for OA trials. Student's t-tests (or Mann-Whitney U tests when data were not normally distributed) were used to detect statistically significant differences in mean EMG activity between OP and OA trials over this interval. An OP/OA ratio greater than 1 meant that more mean EMG activity was present over the 50-100 ms interval during OP than OA trials and a ratio less than l indicated that less EMG activity was present during OP trials over that interval.

For illustration and statistical analysis across subjects, data were normalized to the corresponding mean over the 100 ms interval prior to contact in the OP trials. All descriptive statistics are given as the mean $\pm$ one standard error (SE). For all tests statistical significance was accepted when $P<0.05$.

5.3 Results

5.3.1 General Movement Characteristics

Subjects were requested to grasp, lift and replace an object using a precision grip. Mean EMG activity and grip aperture for a single subject (S7 in Table 5-1) during OP trials (n=93) are shown by the thick solid lines in Figure 5-2. The thick vertical dashed line in this and in all subsequent figures represents the time of first contact of one or other digit with the object (see Methods). For this subject, the whole task (from movement onset to return of the digits to the approximate starting position) took 2.0 ± 0.1 s (mean $\pm$ 1 SE). Across the first 9 subjects this duration averaged 2.0 ± 0.2 s. The task was divided into 4 temporal phases. 1.) Movement onset to first digit contact with the object (vertical line in Figures) averaged 153 ± 20 ms across the 9 subjects. The thumb and index finger

usually contacted the object asynchronously. The average difference between contact times was approximately 20 ms. 2.) First contact to object lift-off averaged 269 $\pm$ 45 ms. 3.) The duration of the lift (lift-off to replacement of the object on the table) averaged 1.02 $\pm$ 0.09 s. 4.) Time from replacement of the object to return of the digits to the approximate starting position averaged 0.6 $\pm$ 0.1 ms.

Mean data from OA trials (n=33) for subject S7 are shown by the thin lines in Figure 5-2. These trials were realigned such that the estimate of when contact would have occurred is at time zero (vertical dashed line, see Methods). In most trials in which the target was absent the digits continued moving, though often decelerating, until they touched each other approximately 75 ms after contact would have been made. In 3 subjects, the digits occasionally (in approximately 20% of OA trials) rapidly re-extended, then flexed again beginning approximately 100 ms after contact would have occurred as though in search of the object.

5.3.2 Peripheral Afferent Contributions to EMG Activity

The main focus of this study was to investigate the contribution of the sensory contact signal to EMG activity during human grasp. Therefore, EMG activity was compared between OP and OA trials, the difference being the presence or absence of contact-evoked sensory input, respectively. Figure 5-2 shows large differences in EMG activity between these two conditions for subject S7, developing shortly after contact with the object. These data are replotted in Figure 5-3 on an expanded time scale. Mean raw data and mean binned data are shown on the left and right sides, respectively. Note that the binned data were calculated for the 0-98 ms interval from the corresponding data on the left side (i.e. data between the vertical dashed lines). The left side of Figure 5-3 shows clear differences in EMG activity within the first 100 ms after contact. Statistical analyses of the binned data from this subject (right side of Figure 5-3) indicated that these discrepancies became significantly different 50, 50, 40, and 40 ms after contact for FDI, Thenar, FD and ECR, respectively. Table 5-1 summarizes the results of statistical tests for each subject. Subjects are listed in the order in which they participated in the

experiments and are referred to throughout this paper by the subject code as indicated in this Table and in Table 5-2. Summarized are the latency and the magnitude (OP/OA ratio) of the discrepancies in EMG activity between OP and OA trials. Latencies indicate the earliest latency (after time zero) at which the mean binned EMG activity in OP and OA trials became significantly different. Within 100 ms after contact with the target, significant differences were found in at least one corresponding bin in all subjects and in 40 of the 46 muscles sampled (see Latency measures Table 5-1, FCR data not shown). The shortest latency at which these differences appeared was 30 ms after contact, which was seen in 7 muscles (4 subjects).

The magnitude of the difference in EMG activity between OP trials and OA trials was expressed as the OP/OA ratio (Table 5-1, see Methods). This ratio was calculated from the mean EMG activity levels over the interval 50-100 ms after time zero. More EMG activity was recorded in OP trials than in OA trials over this interval in 33 of the 46 muscles sampled (OP/OA ratio >1). Statistical significance was reached in 24 of these cases. In 12 of the 46 muscles sampled, less EMG activity was recorded during OP trials compared to OA trials (OP/OA ratio <1). This was significant in 8 cases. The OP/OA ratio ranged from 0.4 (S4, thenar) to 4 (S1, FDI).

In general, OP trials showed more activity than OA trials beginning approximately 40-50 ms after contact and lasting throughout the data collection period. However, there were clear exceptions. Characteristics of responses found in the individual muscle groups are described below.

FDI

Mean FDI EMG activity, averaged across all 12 subjects, is shown in the top panel of Figure 5-4. Mean raw data and mean binned data are shown on the left and right sides, respectively (note different time scales). The mean raw data indicate that OP trials began to show more EMG activity than OA trials 40-50 ms after contact. However, this did not reach statistical significance in the individual bins across subjects over the range tested. This is likely due to the large amount of inter-subject variability observed in this muscle (see Table 5-1 and below).

Analysis of the binned data from individual subjects showed significant differences in mean EMG activity during the first 100 ms between OP and OA trials in 11/12 subjects (see Latency in Table 5-1). The onset of these differences ranged from 30 to 80 ms after contact with the object and averaged 49 $\pm$ 6 ms across all subjects. The shortest latency response (30 ms) was seen in 4 subjects.

9/12 subjects showed significant OP versus OA differences in mean EMG activity in the interval 50-100 ms after time zero (see Table 5-1). The OP/OA ratio ranged from 0.6 to 4 and averaged 1.6 over all subjects. Six subjects showed significantly more FDI EMG activity in OP trials. This is reflected in the grand average (Figure 5-4) and an example from a single subject (S7) is shown in the top panel of Figures 5-2 and 5-3. Mean EMG activity for this subject was 2.4 times greater in OP trials than OA trials, averaged over the 50-100 ms interval (see Table 5-1). In contrast, 3 subjects showed significantly less FDI activity in OP versus OA trials. In 2 of these (S9, S12) the discrepancy was quite large (OP/OA ratio=0.6). In subject S9 the difference was brief (60-88 ms) but clear. This was the only case across all subjects and muscles sampled in which the response was consistent with inhibition evoked by electrical stimulation of the digits during a static grasp (see Figure 5-5). In subject S12 significance emerged 70 ms after contact and remained throughout the data collection period, qualitatively similar to that often observed in the thenar muscle group (see below). Subject S8 showed a small but significant decrease in EMG activity from 50-100 ms after contact in the OP trials.

Thenar

Mean raw and binned thenar EMG activity, averaged across 10 subjects, is shown in the second panel from the top in Figure 5-4. The traces began to diverge at approximately 60-70 ms after contact, though statistical significance was not reached until the 90-98 ms bin.

Analysis of the binned data from individual subjects showed significant differences in mean EMG activity between OP and OA trials in 7/10 subjects within the first 100 ms after contact (see Latency in Table 5-1). The onset of these differences ranged from 40 to 80 ms after contact and averaged 63 $\pm$ 5 ms across all subjects.

5/10 subjects showed significant OP versus OA differences in mean EMG activity over the 50-100 ms interval. 8/10 subjects showed less mean EMG activity in OP trials, though this was significant in only 4 cases. An example for a single subject is shown in the left of Figure 5-7 (subject S10B). The OP/OA ratio in this subject was 0.7 (see Table 5-1). In contrast, 3 subjects showed more thenar EMG activity in OP trials. However, this was significant only in subject S5 (OP/OA= 1.8). In 5 subjects there were no significant OP versus OA differences in thenar activity over the 50-100 ms interval. Mean OP/OA ratio across all subjects for the thenar muscles was 0.9.

FCR

In 1 of the 2 subjects in whom data were recorded from FCR, a significant OP versus OA difference was identified 60 ms after contact with the target. In both subjects the OP/OA ratio was 1.1 and there was no significant difference in EMG activity between OP and OA trials over the 50-100 ms interval in either case.

Finger Flexors

Data were recorded from the finger flexors in 10 subjects (FD, n=8; FPL, n=2). Mean raw and binned data are shown in Figure 5-4 (third panel from the top). EMG activity in OP trials was clearly larger than that in OA trials beginning approximately 40 ms after contact. Statistical analysis across all subjects showed that this difference was significant from 60 to 98 ms after contact.

Analysis of binned data from individual subjects showed significant differences in mean EMG activity between OP and OA trials prior to 100 ms after contact in the finger flexors of all subjects. Response latencies ranged from 40 to 80 ms and averaged 52 ± 5 ms (see Table 5-1).

8/10 subjects showed significantly more mean activity in the interval 50-100 ms from time zero in OP trials than in OA trials. OP/OA ratios ranged from 1.2-3.4 in these subjects. Examples of significant responses from individual subjects are shown in Figures 5-3 and 5-7 (FD, left side). The OP/OA ratios for these subjects were 3.4 and 1.4, respectively. One subject (S5) showed a slight, but significant, decrease in mean finger

flexor EMG during OP trials (OP/OA ratio =0.9). Across all subjects OP/OA ratios averaged 1.8.

Wrist Extensors

Data were recorded from the wrist extensors in all 12 subjects (ECR, n=6; ECU, n=6). Mean raw and binned data are shown in Figure 5-4 (fourth panel). As for the finger flexors, these data also show a clear increase in OP versus OA EMG beginning approximately 40 ms after contact. Statistical analysis across all subjects showed that the difference was significant from 50 to 98 ms after contact.

Analysis of binned data from individual subjects showed significant differences in mean EMG activity between OP and OA trials prior to 100 ms after contact in 11/12 subjects. Response latencies in the wrist extensors were the most consistent of all the muscle groups tested, though they still ranged from 30 to 70 ms after contact. Across the 11 subjects the mean latency was 46 $\pm$ 4 ms.

The OP/OA ratios in the wrist extensors were also the most consistent of all the muscle groups tested. All subjects showed more wrist flexor EMG activity in OP than in OA trials over the 50 to 100 ms interval. This was significant in 9/12 cases (OP/OA ratios in these cases ranged from 1.4 to 3.6). Examples of responses for 2 subjects who showed significantly more wrist flexor EMG activity during OP trials are shown in Figures 5-3 and 5-7 (left side). Mean OP/OA ratios in these subjects were 3.6 and 2.4, respectively. On average across all subjects the OP/OA ratio in the wrist extensors was 1.9.

5.3.3 Digital Anesthesia

The OP-OA experiments were repeated before and during anesthesia of the index finger and thumb in 4 subjects. This procedure eliminated all but a slight cutaneous sensibility in the affected digits (see Methods). Reflexes evoked by electrical stimulation of the index finger and thumb at 3 times perceptual threshold, averaged across all subjects (n=4), are shown in Figure 5-5. These data were recorded before the anesthesia and during anesthesia immediately prior to the first block of post-injection grasp trials. The

anesthesia effectively abolished cutaneous reflex responses in all subjects. In 2 subjects (S10B, S11) some cutaneous sensibility returned during the second block of trials post-injection (see Methods); therefore those trials were not included in the analysis. Interestingly, responses recorded during these trials with reduced, but not absent, cutaneous sensibility tended to be intermediate between those from control and fully anesthetized trials.

The anesthesia impaired the subjects' ability to lift the object. In all sessions the object occasionally slipped or dropped to the table. This often occurred without the subject being immediately aware of it. These slips and drops tended to decrease in frequency throughout the data collection period. In general muscle activity levels and patterns during OP trials over the whole grasp movement were quite similar in pre- and post-injection trials. However, there were some instances where more EMG activity was seen during anesthesia.

Mean data across the 4 subjects, before and during digital anesthesia, are shown on the left and right sides of Figure 5-6, respectively. On average, the anesthesia greatly reduced the OP versus OA differences in FD and ECR but suprisingly caused slight increases in these differences in FDI and the thenar muscles. Table 5-2 summarizes the effects for individual subjects. With normal sensibility significant OP versus OA differences were found over the interval 50-100 ms after contact in 12/16 muscles sampled. Anesthesia abolished or reduced these differences in 9 of these muscles, but surprisingly enhanced them in 3 cases (S12, FDI and Thenar; S11, ECR).

The effect of anesthesia on EMG activity is shown for subject S10B in Figure 5-7. Removal of cutaneous feedback from the digits completely abolished all significant OP versus OA differences over the 50-100 ms interval in this subject (see Table 5-2). It is therefore interesting that during anesthesia this subject had relatively few slips or drops of the object compared to the other subjects. In the other subjects, significant OP versus OA differences were present during anesthesia in the 50-100 ms interval in 9/12 muscles. In 2 cases (S6B FDI & thenar) these differences emerged in muscles which showed no significant differences with normal sensibility. With some exceptions, the differences during anesthesia were qualitatively similar to, though smaller than, the differences seen

with normal sensibility. Details of the effects of anesthesia on individual muscle groups are described below.

FDI

Mean responses in FDI across the 4 subjects before and during digital anesthesia are shown in the top panel of Figure 5-6. These data suggest a lack of any OP versus OA difference with normal sensibility but less OP activity from about 60 to 150 ms after time zero during anesthesia.

