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EFFECTS OF LOCALISED COOLING AND WARMING ON NEUROMUSCULAR CONTROL IN YOUNG AND OLDER WOMEN

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CONTENTS

ABSTRACT

The present thesis investigated the effects of localised warming (increased muscle temperature ~3/4 °C) and cooling (decreased muscle temperature ~3/4 °C) of the lower limbs on neuromuscular control in young (18-26 years) and older (65-75 years) healthy women. The principal aims were to investigate the effects of temperature on 1) maximal voluntary isometric and isokinetic contractions, and the electromyographic signal; 2) the H reflex and maximal compound action potential and the H_{max}/M_{max} ratio; 3) postural control; 4) force fluctuation during a fine motor control task.

Different responses to temperature were observed between the young and older groups. For example, cooling was found to reduce the isokinetic torque output when compared to the control condition in the young (average reduction ~7%), but not in the older adults. Similarly the H_{max}/M_{max} ratio, an indication of spinal reflex excitability, was increased following cooling in the young subjects only (by 28%). In both groups, however, H reflex onset latency decreased with warming (by 5.3%) and increased with cooling (by 5.5%). This led to hypothesises that the temperature related change in reflex onset would affect the proproceptive response during postural control; however, no effect of temperature on postural control was found in either group following either warming or cooling. In the final study, the effects of cooling were again different between the groups, with the force fluctuations during low intensity isometric tasks increasing as a result of cooling compared to the control condition in only the older subjects (mean increase 35%).

In conclusion, older individuals show a different response to cooling compared to young subjects. Whilst cooling does not affect gross motor tasks and postural stability in the older subjects, it does affect the ability of an older individual to perform fine motor tasks. Warming, however, had little effect on neuromuscular control in either group.

CHAPTER 1

GENERAL INTRODUCTION

Investigations in the field of thermoregulation allow us to understand how the body responds physiologically to the stresses of altered temperature. Of particular significance is the effect of temperature on the neuromuscular system which ultimately controls human movement. In young healthy individuals, altered temperature influences the transmission properties of the nerve and muscle fibres, as well as the contractile properties of the muscle fibres, resulting in changes in the neuromuscular control both during gross and fine motor tasks (Rutkove 2001, Farina et al. 2005, Gray et al. 2006). Indeed, previous studies conducted on young individuals have focused mostly on maximal performance tasks such as sprint cycling and vertical jump tasks, whereby warming is seen to benefit the performance (Gray et al. 2006, Sargeant 1987, Stewart et al. 2003) and cooling detriment the performance (Davies and Young 1983, Oksa et al. 1997, Sargeant 1987). The outcome of these investigations may have a practical relevance for the athletic population, however, they could be considered as less relevant to everyday situations whereby movements are performed at low velocity and intensity. In contrast to the investigations in young healthy individuals, relatively little attention has been given to the effects of altered temperature in individuals with impaired neuromuscular systems, such as older individuals.

An abundance of literature exists on the effects of ageing on the neuromuscular system (Macaluso and De Vito 2004, Roos et al. 1997, Vandervoort 2002). However, while this area continues to be well researched, relatively little attention is given to the thermoregulation systems of the older individual with most of the studies focusing on responses such as vasoconstriction/ dilation, metabolic heat production, sweating and cardiovascular function (for review see: Florez- Duquet and McDonald 1998, Kenney and Munce 2003, Smolander 2002). The thermoregulation system of the aged individual is an area which has still to be fully understood; what is clear from the available studies, however, is that the older individuals have a reduced ability to adapt to changes in the thermal environment, displaying a relative inability to maintain core temperature when exposed to cold and, to a lesser extent, warm environments (Collins et al. 1977, Fox et al. 1973, Horvath and Rochelle 1977, Lybarger and Kilbourne 1985, Yousef and Golding 1989). What has not, as yet, been investigated is the changes that occur with altered temperature at the neuromuscular level in older individuals.

A recent publication by the Scottish Executive entitled "Scottish House Condition Survey: Fuel Poverty Report - 2003/04", published in 2006, reports that 35% of single pensioners and 27% of pensioner couples could barely afford to keep their house warm in the winter months in Scotland. As older individuals have a higher level of sedentaryism during a typical day when compared to their younger counterparts (Davis and Fox 2006), it is likely that the temperature of limbs will be more affected by environmental temperature than in more active younger individuals. A well documented consequence of ageing is an impaired neuromuscular function, which consequenctly reduces muscular strength and power (Bazzucchi et al. 2004, Macaluso et al. 2002, Macaluso and De Vito 2003), worsens balance (Baloh et al. 1998, Maki and McIlroy 1996) and worsens fine and gross motor control (Tracy and Enoka 2002, Vaillancourt et al. 2003). These parameters, in the most extreme phases of life, for example people in their 8-9th decade, continue to worsen in such a way that eventually the individual is unable to live independently, with obvious negative consequences on the quality of life. By understanding whether older individuals respond similarly to young individuals to altered temperature, for example, with cooling further impairing maximal performance or, on the contrary, with warming enhancing the maximal performance, this could potentially offer clinicians and health practitioners a new means of aiding older individuals in performing day to day tasks as well as highlighting the potential dangers of living in insufficiently heated housing.

Along with the mechanical output data, the use of both surface and intramuscular electromyography (EMG) will be used to try to understand the effects of temperature on the neuromuscular system comparing healthy young and older individuals. The following studies cover a range of motor control aspects important to an older individual, ranging from very fine motor control to gross maximal motor control, with the inclusion of both voluntary and reflexively activated contractions. Therefore, the primary aim of this thesis is to investigate the effects of both local cooling and warming of the lower limbs (without modifications in the core temperature) on neuromuscular control in young and older woman. Women are the focus of these studies because older women tend to reach levels of neuromuscular function below the thresholds for an independent life before men (Katz et al. 1983, Skelton et al. 1994).

The thesis is presented in the following chapters:

Chapter 2: This chapter provides a review of literature as a background to identify the research aims and objectives investigated in the following studies of the thesis.

Chapter 3: The aim of the first study was to look at the effects of altered local temperature on torque and EMG parameters during maximal isometric and isokinetic contractions in young and older females.

Chapter 4: The second study had the aim of looking at the effect of both local cooling and warming on the soleus H reflex and M wave in both young and older females.

Chapter 5: The purpose of the third study was to look at the effect of both local cooling and warming on static postural control in young and older females.

Chapter 6: The final study looked at the effects of altered local temperature on fine motor control by investigating the effects of local cooling and warming on the force fluctuations during low-level isometric contractions and on discharge characteristics of single motor units.

Chapter 7: The purpose of the final chapter was to draw together the main findings of the studies conducted for the thesis, discuss the potential clinical importance of the findings and offer future directions for the area of research.

CHAPTER 2

REVIEW OF LITERATURE

SECTION 1a: MAXIMAL NEUROMUSCULAR PERFORMANCE

Maximal neuromuscular performance is commonly assessed by means of dynamometric tests aimed at measuring maximal strength and power, with simultaneous assessment of neural characteristics mostly through electromyographic (EMG) techniques. Muscle strength can be defined as the force generated by an individual. As all human motion involves the rotation of body segments around their joint axes, torque represents the rotational effect of a force with respect to its axis (Enoka 2001). Common measurements of muscle strength include isometric, isotonic and isokinetic modalities. Maximal strength is measured during isometric contraction, in which there is no change in muscle length, whilst power is generated in actions that involve movement and is calculated as the product of torque and speed at which movement occurs.