However, before anesthesia significant OP versus OA differences were found from 50-100 ms after contact in 3/4 subjects (see Table 5-2). Subjects S10B and S11 showed about twice as much EMG activity over this interval in OP trials compared to OA trials before anesthesia (OP/OA ratios of 2 and 2.1 respectively). Anesthesia totally abolished this difference in both subjects (see Figure 5-7 and Table 5-2). One subject (S6B) showed no significant OP versus OA difference before the anesthesia but significantly less EMG activity in OP trials during anesthesia (OP/OA ratio 0.6). The remaining subject showed significantly less activity during OP trials before the anesthesia (OP/OA ratio 0.6) and this discrepancy was somewhat augmented (OP/OA declined to 0.5) during the anesthesia. Across all subjects the OP/OA ratio was 1.4 before anesthesia and 0.8 during anesthesia.

Thenar

Mean responses in the thenar muscles across the 4 subjects before and during anesthesia are shown in the second panel in Figure 5-6. These data show similar OP versus OA differences before and during anesthesia. With normal sensibility 2 of these subjects (S10B, S12) showed significantly less EMG activity during OP trials (see Table 5-2). In subject S10B this difference was eliminated by anesthesia (Figure 5-7), but in subject S12 it was augmented. One of the 2 subjects who showed no significant OP versus OA difference before the anesthesia showed significantly less OP activity during the anesthesia. Across all subjects the mean OP/OA ratio was 0.8 before anesthesia and 0.7 during anesthesia.

FD

Mean responses in FD across the 4 subjects before and during the anesthesia are shown in the third panel of Figure 5-6. These data show a large OP versus OA difference before the anesthesia that was markedly reduced during anesthesia. With normal sensibility, significantly more FD EMG activity was seen in OP than in OA trials in 3/4 subjects. The anesthesia completely abolished these differences in one subject (S10B) and reduced them in the other two (S6B, S11). In the remaining subject no significant OP versus OA differences were identified before or after the anesthesia. Across all subjects the OP/OA ratio was 1.8 before anesthesia and 1.3 during anesthesia.

ECR

Mean responses in ECR across the 4 subjects before and during the anesthesia are shown in the fourth panel of Figure 5-6. As in FD, ECR also showed evidence of large contact-evoked responses before the anesthesia that were reduced during anesthesia. With normal sensibility all subjects showed significantly more ECR activity in OP than in OA trials (see Table 5-2). Digital anesthesia completely abolished this difference in subject S10B (see Figure 5-7) and reduced the differences somewhat in two of the other subjects. In the remaining subject the large OP/OA ratio (2.2) was augmented during the anesthesia (to 2.8). Across all subjects the OP/OA ratio was 2.0 before anesthesia and 1.7 during anesthesia.

5.3.4 Reaction Time

The minimal latency for a volitional response in FDI to somatosensory stimulation of the contralateral fingertip was investigated in 8 subjects. Mean reaction time was 190 $\pm$ 14 ms (range 136-236). The mean minimal reaction time calculated from individual trials was 113 $\pm$ 5 ms (range 92-140).

5.4 Discussion

In the present study we investigated how sensory feedback from the hand helps to shape motor output during human grasp. Specifically, we investigated how the burst of afferent activity known to be evoked when the digits contact the target object (Westling and Johansson, 1987; Johansson and Westling, 1991) contributes to the EMG activity in muscles involved in the task. Data from trials in which subjects performed a standardized precision grasp task were compared to trials in which the target object, and therefore the afferent contact signals, were unexpectedly absent. The results clearly show contact-evoked changes in EMG activity emerging shortly after contact with the object (see Figures 2-4). In individual subjects, significant differences were apparent 30 ms after first contact of the index finger or thumb with the object in 7/46 muscles (see Table 5-1). These contact-evoked changes were often quite large. In one subject (S1 in Table 5-1), 4 times more mean activity was recorded in FDI from 50-100 ms after contact (time zero) in OP trials versus activity over the same interval during OA trials (OP/OA ratio = 4, see Table 5-1). However, in 2 subjects the same comparison showed significantly less activity in FDI over this interval (OP/OA ratio = 0.6-0.8). Qualitatively, the contact-dependent components of EMG activity in the present study were similar to those described in experiments with cats in which extensor EMG in the load-bearing phase of the locomotor step cycle was compared with and without ground support (Gorassini et al. 1994). Similar sensory-driven EMG activity has been seen in human grasp during experiments in which a ball was dropped into a hand-held receptacle, causing it to slip between the subject's thumb and fingers. Slip-evoked compensatory EMG responses were absent when the ball was unexpectedly prevented from landing in the receptacle (Johansson and Westling, 1988a).

In our study, contact-evoked responses in the intrinsic hand muscles (FDI and thenar) were somewhat variable across subjects. Most often there was more FDI EMG activity during OP trials compared to OA trials (significant in 6/12 subjects). However in 3 subjects, significantly less activity was recorded in FDI during OP trials, contrary to our initial hypothesis. This latter pattern was seen in the thenar muscles in 8 of 12 subjects,

though the discrepancy was significant in only 4 cases. With hindsight, we should not have expected a simple contact-evoked excitation of the thenar muscles, given their functional role in the present task (see Functional Implications below). Responses in the extrinsic muscles (finger flexors and wrist extensors) were more consistent across subjects. Significantly more EMG activity was recorded in OP than OA trials in 17/22 extrinsic muscles sampled. In only one case (subject S5, finger flexors) was significantly less activity recorded in OP trials.

5.4.1 Receptor Origin

The obvious candidates for the receptors of origin of these contact-evoked responses are cutaneous receptors in the digit tips. These receptors are ideally situated to signal the moment of contact with a grasped object (Johansson, 1996) and microneurographic studies have shown characteristic changes in their firing rates upon contact (Westling and Johansson, 1987; Johansson and Westling, 1991). The role played by these receptors in the rapid adaptations to slips of grasped objects has been well documented (Johansson and Westling, 1984; Johansson and Westling, 1987; Johansson et al. 1992). It has also been shown that these receptors encode the frictional characteristics of the object surface (Johansson and Westling, 1984; Westling and Johansson, 1984) and that this information is utilized to adjust grip forces independently at the digits (Edin et al. 1992; Burstedt et al. 1997). Previous studies have also shown that removal of this feedback by digital anesthesia often delays the development of appropriate grip forces (Westling and Johansson, 1984) and can even affect movement kinematics throughout the reaching and grasping trajectory (Gentilucci et al. 1997). Our results show that these receptors play an important role in initiating short-latency contact-evoked responses in EMG activity. Removal of feedback from the digits by anesthesia completely abolished OP versus OA differences in one subject (see Figure 5-7) and reduced the differences in 5 of the remaining 8 muscles (3 subjects) in which there were significant differences with normal sensibility. These changes in contact-evoked EMG activity likely underlie the

delay in the development of appropriate grip forces seen previously (Westling and Johansson, 1984).

However, the digital anesthesia did not eliminate all contact-dependent EMG responses in the present study. Significant responses were present in 9 muscles after all cutaneous feedback from sites distal to the metacarpophalangeal joints of the index finger and thumb was removed. This suggests that receptors other than cutaneous receptors in the digits can also play a role. In 3 cases OP versus OA differences were augmented during skin anesthesia. The receptor populations which mediate these contact-dependent responses may vary both between and within subjects. The removal of all contact-evoked responses by skin anesthesia in subject S10B (Figure 5-7) suggests that this subject relied primarily on cutaneous feedback from the digits to signal contact. In contrast, other subjects showed contact-driven responses during the anesthesia which must have originated from other afferent sources. Even within a subject it appears that different receptor populations may mediate the contact-driven responses in different muscles. For example in subject S11, digital anesthesia abolished OP versus OA differences in FDI but augmented them in ECU (see Table 5-2). With the full complement of receptor populations to choose from the nervous system may preferentially utilize signals from skin receptors in the digits which provide the most reliable or functionally relevant signal. When this feedback from the digits is not available the nervous system may switch to alternate afferent sources. These afferent sources may include cutaneous receptors remote from the digits which are known to be active during finger movements and have been shown to be involved in adaptations during slips (Hager-Ross and Johansson, 1996). Also, chronic recordings in cats (Prochazka and Gorassini, 1998) suggest that muscle spindle receptors may provide suitable contact-related signals. It seems unlikely that muscle forces would build up quickly enough after first contact to significantly activate Golgi tendon organs (in part due to the asynchronous nature of thumb and finger contact) in time to mediate the EMG responses. Similarly, joint receptors probably play a minimal role as they are active primarily at the extreme ranges of joint rotation (Burgess and Clark, 1969; Ferrell, 1980).

5.4.2 Neural Pathways

In general, the sensory signals evoked by contact with the object initiated changes in EMG activity starting between 30-50 ms after contact and persisting throughout the data collection period. The afferent signals responsible likely follow several routes through the nervous system. The resulting changes in EMG activity probably reflect the summation of activity in all these pathways. In 9 subjects (15/46 muscles) the leading edge of the changes occurred 30-40 ms after contact. Responses as rapid as these are presumably mediated segmentally; longer latency components of the response in the range 50-70 ms likely involve ascending pathways, cerebellum and sensorimotor cortex (Jenner and Stephens, 1982; Macefield et al. 1996). Motor cortical excitability changes during reaching and grasping have been studied (Datta et al. 1989; Johansson et al. 1994; Schieppati et al. 1996; Lemon et al. 1996). Excitability has been shown to increase during reaching in regions controlling extrinsic muscles, and increase during grasping in regions controlling intrinsic hand muscles (Lemon et al. 1996). It is thought that the apparently high excitability in cortical regions controlling intrinsic muscles at the time of contact with the object "may reflect a powerful interaction, at the cortical level, between cutaneous inputs signaling contact with the object" and motor cortex excitability (Lemon et al. 1996). Similarly, the interaction between cutaneous inputs from the hand and motoneuronal excitability is also somewhat task-dependent (Evans et al. 1989). The extent to which continuing sensory input acting through segmental circuits contributes to EMG activity at medium and longer latencies is not clear.

The fastest voluntary reaction time we recorded in FDI in response to pulsatile contralateral somatosensory stimulation of the digits during a single trial was 92 ms. Allowing 12 ms for interhemispheric transfer of motor commands (Schieppati et al. 1985) we feel that any EMG activity more than 80 ms after contact for intrinsic muscles and 75 ms for extrinsic muscles could conceivably include voluntary components. Propriospinal mechanisms and sensory input to them have been shown to contribute to the control of reaching and grasping movements in cats (Alstermark and Lundberg, 1992). This may also apply to human grasping (Pierrot-Deseilligny, 1996). Abnormal grip forces seen in

patients with disorders of the cerebellum (Muller and Dichgans, 1994)or basal ganglia (Muller and Abbs, 1990) suggest that these structures may also be also involved.

In summary the contact-related EMG activity we observed likely involves several neural routes and a number of central nervous structures all of which contribute to different extents and at different latencies after contact.

5.4.3 Functional Implications

Our results show that, on average, the sensory contact signals initiated changes in EMG in that were functionally relevant to the task at hand (see Figure 5-4). Typical response patterns included contact-driven enhancement of the activity in the prime movers (FDI, finger flexors). This would contribute to the build-up of pinch-grip forces required to lift the object from the table. Also, all subjects showed a contact-evoked enhancement of the activity in the wrist extensors which would help to stabilize the wrist for the lift. The coactivation of muscles controlling the fingers and wrist during precision grip is thought to contribute to grasp stability (Werremeyer and Cole, 1997). The most common response in the thenar muscles was less activity when the object was present. These muscles do not act as agonists in the present task as evidenced by the inverse modulation of thenar and FDI EMG in Figure 5-2. This pattern of activity during precision grip has been shown previously in abductor pollicus brevis (a thenar muscle) (Johansson and Westling, 1988b). The contact-driven decrease may serve to terminate activity in muscles which oppose the movement. The somewhat variable responses in the thenar muscles may reflect the non-specific nature of surface EMG recording from the three muscles of the thenar eminence which perform different biomechanical functions. The variability in responses in FDI are more difficult to explain and may reflect individual motor strategies.

Our results highlight the importance of afferent signals in regulating phase transitions in movements: only when contact signals were present were successive phases of the motor program for the grasp executed (see Figure 5-2). This is consistent with studies showing a delay in the onset of appropriate grip forces while grasping during

digital anesthesia (Westling and Johansson, 1984). Also, afferent signals evoked when a hand-held object contacts the table are important in terminating motor commands for grasp (Johansson and Westling, 1988b). Similar afferent-controlled phase transitions are seen in the cat step cycle (Pearson and Collins, 1993).

Our results may have relevance for the sensory control of grasp in active orthotic devices for people with spinal cord injury or stroke (Hoffer et al. 1996; Prochazka et al. 1997). Such a device could utilize sensors on the digits to detect contact with objects in order to trigger stimulation of specific muscle groups to mimic the role of the contact signal in human grasp or other tasks. To avoid inappropriate force application such a device may have to modulate the feedback gain according to the task. Indeed, there are many examples of task-dependent gain modulation of sensory pathways throughout the nervous system (Prochazka, 1989) and grip forces are known to be adjusted according to the properties of the held object (Johansson and Westling, 1984; Westling and Johansson, 1984). Infant grasping tends to be indiscriminately strong and it could well be that one of the important functions of motor learning is to develop appropriate task-dependent sensory gain control.

Our results underline the important role of cutaneous feedback, including segmental mechanisms, in controlling hand and finger movements. It has long been known that cutaneous receptors are crucially important in the control of hand movements (Mott and Sherrington, 1895) and in recent years there has been a resurgence of interest and research into the precise role of these receptors and their central actions (Edin and Johansson, 1995; Johansson, 1996; Collins and Prochazka, 1996b; Gentilucci et al. 1997).

5.4.4 Summary

Our study showed that sensory input signaling first contact with a grasped object is responsible for a significant amount of the subsequent activation of the hand muscles. The onset latencies of sensory-dependent EMG activity were mostly less than voluntary reaction time, suggesting mediation by more automatic mechanisms. Abolishing cutaneous sensory input from the fingertips changed and in some cases eliminated the

contact-related components of EMG. This indicates that skin input plays a dominant role in the short-latency control of grasp onset, as previously shown for adaptations of grasp to load or load changes. The variation in contact-related EMG patterns we observed between muscles and also between subjects suggested that sensorimotor integration during grasp is highly task-dependent and may also vary from one individual to another.

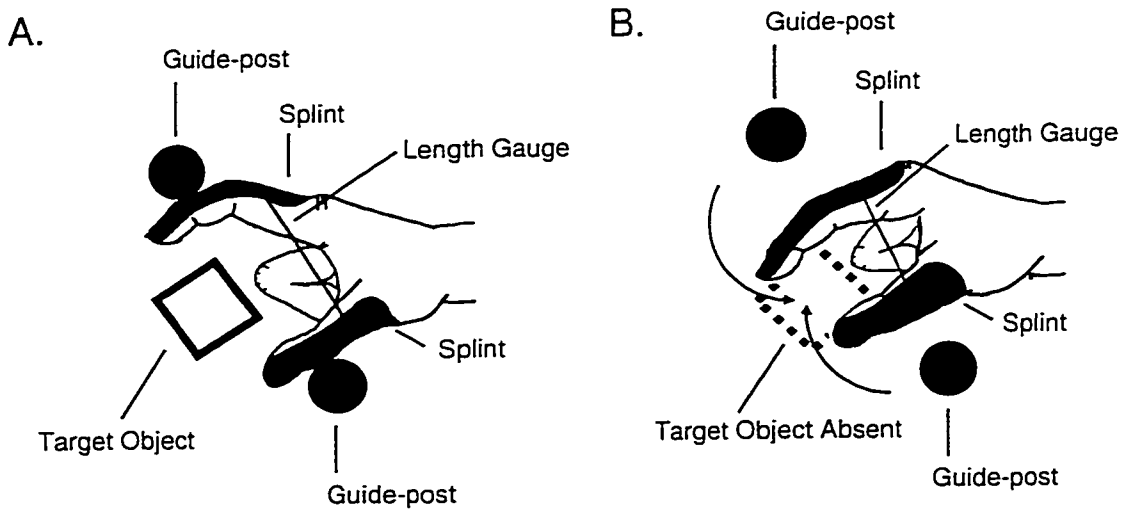

Figure 5-1. Diagram of the experimental paradigm.
A. Standardized starting position for the hand. Before each trial the digits were extended to adjustable guide-posts. B. Example of a trial in which the target object was unexpectedly absent (object absent: OA).

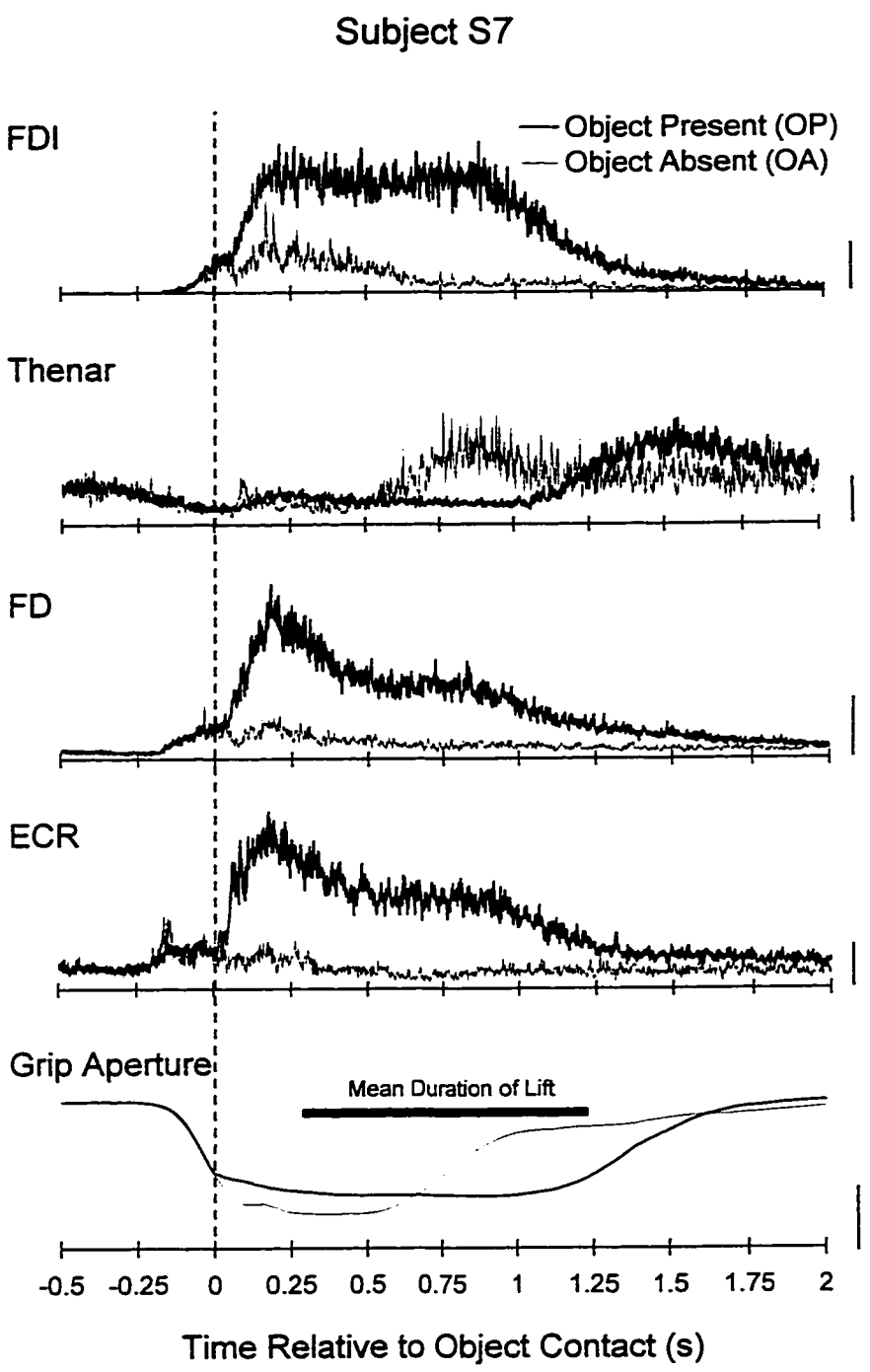

Figure 5-2. Mean rectified EMG in 4 muscles for a single subject.
Data for subject S7 are shown for OP trials (n=93) and OA trials (n=33). The moment of first contact with the target in OP trials is shown by the vertical dashed line. The horizontal solid line over the grip aperture trace shows the average length of time the target object was lifted off the table. Calibration bars = 50 μV for EMG data and 2 cm for grip aperture.

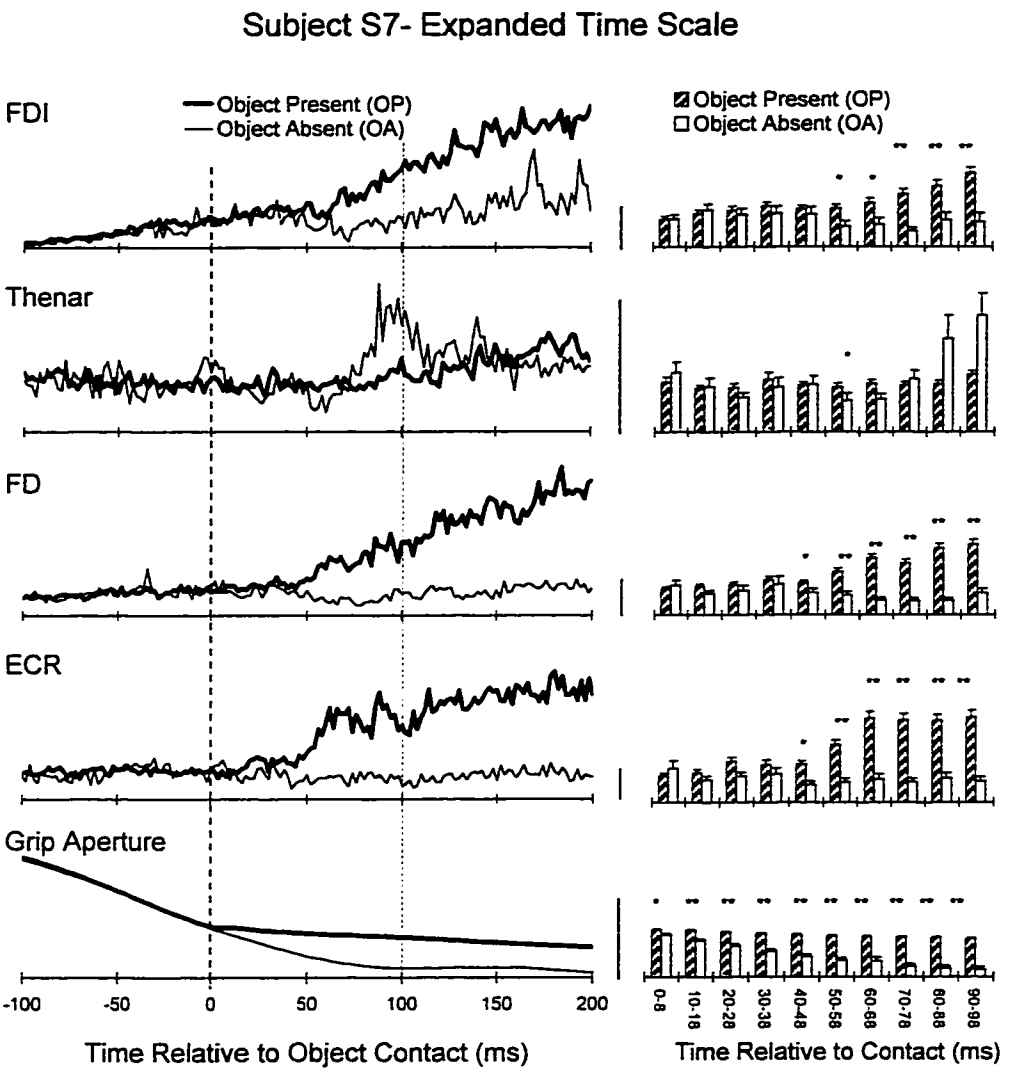

Figure 5-3. Portion of the data in Figure 5-2 shown on an expanded time scale. Left: mean rectified EMG data shown from 100 ms before to 200 ms after contact with the object. The moment of first contact with the target in OP trials is shown by the thick vertical dashed line. Right: mean EMG data binned in 8 ms bins from corresponding data over the interval between the two vertical dashed lines in left side of the Figure (0-98 ms). Calibration bars = 25 μV for EMG data and 2 cm for grip aperture. Statistical significance: *<0.05, ** < 0.0001.

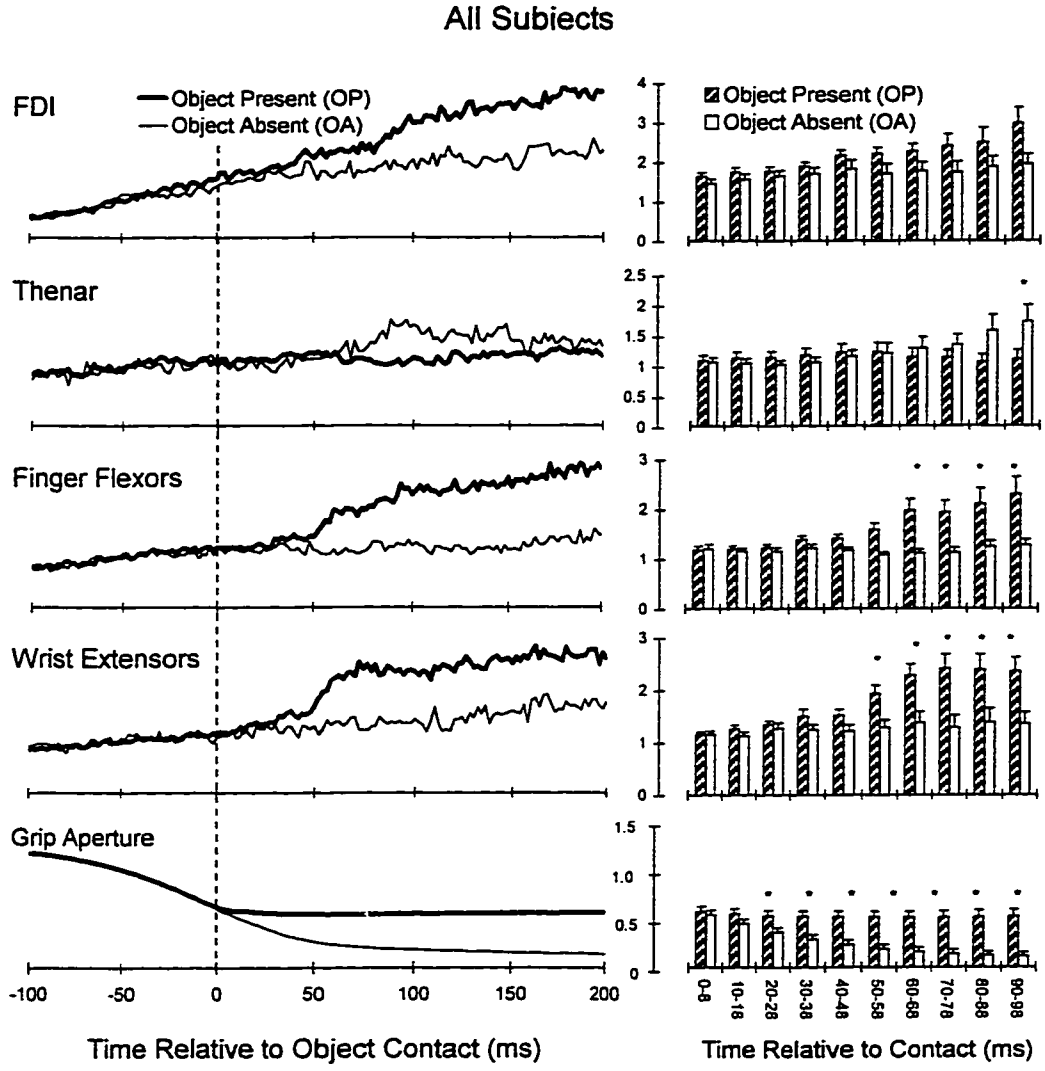

Figure 5-4. Mean data across all subjects.
Data for each subject were normalized to the corresponding mean during the 100 ms prior to contact in the OP trials. Left: mean rectified EMG data from 100 ms before to 200 ms after contact with the object in OP trials. Right: mean EMG in 8 ms bins from the moment of contact with the object to 98 ms after contact. Statistical significance: *<0.05.