The control of muscle performance by the nervous system is accomplished by electrical signals sent from the motor neurons to muscle fibres. Surface EMG is used as a tool to identify the mechanisms involved in various adaptations within the neuromuscular system (Enoka 2001). The central nervous system controls muscle force by motor unit recruitment and motor unit discharge modulation (Farina et al. 2002b). The surface EMG comprises of the sum of the electrical contributions made by the active motor units as detected by the electrodes placed on the skin overlaying the muscle. The amplitude of the surface EMG signal is related to the motor unit activity, that is, the recruitment and discharge rates of the active motor units. Average rectified value (ARV) and the root mean square (RMS) are two of the variables that are used to describe the amplitude of the signal. Analysis in the frequency domain includes the mean frequency (MNF) and the median frequency (MDF). This analysis has most commonly been used to study fatigue (e.g. Bazzucchi et al. 2004, Merletti et al. 2002), however, it may also be used as a method of inferring changes in motor unit recruitment. As with the measurement of muscle fibre conduction velocity (MFCV), estimated from the delay between signals using two or more surface EMG recordings (Bigland-Ritchie et al. 1981, Merletti and Lo Conte 1995, Merletti et al. 1990), the recruitment of progressively larger motor units with higher conduction velocities should determine an increase in MNF and MDF and global MFCV, with the maximal value of each variable indicating full motor units' recruitment (Solomonow et al. 1990). The MNF and MDF have been found to have a linear relationship with MFCV (Arendt- Nielsen and Mills 1985, Stulen and De Luca 1978) and both sets of variables have been used as a method of estimating muscle fibre type proportions (Gerdle et al. 1991, Kupa et al. 1995, Moritani et al. 1985, Wretling et al. 1987, Farina et al. 2006).

SECTION 1b: MAXIMAL NEUROMUSCULAR PERFORMANCE AND AGEING

As early as 1835, the reduced maximal strength of older individuals has been researched (Quetelet 1835). This decrease in strength has been clearly demonstrated via the use of isometric and isokinetic tests. After around the 2nd or 3rd decade of life, maximal strength of the muscle starts to decrease, however, these changes are minor until the 5th – 6th decade whereby the rate of decline is dramatically accelerated at a loss of about 10-15% per decade (Frontera et al. 1991, Kallman et al. 1990, Vandervoort and McComas 1986). Many studies have reported regional differences in the reduction of strength with the lower body being more affected than the upper body (Candow and Chilibeck 2005, Janssen et al. 2000, Lynch et al. 1999). Males and females appear to show comparable age related trends when their values are expressed relative to muscle mass or muscle cross-sectional area (Doherty et al 1993, Lindle et al. 1997, Vandervoort and McComas 1986). As females have lower initial strength values they will reach levels of strength below the threshold necessary to accomplish basic daily activities before males; therefore, it has been suggested that they should be the first group targeted in intervention and rehabilitation studies (Skelton et al. 1994).

Muscle power is seen to decline with ageing at an even greater rate than strength at 3-4% per year as compared to 1-2% per year between the ages of 65 and 89 years (Metter et al. 1997, Skelton et al. 1994). Critical levels of muscle power are necessary in older people to accomplish daily living activities like climbing stairs, rising from a chair or using public transport, and thus, the maintenance of independent living are above all related to the ability to generate power specifically at low velocity.

Many studies have investigated the relationship between strength and power, most commonly of the knee extensors, and the persons ability to perform day to day activities, for example strength and power have been shown to be related to chair rise time (Hughes et al. 1996, Skelton et al. 1995), step height (Macaluso et al. 2003, Skelton et al. 1995), walking speed (Gibbs et al. 1996, Rantanen and Avela 1997, Schlicht et al. 2001) and balance (Holviala et al. 2006, Orr et al. 2006).

The major cause of the loss in strength and power is sarcopenia. Sarcopenia is defined as the loss of muscle (Evans 1995). Muscle mass in males and females is reported to decline at a rate of 1.9 and 1.1 kg/decade, respectively, after the 5th decade of life and, as with the muscle strength, a preferential loss to the lower body has been reported (Janssen et al. 2000). Older individuals (aged between 60 and 80 years) have a 14- 26% smaller muscle mass than the young subjects (Hakkinen et al. 1998, Kent-Braun and Ng 1999, Klein et al. 2001, Macaluso et al. 2002, Overend et al. 1992). The decrease in muscle mass alone, however, does not explain the decrease in strength and power with ageing, as the difference exists even after normalisation for muscle cross sectional area (Jubrias et al. 1997, Kallman et al. 1990, Klein et al. 2001, Macaluso et al. 2002).