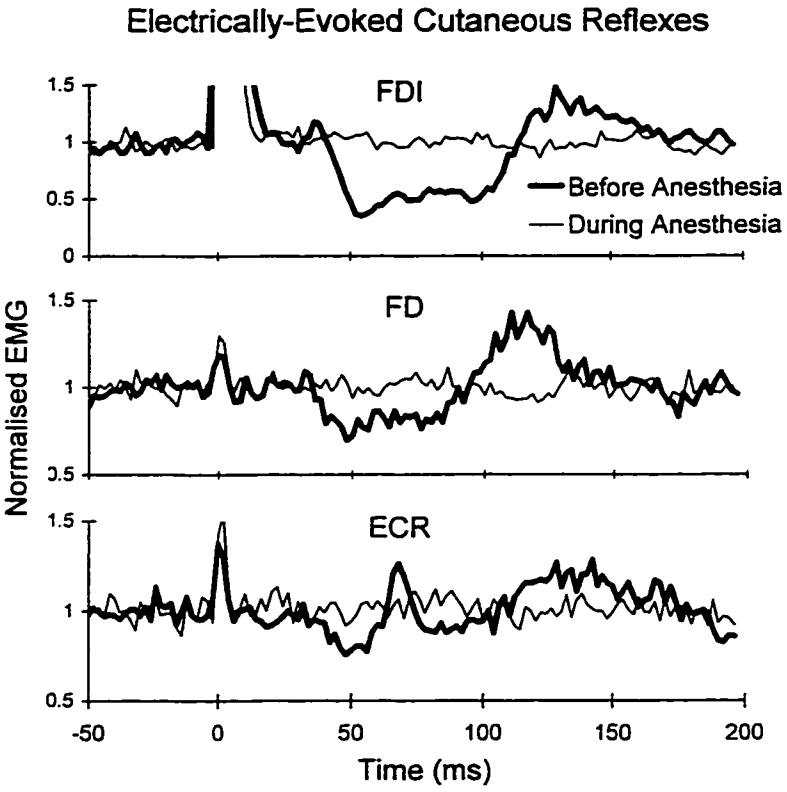

Figure 5-5. Electrically-evoked cutaneous reflexes before and during digital anesthesia.
Data for each subject were normalized to the corresponding mean during the pre-stimulus 100 ms. Averaged responses in three muscles to stimuli delivered at time zero (n=100). Deflections in first 10 ms are stimulus artifacts.

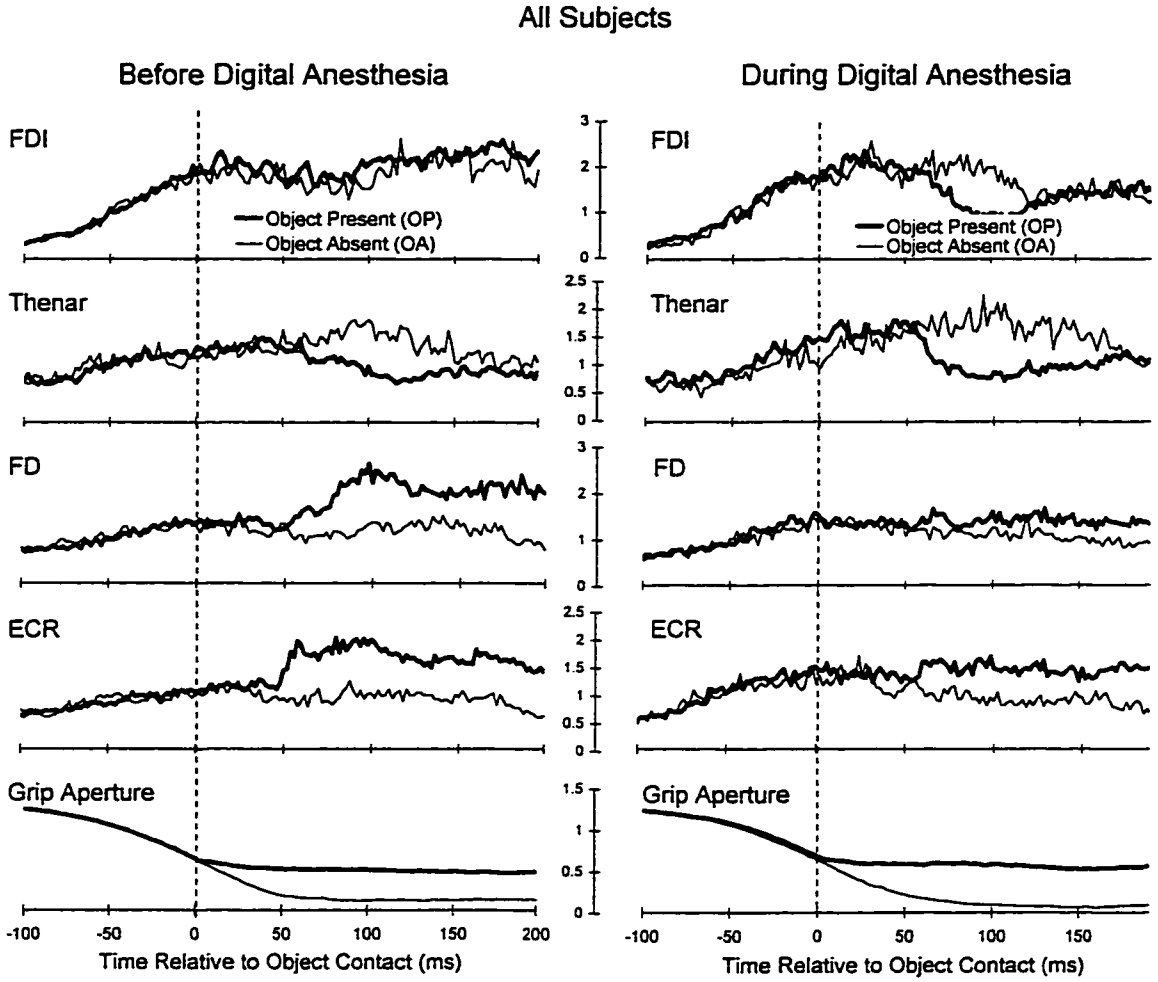

Figure 5-6. Mean effect of anesthesia on contact-dependent responses.
Rectified EMG data across four subjects before anesthesia (Left side) and during anesthesia (Right side). Data for each subject were normalized to the mean activity during the 100 ms prior to contact in the OP trials.

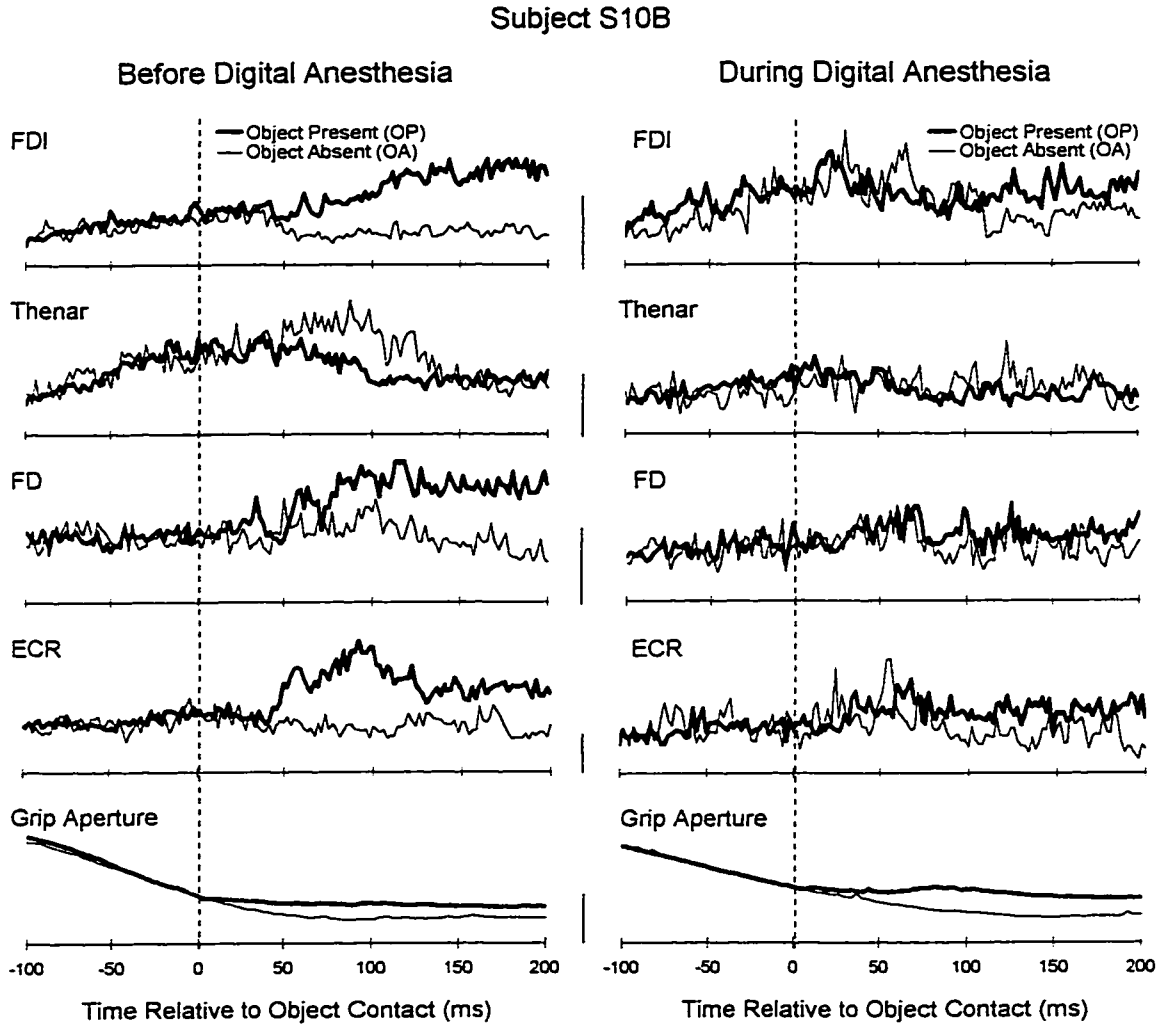

Figure 5-7. Mean rectified EMG data from a single subject before (left) and after (right) digital anesthesia.
Note the abolition of differences between OP and OA trials during anesthesia. Calibration bars = 25 μV for EMG data and 2 cm for grip aperture.

Table 5-1. Summary of contact-evoked changes in EMG activity for individual subjects.

Shown are the latency and magnitude of differences in mean EMG between OP and OA trials. Latency values show the time after contact with the object at which mean EMG activity during OP trials became significantly different than that in corresponding OA trials. Magnitudes are expressed as the OP/OA ratio and were calculated by dividing the mean EMG activity over the 50-100 ms interval in OP trials by the mean activity over the same interval during OA trials. Statistical significance: *<0.05, ** < 0.0001, "ns" denotes no significant difference.

	Latency (ms) & OP/OA Ratio							
	FDI		Thenar		Finger Flex.		Wrist Ext.	
Subject	Latency	OP/OA	Latency	OP/OA	Latency	OP/OA	Latency	OP/OA
S1	40	4.0 **	ns	0.8 ns			70	1.4 ns
S2	30	2.1 **	70	0.6 *	40	1.5 **	30	1.7 **
S3	30	1.4 ns			40	1.9 *	40	1.5 *
S4	80	1.0 ns	60	0.4 **	70	1.2 *	50	1.9 **
S5	ns	1.2 ns	40	1.8 *	80	0.9 *	60	1.4 *
S6a	30	1.5 **	80	0.8 **	30	1.3 **	50	2.6 **
S7	50	2.4 **	50	0.8 ns	40	3.4 **	40	3.6 **
S8	50	0.8 *	ns	0.9 ns			ns	1.2 ns
S9	60	0.6 *	ns	1.2 ns	70	1.3 *	30	1.2 ns
S10a	70	2.0 **			50	2.8 **	50	2.5 **
S11	30	2.1 **	70	0.8 ns	50	2.3 **	50	2.2 **
S12	70	0.6 **	70	0.7 **	50	1.1 ns	40	1.7 **
Mean	49	1.6	63	0.9	52	1.8	46	1.9

Table 5-2. Summary of the effect of digital anesthesia on the magnitude of contact-evoked changes in EMG activity between OP and OA trials.
Magnitudes are expressed as the OP/OA ratio which was calculated by dividing the mean EMG activity over the 50-100 ms interval in OP trials by the mean activity over the same interval in OA trials. Statistical significance: *<0.05, ** < 0.0001, "ns" denotes no significant difference.

	Muscle Group (OP/OA ratio)			
Subject	FDI	Thenar	FD	ECR
S10b				
before	2.0 **	0.7 **	1.4**	2.4**
During	0.8 ns	0.8 ns	1.2 ns	1.2 ns
S6b				
Before	1.0 ns	0.9 ns	2.3**	1.6**
During	0.6 **	0.6 **	1.6**	1.4**
S11				
Before	2.1 **	0.8 ns	2.3**	2.2**
During	1.1 ns	1.0 ns	1.3*	2.8**
S12				
Before	0.6 **	0.7 **	1.1 ns	1.7**
During	0.5 **	0.4 **	0.9 ns	1.3**
Mean				
Before	1.4	0.8	1.8	2.0
During	0.8	0.7	1.3	1.7

5.5 References

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6.0 Task-Dependence of Stretch Reflexes During Human Precision Grip Movements

6.1 Introduction

It is well known that the gain of reflex pathways from muscle receptors in the leg can be modulated prior to and during tasks (Pierrot-Deseilligny & Lancert, 1973; Capaday & Stein, 1986; Dietz *et al.*, 1990). Much of this modulation is independent of background electromyographic (EMG) activity and apparently originates presynaptically to the motoneuronal membrane (Brooke *et al.*, 1991; Capaday & Stein, 1986; Capaday & Stein, 1987). This is important as it shows that mechanisms within the central nervous system (CNS) can regulate afferent transmission, presumably according to the requirements of the task. Compared to the leg there have been fewer studies of the regulation of proprioceptive reflex pathways in the upper limb. The upper limbs perform more varied and complex tasks than the lower limbs which may be more reliant on afferent feedback and a much greater area of the cortex is devoted to the control of their movements (Penfield & Rasmussen, 1950).

The available evidence shows that proprioceptive reflexes of the upper limb are also modulated. Several studies have investigated task dependence of stretch-evoked EMG responses in arm muscles. These responses are initiated primarily by excitation of muscle receptors (Bawa & McKenzie, 1981; Burke *et al.*, 1983) and, at similar background EMG levels, changes in their amplitude reflect gain modulation of signals traversing both segmental and supraspinal pathways (Matthews *et al.*, 1990; Marsden *et al.*, 1977). During *static* trials, EMG responses were larger when subjects were instructed to maintain a constant position versus maintain a constant force, in several muscles controlling the hand. (Akazawa *et al.*, 1983; Doemges & Rack, 1992a; Doemges & Rack, 1992b). Stretch reflexes are also modulated during *movement* of the upper limb. The amplitude of stretch reflexes in muscles controlling the elbow were extensively

modulated throughout a cycle of elbow movement, independent of the background EMG activity (Dufresne *et al.*, 1980; MacKay *et al.*, 1983). A recent study has shown that stretch reflexes in the long flexor of the thumb (FPL) are attenuated during thumb movements, compared to static trials (Wallace & Miles, 1998). However, this is contrary to the results of the early studies of Marsden et al. (Marsden *et al.*, 1976) which showed no such attenuation during similar movements.

The role of these proprioceptive reflexes in the control of grasp is not well understood. Potentially, they could contribute to the EMG activity required to perform the task. During locomotion, feedback from muscle receptors is thought to account for as much as 60% of the EMG activity in the soleus muscle (Yang *et al.*, 1991). We have recently shown an important role for afferent feedback in the initiation of EMG activity during human grasp (Collins *et al.*, 1998). The sensory volley evoked by contact with the target object was shown to initiate changes in EMG activity at a latency of approximately 50 ms (Collins *et al.*, 1998). Digital anesthesia impaired the contact-dependent EMG responses showing the importance of cutaneous feedback from the digits to these responses. However, the anesthesia rarely abolished and in some cases did not alter the responses, indicating that other receptors are involved. (Collins *et al.*, 1998). These may include cutaneous and muscle receptors remote from the digits. Some evidence that pathways from muscle receptors are augmented during grasp was provided by Traub et al. (1980) who showed larger reflexes when subjects held a glass of sherry compared to control trials.

The present experiments were designed to answer two main questions: 1. Are stretch reflexes in hand muscles attenuated during index finger movement, compared to stationary controls? 2. If so, can some of the movement-induced attenuation be altered by changing the demands of the task? To address these questions, EMG responses to rapid extension of the index finger were compared between static trials and two movement tasks involving index finger flexion. To answer the first question we compared stretch reflexes recorded during the static trials to those from trials when subjects were instructed to simply move the index finger to touch the thumb. We predicted that the reflexes would be attenuated during the movement trials in accordance with findings of a general

suppression of reflex pathways during movement. To answer the second question, we compared reflex amplitudes recorded during the movement tasks described above to those recorded during kinematically-similar movements requiring subjects to grasp and lift a metal weight. During all tasks stretches were applied at approximately the same grip aperture, corresponding to that at the moment the index finger contacted the weight in the latter task. We hypothesized that there would be less movement-related attenuation during the grasp task, to permit the afferent feedback to contribute to the ongoing EMG activity required to perform the task. Some of these data have been published in abstract form (Collins & Prochazka, 1996).

6.2 Methods

Eight subjects (5 male, 3 female) aged 24-32 participated. All gave informed consent and none reported any history of neurological or musculoskeletal disease. Experiments were conducted in accordance with the declaration of Helsinki and the University of Alberta Hospitals Ethical Committee.

6.2.1 EMG Recording

Surface EMG activity was recorded using self-adhesive, silver/silver-chloride electrodes (2.2 x 3.4 cm, Jason Electrotrace). For each subject, pairs of electrodes were placed over the bellies of 2 or 3 of the following muscle groups; first dorsal interrosseus (FDI), flexor digitorum superficialis (FDS) and/or flexor carpi radialis (FCR). Electrodes for FDI were trimmed to approximately 1.5 cm in diameter. The EMG signals were amplified 1000-3000 times, high pass filtered (10 Hz), full-wave rectified, low pass filtered (300 Hz) and digitized at 500 Hz (see below).

6.2.2 Experimental Protocol

During all experiments the subjects were seated comfortably at a table and were blindfolded or seated behind a screen to prevent vision of the right arm distal to the mid-forearm. All tasks were performed with the right hand. Prior to each trial the right arm and hand rested on the table with the wrist fitting snugly between three adjustable supports (see Figure 6-1D). Two thermally-molded splints were form-fitted to the dorsal aspect of the right index finger and thumb to reduce movements at the interphalangeal joints. Grip aperture was monitored using a length gauge mounted between the two splints, just distal to the MCP joints (see Figure 6-1D). The length gauge consisted of a miniature cantilever strain gauge attached to a 1mm diameter silastic tube.

Stretch reflexes were evoked by an imposed extension of the index finger. The perturbation (amplitude-12 mm, rise time- 20 ms, duration 100-125 ms) was applied using a custom-made electromagnetic linear motor. A flexible cable was fixed to the dorsal side of a molded ring (approximately 1 cm width) fitted snugly around the distal interphalangeal joint (see Figure 6-1). During all trials this cable was connected to one of two rings on the electromagnetic motor (see Figure 6-1 and below). The supports and splints ensured that movements were restricted to the MCP joint of the index finger.

6.2.3 Tasks

Data were collected while subjects performed three separate tasks. For each subject, one to three blocks of 40 trials were collected for each task (see below). Before the onset of data collection, subjects were allowed sufficient practice to become familiar and comfortable with each task. Rest periods were incorporated to avoid fatigue. Trials in which stretches were imposed (approximately 50%) were randomly interspersed within each block. For each task the stretches were applied at the same grip aperture corresponding to that at the moment of contact of the index finger with the target object during Task 3 (see below). In this position the tip of the thumb and index finger were approximately 4 cm apart, see Figure 6-1D. The order in which the three tasks were performed was randomized across subjects.

Task 1. Static.

During these trials subjects maintained a steady pinch grip between the thumb, which rested against a support firmly fixed to a bracket on the table, and the index finger, which pulled against the linear motor (see Figure 6-1A and D). Imposed stretches were applied at 2-5 second intervals. Four of the subjects were requested to maintain each of three force levels subjectively rated as low, medium and high. One block of trials was collected at each level. The order of these blocks was randomized across subjects. The other four subjects performed one block of static trials during which they maintained a constant FCR EMG level displayed on an oscilloscope. The level was pre-determined to approximate that during the two movement tasks. Subjects were instructed not to intervene during the imposed stretch.

Task 2. Move.

During these trials subjects were requested to move the index finger to touch the thumb which rested against the thumb support used in the static trials (see Figure 6-1B). One block of trials was collected for each subject. All movements were self-initiated and self-paced. However, if the task order was such that these trials were preceded by Task 3, subjects were asked to perform this movement at approximately the same speed as Task 3. Prior to each trial the thumb rested against the support and the index finger was extended to an adjustable guidepost. Hand position relative to the motor was precisely adjusted to ensure that the flexible cable connecting the index finger to the motor via a hook and ring became taut at a grip aperture predetermined to be equal to that at the moment of finger contacted the weight in Task 3 (see Figure 6-1B and below). The first increase in force detected by the sensitive force gauge located between the cable and the motor was used as a trigger signal to initiate the pull from the linear motor. For perturbed trials, the cable was attached to the closed ring on the motor shaft which held secure, thus delivering the imposed stretch (see Figure 6-1B). For unperturbed trials, the hook on the flexible cable was attached to the open ring on the motor shaft which permitted the hook to slip through. The very slight force transient this caused was sufficient to trigger the

motor but insufficient to be detected by the subject or elicit reflex responses. Between trials the subject extended the index finger while the experimenter re-attached the cable to the motor. Subjects were unable to predict when a trial would involve an imposed stretch.

Task 3. Grasp.

During these trials subjects were requested to grasp a stainless steel weight (3.8x3.8x12 cm high, 750 g) between index finger and thumb and lift it approximately 5 cm (see Figure 6-1B). One block of trials was collected for each subject. All movements were self-initiated and self-paced. However, if the task was such that these trials were preceded by Task 2, subjects were asked to perform this movement at approximately the same speed as Task 2. Hand position prior to each trial and at the time of the imposed stretch was the same as in Task 2 (see Figure 6-1D). Between trials the subject extended the index finger and thumb while the experimenter replaced the weight at the starting position and re-attached the cable to one of the two rings on the motor. For perturbed trials, the base of the weight was clipped to a rigid bracket on the table (see Figure 6-1) so that the surface touching the thumb rigidly blocked thumb movement during the perturbation of the index finger. Subjects were unable to predict when a trial would involve an imposed stretch.

6.2.4 Data Acquisition and Analysis

Data were stored 250 ms before and 500 ms after a trigger signal. For the static trials, the trigger signal was derived from the computer keyboard. The trigger signal also initiated the pull from the motor for perturbed trials. For both movement tasks the trigger signal was derived from the force sensor on the electromagnetic motor (see above). All data were digitized at 500 Hz (Cambridge Electronic Design 1401 A/D interface using Sigavg 6.0 software) and stored on a personal computer.

Data from trials with imposed stretches were averaged together for each subject, task and muscle. Individual subjects' data were included for analysis only when EMG activity over the pre-stretch 30 ms was not significantly different between the three tasks.

If significant differences were present over this interval, up to 5 individual trials were removed from the average for one or more of the tasks, post-hoc to standardize the mean pre-stimulus EMG activity. EMG response magnitudes were calculated over two 30 ms intervals after the stretch for each muscle based on visual inspection of the data. In general, two periods of excitation were seen in the EMG traces approximately 24-54 and 60-90 ms after the onset of the stretch. We have adopted the M1 and M2 nomenclature of Tatton et al. (Tatton *et al.*, 1975) for the early and late responses, respectively. Mean EMG activity was calculated over these intervals for each muscle and task using data from individual subjects. Data for each subject were normalized to the mean EMG activity during the pre-stretch 30 ms period for each respective task.

6.2.5 Statistical Analysis

Tests for statistically significant differences in EMG activity between tasks were conducted on data from individual subjects and across all subjects. Tests on data from individual subjects were conducted using one-way analysis of variance tests (ANOVA) or Friedmans ANOVA when the data were not normally distributed. Tests across all subjects were conducted using one-way repeated measures ANOVA. For all tests statistical significance was accepted when $P<0.05$.

6.3 Results

6.3.1 Movement and Perturbation Characteristics

Tasks 2 and 3 involved voluntary flexion movements of the right index finger MCP joint. Kinematic details during unperturbed trials for these movements, averaged across all subjects, are given below.

The duration of index finger flexion for Task 2, from movement onset to contact of the index finger with the weight, was approximately 0.1 s. Mean rate of change of measured grip aperture of grip aperture closure over this interval was approximately 20

mm/s. This was estimated to be equivalent to an angular velocity of 18 ^{0}/s at the index finger MCP joint. Movement duration for Task 3, from movement onset to contact of the index finger to the thumb support, was approximately 0.2 ms. Mean movement velocity over this interval was approximately 25 mm/s corresponding to an angular velocity of approximately 22 ^{0}/s at the MCP joint.

The perturbation applied by the electromagnetic motor was consistent both within and between subjects. Averaged across all subjects the amplitude of the perturbation was 12 mm $\pm$ 0.3 mm. Within a block of 40 trials the perturbation parameters were maintained within very narrow constraints. The effect of the perturbation on grip aperture is shown for each task in the middle panels of Figures 6-3 to 6-5. Across all subjects and tasks the mean velocity of the perturbation estimated at the MCP joint was approximately 400 ^{0}/s.