Ageing is known to reduce both motoneuron numbers (Campbell et al. 1973, Tomlinson and Irving 1977) and muscle fibre numbers (Lexell et al. 1988) resulting in a decrease in the number of motor units. This decrease in motor unit number has been investigated using both cadaver subjects and EMG techniques (Brown 1972, Brown et al. 1988, Campbell et al. 1973, Tomlinson and Irving 1977). Loss in motor unit number has been estimated to be ~1% of the total number per annum beginning in the 3rd decade of life and increasing in rate after 60 years of age (Tomlinson and Irving 1977). The number of motor units has been reported to be as much as 50% lower in individuals above the age of 60 years compared to young subjects (Brown et al. 1988). Both type I and type II motor units are reduced in number, but there is a preferential loss of the type II motor units (Lexell et al. 1988, Thompson 1994). For example, Larsson et al. (1978) observed an increased relative proportion of type I fibres in 60-65 year old subjects (66% of total muscle) in the vastus lateralis muscle compared to 20-29 year old subjects (39% type I fibres) with no change in the ratio of type IIa and type IIb fibres. Along with the greater loss of the type II motor units, motor unit remodelling occurs such that type II fibres are selectively denervated and innervated by collateral sprouting of axons from the type I motor units (Roos et al. 1997). It is suggested that the type II fibres which are reinnervated by slow motor units axons actually become (or approximate) type I fibres, with respect to physiological and biochemical properties (Kugelberg 1976). These changes are accompanied by an increase in size or innervation ratio, such that each motor neuron innervates more muscle fibres in older than young muscle. Through use of macro EMG techniques, an increase in motor unit size is seen in older individuals over 60 years indirectly indicting an increased number of muscle fibres per motor unit (de Koning et al. 1988, Stalberg and Fawcett 1982, Stalberg et al. 1989).

Not only there is a decrease in type II muscle fibre number but there is also a decrease in the fibre size. This is seen only for the type II fibres, without a change in size of the type I fibre (Grimby et al. 1984, Lexell et al. 1988, Porter et al. 1995). In the 3rd and 4th decade of life, the mean cross sectional area of the type II fibres in the quadriceps femoris muscle exceeds that of type I fibres by approximately 20% (Brooke and Engel 1969), but by the age of 85 years the area of the individual type II fibres is less than 50% of that of the type I fibres (Tomonaga 1977).

The alteration in the innervation ratio may be responsible for the lower motor unit discharge rate in older individuals compared to younger subjects at MVC (Connelly et al. 1999, Kamen et al. 1995). A substantial decrease in discharge rate of 64% has been reported (Kamen et al. 1995). There are few studies, however, which have investigated motor unit discharge at high contraction levels due to the technical difficulties in discriminating the discharge pattern of individual motor units (Roos et al 1997). The decreased maximal discharge rate may also be affected by age related limitations in excitability of the corticospinal tract (Rossini et al. 1992) and motor neurons (Engelhardt et al. 1989) or a reduction in central drive (Yue et al. 1996).

The ability to fully activate the muscle during voluntary isometric contractions has been a focus of research recently, yet the findings are inconsistent with some studies showing that older individuals voluntarily activate a lower percentage of the complete activation capacity than young subjects during MVC (Morse et al. 2004, Stevens et al. 2003, Yue et al. 1999), while other studies have shown that older and young subjects have the same activation capacity (De Serres and Enoka 1998, Kent-Braun and Ng 1999, Klass et al. 2005, Phillips et al. 1992). Voluntary strength testing, however, is thought to be preferable to electrical stimulation, since stimulation determines full synchronisation of motor units which is unlikely to occur in real life (Solomonow et al. 1994).