6.3.2 Stretch-Evoked EMG Responses

To test for task dependent changes in reflex amplitude independent of the muscle or response latency we combined the M1 and M2 response amplitudes from all the muscles (n=30). Significant differences were identified between all three tasks as shown in Figure 6-2. The stretch-evoked responses were significantly larger during Task 1 (Static) than during both movement tasks. Between the movement tasks, responses were significantly larger during Task 3 (Grasp) than Task 2 (Move).

The stretch-evoked responses in individual muscle groups are described below. Numerical descriptions are normalized to the mean EMG activity over the pre-stretch 30 ms for each task.

FDI

Mean rectified FDI EMG activity recorded during perturbed trials while subjects (n=5) maintained a static pinch grip is shown by the thick lines in the top two panels of Figure 6-3. In this and all subsequent figures, data for a single subject are shown in A and averaged across all subjects in B. The EMG data are replotted as the solid bars in the

respective lower panels, normalized and averaged over three 30 ms intervals (pre-stretch 30 ms, M1, M2). Mean M1 response amplitude across all subjects during the static trials was 1.6 (range 1.1-1.9, normalized to pre-stretch 30 ms). In 4/5 subjects this was followed by a larger M2 response as shown in Figure 6-2. On average M2 amplitude was 2.0 (range 1.0-2.6) and the M1/M2 ratio for this muscle was 0.8.

Across all subjects the mean amplitude of the M1 response in FDI was not significantly different between tasks (see Figure 6-3B, bottom panel). Despite this, task-dependent differences were seen in the individual data from 3/5 subjects. In 2 subjects M1 was significantly smaller (see Figure 6-2A) and in 1 subject M1 was significantly larger, during Task 2 compared to both other tasks.

The amplitude of the M2 response in FDI was highly task-dependent. As shown in Figure 6-3B, averaged across all subjects, the large M2 response seen during the static trials (amplitude 2.0) was absent during both movement tasks. The corresponding amplitudes for move and grasp tasks were 1.0 and 0.9, respectively. A similar attenuation is shown for a single subject in Figure 6-3A. There was no significant difference in M2 amplitude between the two movement tasks averaged across all subjects.

FDS

Mean rectified FDS EMG activity during static trials is shown by the thick lines in the top two panels in Figure 6-4. These data are replotted as solid bars in the respective lower panels, normalized and averaged over the three 30 ms intervals. Of the three muscles studied, the relative amplitudes of M1 and M2 in FDS were the most variable between subjects. Across all subjects (n=4) M1 amplitude was 3.2 (range 1.8-5.5) and M2 amplitude was 2.5 (range 0.9-4.3). This corresponds to a M1/M2 ratio of 1.3 for this muscle.

Figure 6-4B shows that the amplitude of the M1 response in FDS was significantly attenuated during both movement tasks, compared to the static trials. However, as shown in Figure 6-4A the movements did not attenuate M1 in all subjects.

Across all subjects, M2 amplitudes in FDS were not significantly different between tasks (see Figure 6-4B). The expression of M2 could be quite variable even

within a single subject. For example, the subject in Figure 6-4A showed a large M2 response during the grasp task which was absent during the other two tasks. This is despite the presence of similar M1 responses for this subject in all three tasks. In contrast, in another subject (not shown) M2 was present during the static task but was absent during both other tasks.

FCR

Mean rectified FCR EMG recorded during static trials is shown by the thick lines in the top two panels of Figure 6-5. Responses in this muscle were dominated by M1 the normalized amplitude of which averaged 5.2 across all subjects (range 1.7-12.7). Typically (4/6 subjects), M1 was followed by a very small M2 response as can be seen for one subject in Figure 6-5A. However, in two subjects M1 and M2 were of similar amplitude. Mean M2 amplitude across all subjects was 1.9 (0.8-3.3) and the M1/M2 ratio for this muscle was 2.7.

Across all subjects, M1 was significantly attenuated during both movement tasks compared to the static trials (see Figure 6-5B). This attenuation was significant in each of the 6 subjects. Across all subjects there was no significant difference between the two movement tasks. In individual data, in three subjects there was no difference between the movement tasks and in the other three M1 was larger during the grasp trials.

As can be seen in Figure 6-5B, M2 responses were generally small in FCR. Despite this, across all subjects M2 was significantly attenuated during the move task compared to the static trials (see Figure 6-5B, bottom panel).

6.4 Discussion

We compared the amplitude of stretch reflexes in hand muscles between static trials and two tasks requiring flexion of the index finger. In all three muscles studied, reflexes were significantly attenuated during both movement tasks, compared to the static task. Across all muscles, reflexes were significantly larger during the grasp and lift task compared to when subjects simply moved the index finger to touch the thumb. The

results show that proprioceptive reflexes are attenuated during index finger movements and that this attenuation can be modified according to the task.

6.4.1 Experimental Control

We do not believe that the observed differences in reflex amplitudes arose from methodological differences between tasks. Stretches were evoked at the same hand position and grip aperture for each task. The index finger, thumb and wrist were well supported to restrict movements to the index finger MCP joint. The activation level of the muscles was relatively consistent between tasks. Data were only included for analysis when mean EMG activity over the pre-stretch 30 ms interval was not significantly different between tasks. The perturbation delivered by the electromagnetic motor was consistent both within and between.

6.4.2 Afferent Origin and Neural Pathways.

It is generally agreed that imposed stretches predominantly excite primary muscle spindle receptors and to a lesser extent cutaneous and secondary muscle spindles receptors (Bawa & McKenzie, 1981; Burke *et al.*, 1983). Experiments during digital anesthesia occasionally attenuated but never abolished stretch-evoked responses showing the importance of feedback from muscle spindles to these responses (Jaeger *et al.*, 1982).

In our study we calculated the EMG responses to the stretch over two intervals relative to the onset of the stretch: M1 (24-54 ms) and M2 (60-90 ms). This nomenclature was adopted from the early work of Tatton et al. (Tatton *et al.*, 1975). These responses are believed to arise from neural signals traversing two pathways through the CNS. The M1 component is almost certainly a spinal reflex response. Consensus on the neural pathway for the M2 component has been slower in coming but it is now generally agreed that a supraspinal route including the motor cortex is involved (Matthews, 1991). However, the extent to which supraspinal pathways contribute to long latency responses may vary between different muscles of the upper limb (Thilmann *et al.*, 1991).

In the static trials in our experiments the relative amplitude of M1 and M2 depended on the distal-proximal location of the muscle. Mean M1/M2 ratios across subjects increased from 0.8 to 1.3 to 2.7 for FDI (most distal), FDS and FCR (most proximal), respectively. This predominance of the long-latency response in distal muscles and of the short latency response in more proximal muscles has been previously reported and is thought to reflect a greater cortical control over the distal musculature.

6.4.3 Task-Dependent Reflex Modulation

The first question addressed in these experiments was: Are reflexes in hand muscles attenuated during index finger flexion? Our results showed consistent and significant attenuation of stretch reflexes in all muscles during both movement tasks, compared to the static trials. This is in agreement with findings of stretch reflex attenuation in both the upper and lower limbs during movement (Dietz *et al.*, 1990; Wallace & Miles, 1998). Indeed, our experiments may not have revealed the maximal difference between static and movement tasks, because reflex amplitudes may have been larger when subjects maintained a constant position than when they maintained a constant force as they did in our study (Doemges & Rack, 1992a). The attenuation during movements may prevent saturation of the reflex pathways by afferent traffic associated with movement and permit the motoneuronal pools to remain receptive to other inputs.

Several sources could account for the attenuation of reflex amplitude between the static and movement tasks. Differences in fusimotor drive or spindle unloading between the static and movement tasks could result in changes in the afferent volley evoked by the stretch. Though there is little evidence for dissociation of alpha and gamma drive in humans (Prochazka, 1996), we cannot rule out that spindle unloading may have contributed. Reafference from peripheral receptors has been shown to attenuate spinal and supraspinal reflex responses from muscle receptors of the human leg (Brooke *et al.*, 1997). The evidence to support this sensory gating of reflex pathways includes attenuation of H reflexes during passive movements (McIlroy *et al.*, 1992) and following tendon taps (Cheng *et al.*, 1995). More direct evidence from reduced preparations

identifies a significant role for muscle spindle feedback from leg extensor muscles (Misiaszek *et al.*, 1995; Misiaszek & Pearson, 1997). A similar mechanism may exist in the upper limb as suggested by the attenuation of FCR H reflexes during passive movements (Tarkka & Larsen, 1987). There is also clear evidence that the CNS can modify reflex pathway gains independent of peripheral feedback. This is supported by changes in reflex gain in the absence of changes in peripheral feedback such as that observed prior to movement (Cole & Abbs, 1987) and, between different static tasks (Doemges & Rack, 1992a). It is likely that both peripheral and central sources contribute to the movement-associated attenuation of stretch reflex amplitudes.

The second question we addressed was: Can some of the movement-induced attenuation be altered by changing the demands of the task? Our results supported the hypothesis that the attenuation is less when the task is more demanding. This would ensure that muscle receptor feedback elicited at the moment of contact with the object during human grasp could contribute to the EMG activity required to perform the task. Feedback from cutaneous receptors also contributes to EMG activity at this point during human grasp (Collins *et al.*, 1998) and it may be that cutaneous reflexes are also modulated in a task-dependent manner during this task.

The kinematic similarities between the two movement tasks make it likely that afferent feedback and spindle unloading were similar between the two tasks. Hence, the observed differences in individual subjects' data likely reflect a descending control of the afferent pathways. Interestingly, our results show that this control can be exerted independently over M1 and M2 response pathways. Within individual subjects the task-dependent changes were not always similar for M1 and M2. This can be seen by the appearance of the large M2 response only during the grasp task in Figure 6-4A. This is despite the similarity of M1 amplitudes between tasks for this subject.

The presence of movement-induced attenuation of stretch reflexes in the present study was clear and generally consistent across subjects. However, the difference in reflex amplitudes between the two movements tasks, though significant was rather variable between subjects. This variability may represent individual motor control strategies that differ in the extent to which afferent feedback is utilized during

movements. Such differences in motor strategies may be related to motor skill. A recent report has shown a significant correlation between the ability to inhibit stretch reflexes in the wrist flexors and fast reaction times in the wrist extensors (Kizuka *et al.*, 1997).

6.4.4 Conclusion

Many studies have identified the attenuation of proprioceptive reflexes during movement. The present results extend these finding to stretch reflexes in hand muscles during index finger flexion. The attenuation was found for reflexes traversing both spinal and supraspinal pathways and likely originates from several sources. Reflex amplitudes were significantly larger during movements that required subjects to grasp and lift a weight compared to when they simply moved the index finger to touch the thumb. This may permit signals from muscle receptors to contribute to ongoing activity during the grasp. However, intersubject variability in this task-dependent modulation suggests that individual strategies in the use of afferent feedback may vary.

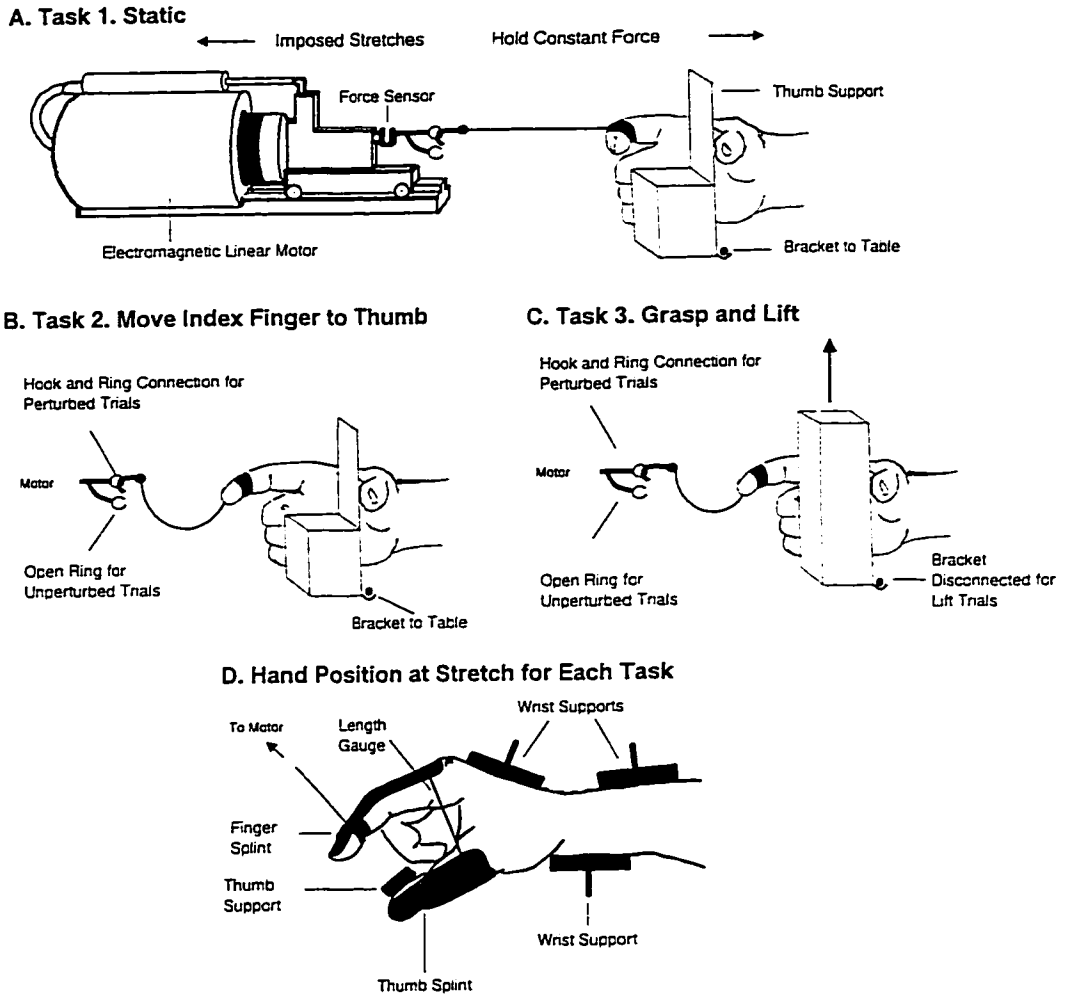

Figure 6-1. Diagram of the experimental set-up.
Stretches reflexes were evoked during three tasks. A. Task 1 Static. Subjects maintained a static pinch grip between thumb and index finger. The electromagnetic motor (not shown for parts B-D) was used to rapidly extend the index finger MCP joint in approximately 50% of the trials during all tasks. B. Task 2 Move. Subjects moved the index finger to touch the thumb. Note the different attachments to the motor for perturbed and unperturbed trials for this and the subsequent Tasks. C. Task 3 Grasp. Subjects grasped and lifted a weight using a similar movement of the index finger as in Task 2. D. Hand position at stretch. The perturbation was applied at the same grip aperture for each task. Note the bracing of the thumb, index finger and wrist.

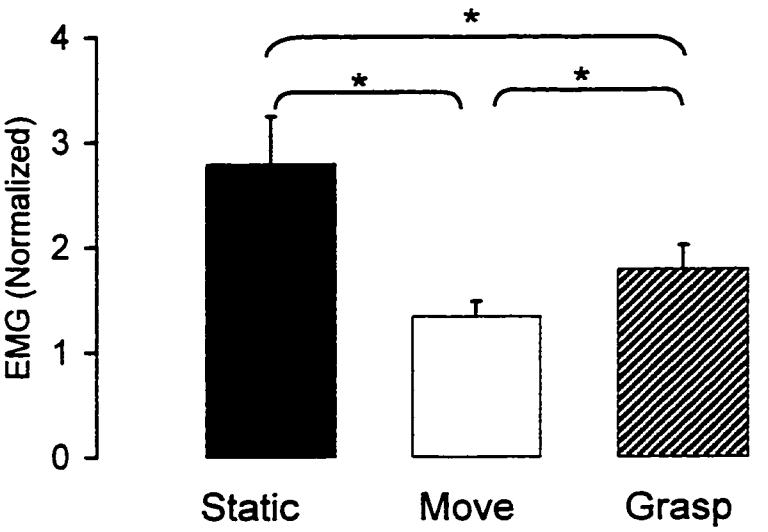

Figure 6-2. Mean effect of task on M1 and M2 stretch reflex amplitudes.
Shown is the mean response amplitude for each task for all three muscles. Amplitudes are normalized to the mean EMG activity over the 30 ms prior to stretch onset. Error bars depict one standard error of the mean. Asterisks denote significant differences.

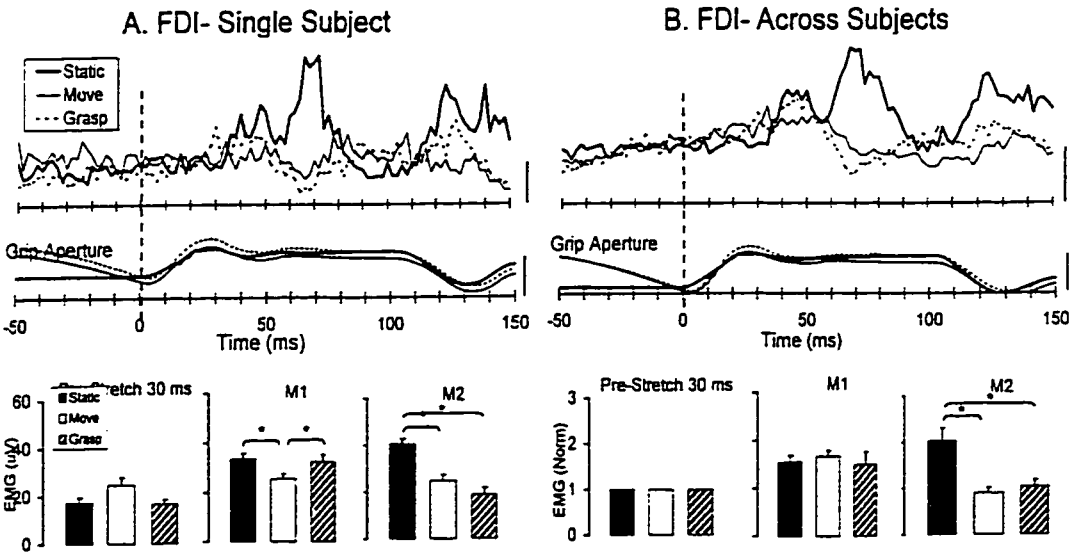

Figure 6-3. Mean FDI EMG activity and grip aperture during all three tasks. Shown are data for a single subject in A and averaged across all subjects (n=5) in B. In A and B, mean rectified EMG activity, grip aperture and mean EMG activity averaged over three 30 ms intervals relative to stretch onset are shown in the upper, middle an lower panels, respectively. The EMG data in Part B are normalized to the mean activity over the pre-stretch 30 ms for each task. Asterisks denote significant differences between tasks. Calibration bars represent 25 μv and 10 mm for the upper and middle panels of Part A and 1 and 10 mm for the upper and middle panels of Part B, respectively.

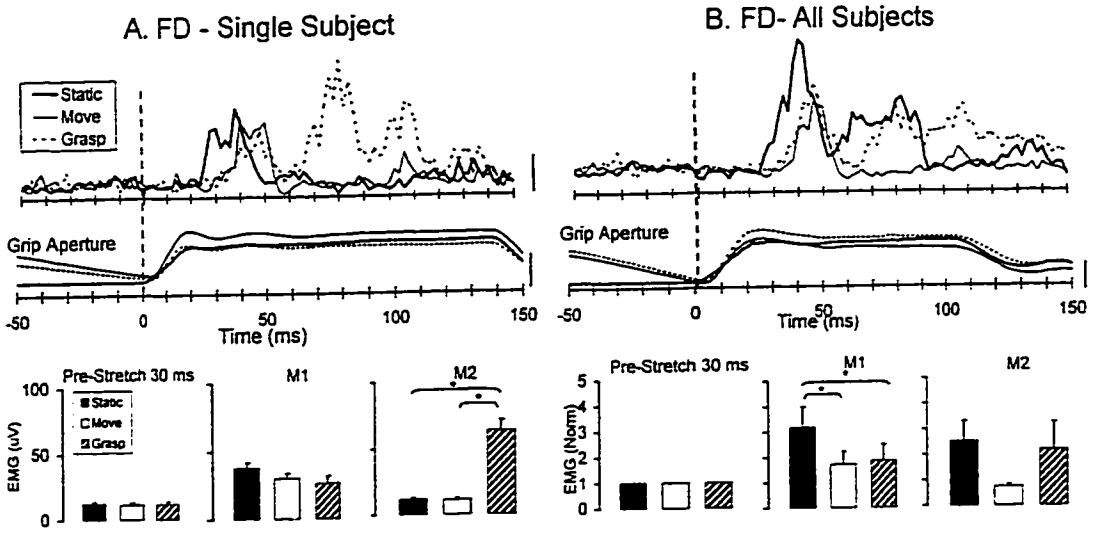

Figure 6-4. Mean FDS EMG activity and grip aperture during all three tasks. Shown are data for a single subject in A and averaged across all subjects (n=4) in B. In A and B, mean rectified EMG activity, grip aperture and mean EMG activity averaged over three 30 ms intervals relative to stretch onset are shown in the upper, middle an lower panels, respectively. The EMG data in Part B are normalized to the mean activity over the pre-stretch 30 ms for each task Asterisks denote significant differences between tasks. Calibration bars represent 25 μv and 5 mm for the upper and middle panels of Part A and 1 and 5 mm for the upper and middle panels of Part B, respectively.

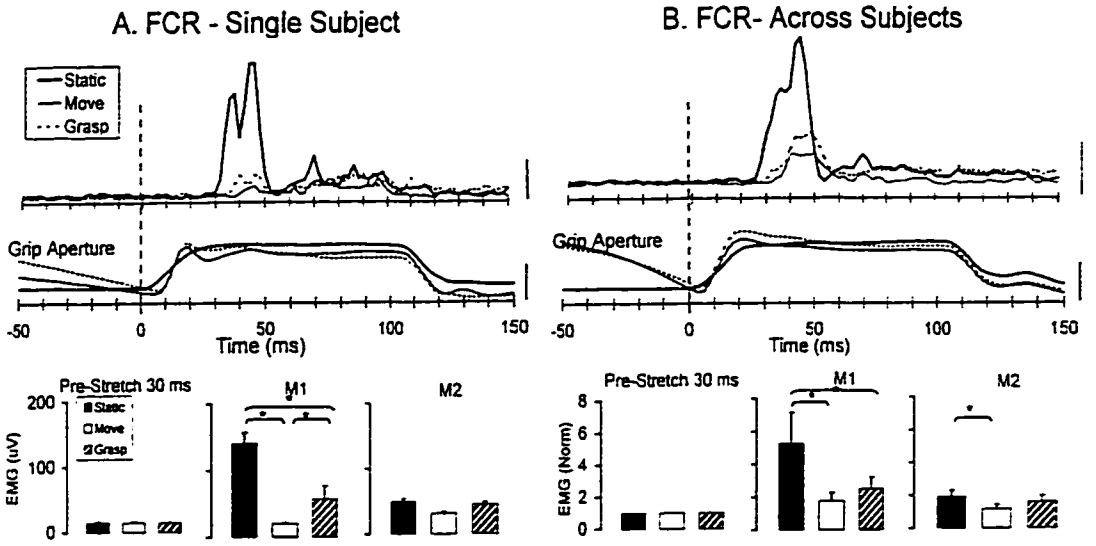

Figure 6-5. Mean FCR EMG activity and grip aperture during all three tasks. Shown are data for a single subject in A and averaged across all subjects (n=6) in B. In A and B, mean rectified EMG activity, grip aperture and mean EMG activity averaged over three 30 ms intervals relative to stretch onset are shown in the upper, middle an lower panels, respectively. The EMG data in Part B are normalized to the mean activity over the pre-stretch 30 ms for each task Asterisks denote significant differences between tasks. Calibration bars represent 50 μv and 5 mm for the upper and middle panels of Part A and 1 and 5 mm for the upper and middle panels of Part B, respectively.

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7.0 General Discussion

This thesis comprises five research projects with a common focus on sensory feedback and the neural control of upper limb movements. Conceptually, the projects can be divided into three groups. Each group is discussed in a separate section below. The first section (7.1) describes attempts to characterise sensory receptor activity from the forelimbs of freely moving cats. The next section (7.2) discusses two projects that investigated the way in which pathways from muscle receptors are gated through the CNS in humans. The third section (7.3) describes specific roles identified for afferent signals in the control of human hand movements. Several potential extensions of the work described in the thesis are outlined in Section 2.4. Some concluding statements are made in Section 2.5.

7.1 Afferent Recordings from Freely Moving Animals

The data in Chapter 2 were obtained using a technique modified in order to record peripheral receptor activity from the forelimbs of freely moving cats. These were the first recordings of forelimb afferent activity during unrestrained movements in any species. The goal was to document this activity during various movements including reaching and manipulative tasks and compare the results to other afferent recordings from cats, monkeys and humans. Over the course of 15 months we implanted 79 microwires in 14 cats. Though clear single unit activity was always present during the implants, in seven animals none was found subsequently. However, sensory activity was evident after recovery in the other seven animals. This generally involved sensory hiss or single units that were too small or unstable to record. Useful data were recorded from 3 animals. One suspected spindle primary ending had a peak firing rate 250 imp/s (see Figure 2-4), which compares to peak rates from hindlimb primaries in the range of 400-600 imp/s. These contrast with the lower maximal published firing rates of 130 imp/s in monkeys (Schieber & Thach, 1985) and 110 imp/s in humans (Macefield & Johansson, 1996). Unfortunately, due to the low yield of our experiments, the question of whether this reflects a real

species difference or differences in the respective experimental protocols is still open. The activity of a forelimb GTO during locomotion was similar to that for hindlimb GTOs. However, during a ramp and hold stretch maximal firing rates only reached 150 imp/s (see Figure 2-3), compared to over 400 imp/s recorded from a hindlimb GTO during similar movements (Appenteng & Prochazka, 1984). However, the data are too limited to formulate any conclusions. Interestingly, data were obtained from a cutaneous receptor (suspected SAII, see Figure 2-2) that had a high degree of directional specificity and would be an ideal candidate for the type of receptor involved in the illusory movements described in Chapter 3 of this thesis.

A persistent difficulty with these experiments was the low number of afferent recordings, compared to similar experiments performed on the hindlimb. We explored many options to increase this yield but were unsuccessful. There were two main differences between our technique and that previously used in the hindlimb. First, there is a much greater range of motion in the cervical region of the spinal cord compared to the lumbar region. The increased motion led to difficulties with electrode stability and may have damaged the microwire assembly. Second, due to the anatomy of the cervical region, we could not implant our microwires in the dorsal root ganglion as done in the hindlimb. Instead, we accessed the afferent fibres as they ascended the dorsal columns. This tract contains myelinated fibres compared to cell bodies located in the dorsal root ganglion which may have reduced our chances of obtaining unitary activity as the electrode tips may have had to reside close to a node of Ranvier to record activity. Also, there may be differences in electrode tip encapsulation between the dorsal columns and the ganglion. Our attempts to identify a reason for the low yield during post-mortems were unsuccessful, largely due to massive regrowth of connective tissue. After the last 5 unsuccessful implants it was decided that the yield was too low to warrant the time, expense and animal sacrifice that were involved. Hence, contrary to the conclusion reached midway through these experiments and stated in Section 2.4, we do not believe that the approach we used was a viable one to obtain these afferent recordings.