In older individuals the amplitude of the surface EMG, RMS/ ARV, is lower during a maximal contraction either in an isometric contraction or an dynamic contraction when compared to young individuals (Hakkinen and Hakkinen 1995, Hakkinen et al.

1998, Macaluso et al. 2000, Moritani and deVries 1980). This is thought to reflect the reduced number of motor units (Esposito et al. 1996) and reduction in the maximal motor unit firing rates in the older individual compared to young subjects (Esposito et al. 1996, Merletti et al. 2002), masking the increase in single motor unit action potential amplitude with ageing, as revealed from intramuscular EMG measurements (Doherty and Brown 1993, Howard et al. 1988, Roos et al. 1999). However, the difference between the groups may also be a consequence of the different thickness or conduction of the layers between the muscle and recording electrodes, as subcutaneous fat acts as a low pass filter for the surface EMG (De Luca 1997, Farina and Rainoldi 1999). Regardless of the difference in absolute RMS values between young and older individuals, Esposito et al. (1996) reported that both groups display a similar trend in the increase of RMS as a function of the level of force, suggesting a similarity in motor unit activation patterns.

Comparisons of the EMG frequency parameters and MFCV between young and older individuals have been conflicting. MNF/ MDF has been reported to decrease with ageing (Bazzucchi et al. 2004, Esposito et al. 1996, Yamada et al. 2002), however, despite the linear relationship between MNF/ MDF and MFCV (Arendt-Nielsen and Mills 1985, Stulen and De Luca 1978), only one study has reported a significant decrease in MFCV in older subjects compared to young subjects (Yamada et al. 2002), whereas Bazzucchi et al. (2004) and Merletti et al. (2002) found no difference. A selective decrease in the fast conducting type II fibres in older individuals, therefore, is not clearly reflected in the MFCV recorded from the surface EMG. Merletti et al. (2002) explain that one of the pitfalls of calculating MFCV from the surface EMG is that the large motor unit action potentials (MUAP) mask the MUAP of the smaller units and the MUAPs identified by the surface electrodes of the young and older individuals may have a similar MFCV and the numbers of motor units identified could be not sufficient to discriminate between the age groups. Additionally, young and older muscles have a different distribution of fast and slow fibres, with young subjects having a more even distribution of fibre types (Lexell et al. 1983), this compromises the comparison of the MFCV when recorded from the surface EMG between young and older subjects.

Surface EMG has been used to assess coactivation levels with ageing. Greater coactivation can reduce the performance of agonist muscles through the opposing mechanical action of the antagonist muscles (Carolan and Cafarelli 1992). Many studies have shown an increased level of coactivation in older subjects during MVC (Izquierdo et al. 1999b, Klien et al. 2001, Macaluso et al. 2002, Valkeinen et al. 2002), however, many authors have also reported no difference between young and older individuals (Klass et al. 2005, Morse et al. 2004, Pousson et al. 2001). This greater coactivation may contribute to reduced force production in older individuals as a linear relationship between the percentage of coactivation and resultant torque has been reported (Simoneau et al. 2005).

SECTION 1c: MAXIMAL NEUROMUSCULAR PEFORMANCE AND TEMPERATURE

Muscle temperature has been repeatedly shown to have a profound consequence on maximal muscle performance. A wide range of techniques has been used to alter muscle temperature including water immersion of the limb (Bigland-Ritchie et al. 1992, Davies and Young 1983, Sargeant 1987), electrical pads (Thornley et al. 2003), ice to the skin (Bolton et al. 1981, Jutte et al. 2001, Bell and Lehmann 1987) and use of prior exercise (Racinais et al. 2005, Stewart et al. 2003). This along with wide variations in the duration and intensity of temperature manipulation, inconsistent methods of reporting muscle temperature, with many studies reporting only skin temperature (e.g. Cheung and Sleivert 2004, Comeau et al. 2003, Farina et al. 2005, Thornley et al. 2003), makes direct comparisons of the different studies rather difficult.