However, we still feel that there are important questions to be addressed by recording upper limb afferent activity during unrestrained movements. Afferent

discharges, especially from the muscle spindle, may be very different during natural movements compared to the more restricted movements that have been investigated to date in human and monkey trials. This may account for the present discrepancies in afferent firing rates between human and animal data. Unfortunately, a suitable technique to obtain these data is not presently available in any species. The development of such a technique in an animal model or an improvement on the stability of existing human microneurographic techniques would provide a significant contribution to our understanding of the sensory control of the upper limb.

7.2 Modulation of Somatosensory Pathways

Our experiments demonstrated a movement-induced attenuation through both spinal and supraspinal somatosensory pathways for muscle receptor signals from the upper limb. We showed for the first time that movement reduces the conscious perception of these signals. This is despite the fact that they are known to be important to our kinesthetic ability (Goodwin *et al.*, 1972) and their attenuation may serve to prevent saturation of the CNS by reafference during movement. The attenuation of ascending sensory signals is widespread. The conscious perception of cutaneous signals is also attenuated by movement (Angel & Malenka, 1982) as are SEPs arising from stimulation of muscle (Grunewald *et al.*, 1984) and cutaneous receptors (Rushton *et al.*, 1981). We also found attenuation of stretch reflexes during index finger movements. This agrees with experiments showing a general attenuation in these pathways during movements of both the upper (Wallace & Miles, 1998) and lower limb (Dietz *et al.*, 1990). Clearly, during movement afferent signals are attenuated in both spinal and supraspinal pathways. However, the relative gating of the different somatosensory pathways through the CNS during movements has not been explored. Thus, it is not clear to what extent spinal and supraspinal pathways share common gating mechanisms during movement. Experiments designed to address this issue are described in Section 7.4.1.

We demonstrated that the attenuation of ascending pathways for muscle receptors can arise from both peripheral and central sources. The attenuation was present during

cyclic stretching of the skin on the dorsum of the hand and immediately prior to a single wrist flexion movement. The contribution from both central and peripheral sources to the modulation of somatosensory pathways of the lower limb is well established (Brooke *et al.*, 1997). Our results suggest that similar mechanisms may be responsible for the gating of these pathways in the upper limb.

We also demonstrated that the movement-induced attenuation of stretch reflexes was less when the task demands were greater. Presumably, this difference arose from central sources. Similar task-dependent changes in reflex amplitude have been shown previously (Doemges & Rack, 1992). It appears that the CNS tailors the gating of the different pathways according to the task requirements. The extent to which such task-dependent modulation is specific to spinal and/or supraspinal pathways has not been explored.

It is sometimes difficult to disentangle modulation that is dependent on the movement per se, from that dependent on the task. Task-dependent modulation infers that something about the task predicates the CNS to alter somatosensory transmission. Such a source must underlie changes in reflex amplitudes between two static tasks. However, differences in reflex amplitudes between static and movement tasks or between two kinematically different movements may arise from peripheral or central regulation of the reflex pathway. Indeed, changes in reflex gains that are specifically due to the *task* can only really be identified when changes in peripheral feedback are ruled out. Accordingly, movement-induced attenuation would be that which is obligatory to the movement itself, arising from peripheral sources as seen during passive movements. Task-dependent differences would then represent the central regulation of the reflex pathways when contributions from peripheral feedback are similar as in the differences between the two movement tasks in our study.

7.3 Roles for Afferent Feedback During Hand Movements

We identified some important roles for cutaneous feedback from the hand. These receptors on the hand dorsum were shown to play important roles in kinesthesia and in the gating of ascending signals from muscle spindle receptors. Afferent feedback from the digit tips, particularly cutaneous feedback, was important for the initiation of EMG activity immediately after contact with the target during human grasp. An important role for cutaneous feedback in motor control is becoming increasingly evident. It has recently been shown that removal of cutaneous feedback from the hand disrupts movement kinematics throughout a reaching task (Gentilucci *et al.*, 1997).

There are reasons to believe that the neural control of the upper limb is unique. A disproportionately large area of the cortex is devoted to the control of the upper limbs, compared to other parts of the body (Penfield & Rasmussen, 1950). Also, the involvement of the propriospinal system is unique to the upper extremity (Pierrot-Deseilligny, 1996). The importance of cutaneous feedback in movement control may be specific to the upper limb. The high density of cutaneous receptors in the digits (Johansson, 1996) and the specialization of cutaneous receptive field characteristics in the hand (Vallbo *et al.*, 1995) suggest a unique role. Also the specialisation of area 2 of the somatosensory cortex to receive cutaneous input (Iwamura *et al.*, 1985) suggests a unique importance for these feedback signals. There is some evidence that the role of these receptors in kinesthesia may be unique to the hand. Removal of this feedback from the hand reduced the ability to detect movements of the fingers (Ferrell *et al.*, 1987). However, removal of this feedback from around the knee augmented the ability to perceive knee movements (Horch *et al.*, 1975). The extent to which the present results are generalisable to other parts of the body is not clear.

7.4 Future Directions

7.4.1 Modulation of Somatosensory Pathways

Most of what we know about the gating of spinal and supraspinal pathways for cutaneous signals comes from experiments comparing the same response to a given stimulus between different tasks (i.e. reflexes, conscious perception *or* SEPs). This has provided a wealth of information regarding transmission through the individual pathways. However, little is known of the *relative* gating of these signals through different pathways in the CNS. Simultaneous measurement of EMG activity, conscious perception and SEPs arising from electrical stimulation of the index finger during different tasks would provide this information. Such experiments would answer several questions including: Does the CNS modulate segmental and ascending pathways to the same extent or is each path modulated separately, according to the task demands? Under what conditions is there independent control over spinal and supraspinal pathways? What is the relationship between SEP amplitude, conscious perception and long latency reflex amplitudes? Under what conditions are these modulated independently? These experiments would shed some light on gating mechanisms that are common to each pathway and would provide insights into the functional relevance of the gating of these pathways.

One technical difficulty with stretch reflex experiments is the necessity for a device with which to apply the stretch, the size and location of which generally restricts the types of movements that can be examined (for example see Figure 6-1A). This is particularly true for the leg and hence a device was developed to deliver imposed flexions at the ankle which could be worn by the subject, thus permitting relatively free movement (Yang *et al.*, 1988). A similar device, adapted to fit the hand and apply stretches at the index finger MCP joint, would permit investigation of the gating of these pathways during a much wider range of movements than is presently possible. The gating of somatosensory pathways may be quite different during these movements compared to the more restricted movements that are presently examined.

A common conclusion of studies showing changes in stretch reflex amplitudes between tasks is that they may arise from changes in spindle discharge between tasks for reasons including changes in fusimotor drive or spindle unloading (Wallace & Miles, 1998). This issue could be resolved using current microneurographic techniques. By simultaneously recording spindle discharges and stretch reflexes during two tasks known to modulate reflex amplitudes the contribution from changes in receptor discharge could be identified. If differences in spindle discharge were detected, the stretch parameters could be adjusted to provide an approximately similar discharge between tasks. In this way, any observed differences in reflex amplitude would have to be centrally mediated.

7.4.2 Roles for Afferent Feedback During Upper Limb Movements

We have demonstrated an important kinesthetic role for ensemble cutaneous feedback from receptors on the dorsum of the hand. This was only the second such demonstration and hence this role is relatively unexplored. Our skin stretch technique only crudely approximated skin strain patterns during natural movements and yet still resulted in illusory movements. A further refinement of the technique to more accurately mimic these patterns would likely result in stronger and more reliable movement illusions. Such a technique could be used in a more detailed study of the relationship between the pattern of stimulation and the resultant illusory movements and shed some light on the kinesthetic acuity of this afferent modality.

There are reasons to believe this important role for cutaneous receptors in kinesthesia may be unique to the hand (see Section 7.3 above). Similar experiments to those described above could be conducted at other joints in the body to address this issue.

Many experiments investigating kinesthesia involve stimulation or removal of a single sensory modality and study of the resulting kinesthetic illusion or deficit, respectively. However, during natural movements afferent signals arise from multiple receptor populations. The extent to which the nervous system utilises different afferent sources and how they interact is not clear and may vary between tasks. Experiments that combine both conflicting and complimentary signals from muscle and cutaneous

receptors may shed some light on the relative contributions from these two receptor populations.

We also demonstrated an important role for the afferent signals evoked by contact with the target during human grasp. These signals were shown to evoke changes in EMG activity appropriate for the task. Presumably these contact-dependent responses would be scaled according to the characteristics of the object to be lifted. Replication of the experiments in Chapter 5 using objects of different weights would identify the extent to which this scaling depends on the task.

7.5 Concluding Remarks

Together these experiments demonstrate the modulation of afferent signals through both spinal and supraspinal somatosensory pathways of the upper limb. This modulation originated from central and peripheral sources and was dependent on the task The experiments also highlighted the importance of feedback from cutaneous receptors in the neural control of the upper limb. The specialisation of the neural control of the upper limb and the way in which transmission through the different somatosensory pathways is gated during various movements requires further investigation.

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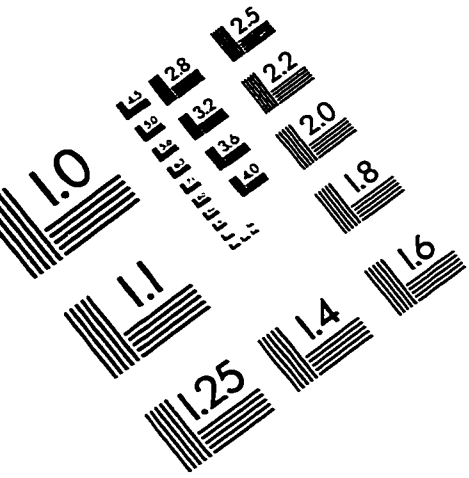
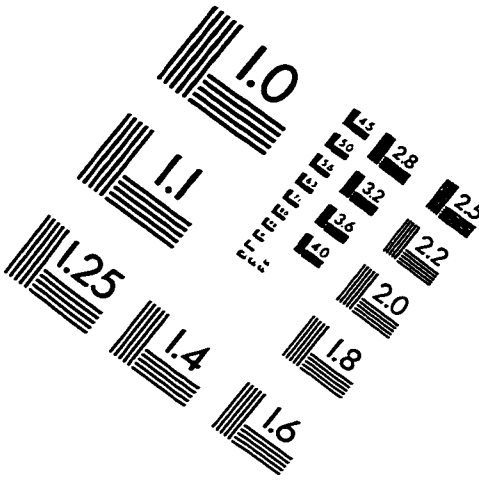
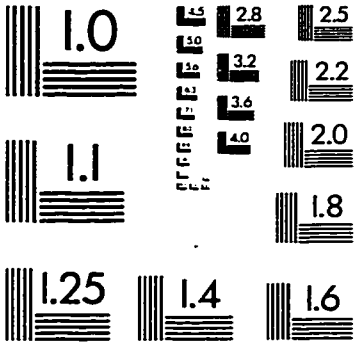
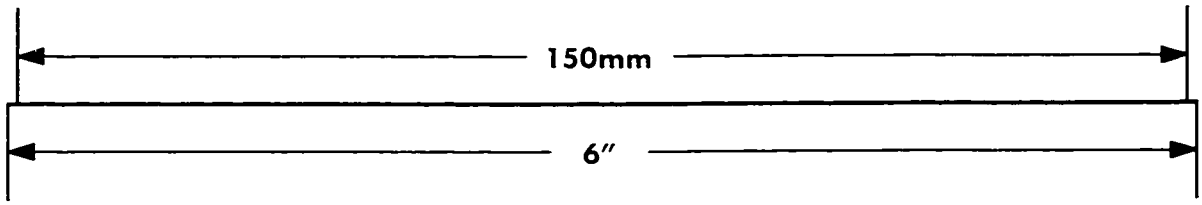
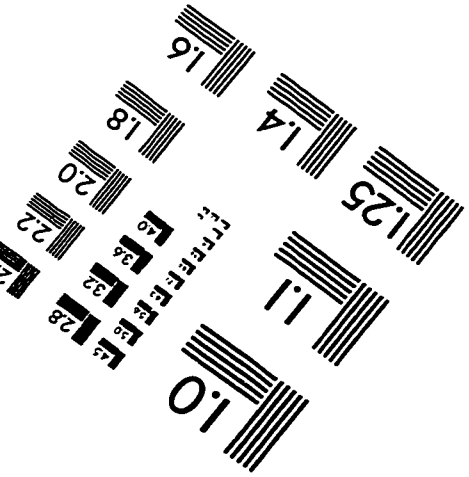
IMAGE EVALUATION TEST TARGET (QA-3)

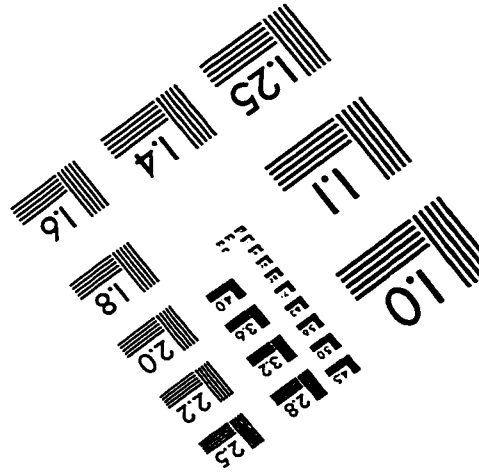












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