The effects of temperature on muscular output during *in vivo* experiments appear to be specific to the velocity component of the muscle contraction and not the force generating ability. It has been consistently shown that when an individual performs a maximal isometric contraction, there is no effect of either cooling or warming on the force (Bergh and Ekblom 1979, Binkhorst et al. 1977, Stewart et al. 2003, Thornley et al. 2003). The benefits of increased temperature and the detriment of decreased temperature to performance are evident in maximal dynamic activities. Warming is seen to increase the power output during sprint cycling (Ball et al. 1999, Gray et al. 2006) while cooling decreases the power output (Davies and Young 1983, Sargeant 1987). Sargeant (1987) described that the effect of cooling the muscle was to decrease the amplitude of the pedalling rate-peak power parabola and to shift the predicted intercept for the maximal pedalling rate to the right, while the effect of warming the muscle was to increase the amplitude and shift the intercept to the left. The same author describes that the temperature effect is greatest when the pedalling velocity is close to, or exceeds, the optimal velocity for power output. Temperature is seen to have similar effects on very high velocity dynamic contractions as seen from the increase in power output during vertical jump (where plantar flexion is reported to exceed 1000 °/s , Bobbert et al. 1986) following warming (Davies and Young 1983, Stewart et al. 2003) and the decrease following cooling (Davies and Young 1983, Ferretti et al. 1992).

In contrast to the high velocity contractions generated during sprint cycling or vertical jump, isokinetic contractions performed on a dynamometer have relatively lower contraction velocities. This velocities produced by the dynamometer are below the optimal velocity for producing maximal force which have lead to somewhat equivocal findings. While Haymes and Rider (1983) reported no difference in torque from between 30 °/s to 300 °/s with muscle cooling, other authors have reported a decrease in torque output following skin cooling (muscle temperature not recorded) at velocities of between 60 and 240 °/s (Bergh and Ekblom 1979, Cheung and Sleivert 2004, Comeau et al. 2003). Bergh and Ekblom (1979) found effects of both cooling and warming on the force during isokinetic contractions but found no velocity dependent effect. These findings appear to be almost entirely due to the local effect of the limb tissue and are independent of core temperature (Cheung and Sleivert 2004, Giesbrecht et al. 1995).

Based on the classical works by Ranatunga (1982, 1984, 1998) on rat muscle, it is generally believed that temperature sensitivity of mechanical and biomechanical properties of slow twitch fibres is greater than that of fast twitch fibres. This has been supported in human subjects during a cycling protocol following warming (Sargeant and Rademaker 1996), but is in contrast to Gray et al. (2006) who observed that the magnitude of the increase in force with warming was correlated to the percentage of fast twitch fibres. However, as highlighted by the authors in the latter study, a higher pedal cadence was used in their study which was beyond the optimal pedal velocity for the slow twitch fibres.

With respect to the recruitment order, Rome (1990) demonstrated, using animal experiments, that following cooling, the recruitment of the fibre types was similar to that under the control temperature, going from slow to fast fibre types; however, a more condensed recruitment curve was reported, whereby more muscle fibres and faster fibre types were recruited at given speeds to compensate for the diminished power output of the fibres. On the other hand, Ranatunga et al. (1987) suggest that the sequence of motor unit recruitment may be altered with cooling with the recruitment order going from fast to slow after cooling as opposed to slow to fast after warming or in normal conditions.

The effects of temperature on the muscle properties are reflected in the surface EMG recordings during isometric and concentric contractions. The amplitude of the RMS is seen to decrease with warming (Petrofsky and Lind 1980, Stewart et al. 2003) and increase with cooling (Mucke and Heuer 1989). While in the power spectrum components, MDF and MNF are seen to increase with warming (Krause et al. 2001, Stewart et al. 2003) and decrease with cooling (Krause et al. 2001, Merletti et al. 1984, Mucke and Heuer 1989, Petrofsky and Lind 1980, Thornley et al. 2003). Few studies have reported the effects of temperature on the MFCV during voluntary contractions: Gray et al. (2006) reported an increase in MFCV with warming compared to control temperature during a sprint cycling; similarly, Farina et al. (2005) reported an increased MFCV of the motor unit at low contraction intensities following warming. In studies with electrical-stimulation induced-contractions a decrease in MFCV with cooling has been reported (Bolton et al. 1981, Dioszeghy and Stålberg 1992), as opposed to an increase following warming (Rutkove et al. 1997). Temperature has a profound effect on the muscle fibre membrane. As Hodgkin and Huxley (1945) first described, the depolarisation of the membrane is due to the inward flux of Na^+ occurring due to the opening of the voltage gated channels along the membrane. After the influx of Na^+ the channel closes and the K^+ channel opens, allowing a removal of K^+ to restore the membrane to its resting potential. Na^+ /K^+ ATPase has the role of continually pumping out Na^+ and bringing in K^+ to maintain the resting potential. Following cooling, both the opening and closing of the Na^+ channels slow, so that the channels are open for longer, increasing the ion flux and therefore, the depolarisation, consequently decreasing the conduction velocity of the action potential along the membrane and increasing the duration and amplitude. Following warming, the opposite occurs, whereby opening and closing of the Na^+ channels quickens, increasing the conduction velocity of the action potential along the membrane and reducing the duration and amplitude (Hodgkin and Katz 1949, Kossler et al. 1989, Stegeman and De Weerd 1982). Depolarisation of the muscle membrane leads to the release of Ca^{++} from the sarcoplasmic reticulum, producing binding of the actin and myosin filaments and therefore muscle contraction. A change in the speed of the depolarisation consequently affects the speed of this binding process (Rutkove et al. 2001).

SECTION 2a: THE HOFFMANN REFLEX (H REFLEX)

The Hoffmann Reflex (H reflex) was first reported by Piper (1912) and first described by Paul Hoffmann (1918). The H reflex response is described as the electrically induced equivalent of the mechanically evoked stretch reflex. Electrical stimulation of a peripheral nerve, which contains both afferent fibres (axons of the muscle receptor) and efferent fibres (axons of the motoneurons), evokes two EMG responses in the connecting muscle, the M wave and the H wave. The elicited response, either an M wave or an H wave or both, depends on the size of the depolarisation caused by the stimulus. The Ia afferent fibres have a larger diameter than the alpha motoneurons, therefore are depolarised at a lower stimulus intensity (Erlanger and Gasser 1968, Kukulka 1992, Li and Bak 1976). At a low stimulus intensity, when the Ia afferents alone are depolarised, a monosynaptic reflex response is produced, seen as the H wave on the EMG recording. With increasing stimulus intensity, further Ia afferent fibres are depolarised, increasing the amplitude of the H wave. Eventually, the stimulus is at an intensity to depolarise the membranes of the alpha motoneurons producing a direct M wave response. As the action potential of the alpha motoneuron travels both orthodromically and antidromically along the fibre after stimulation, there comes a level of stimulation when the action potential of the stimulated alpha motoneuron, travelling antidromically, collides with the action potential of the H wave travelling othodromically along the alpha motoneuron fibre, thus cancelling cancel each other out. With continued increasing stimulus intensity, the H wave will eventually disappear completely, while the M wave will continue to increase until all the alpha motoneurons are depolarised giving rise to the maximum M wave (M_{max}) (Magladery 1955). An example of the EMG recordings with increasing stimulus intensity is shown below (Figure 2.1)

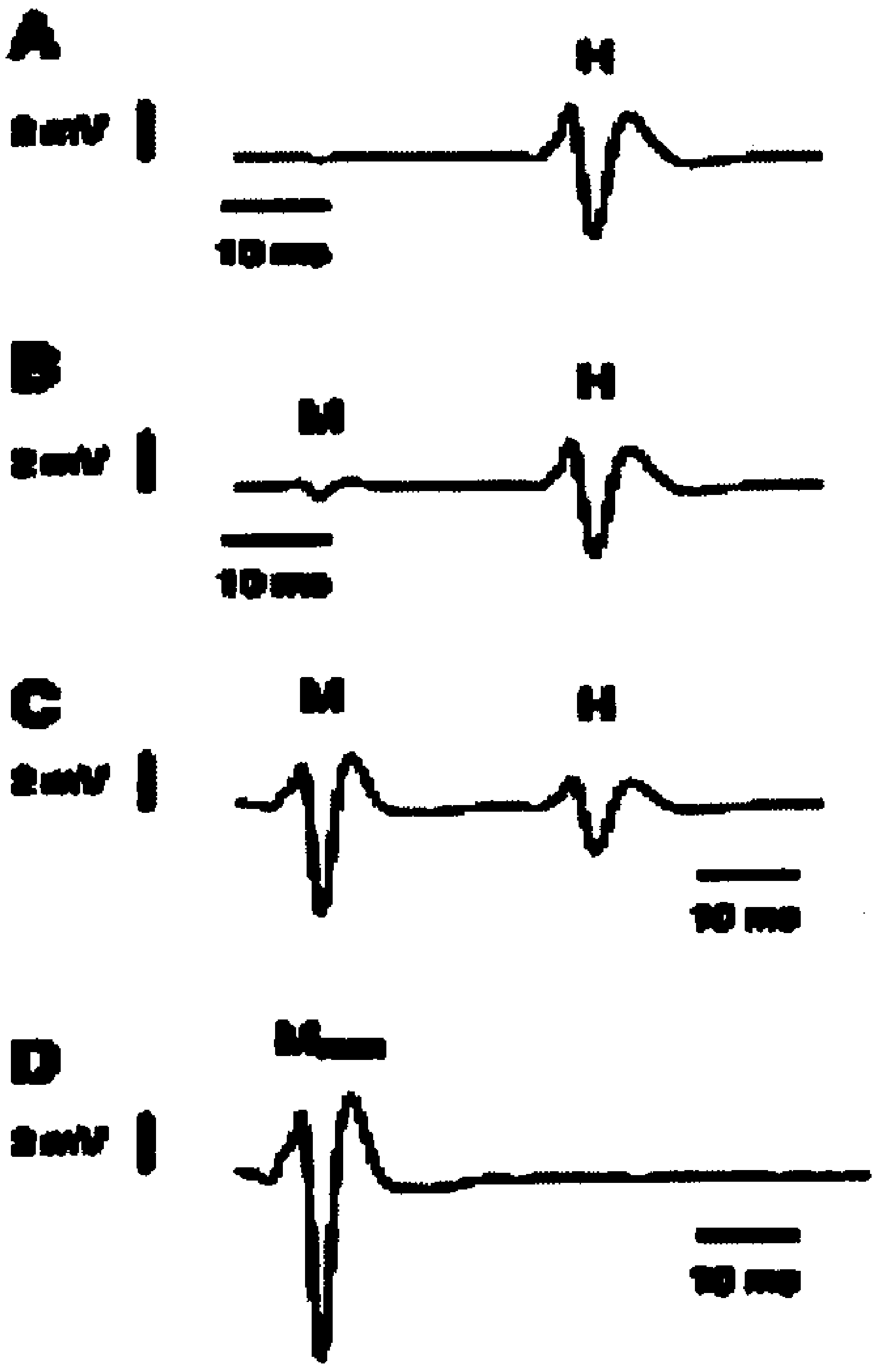

Figure 2.1. An example of the EMG recordings with increasing stimulus intensity. The Y axis is in mV and the X axis in ms. (adapted from Aagaard et al. 2002b).

The recruitment pattern of the Ia afferent and the alpha motoneurones is seen from the H and M wave recruitment curve, shown below (Figure 2.2), where the M wave and the H wave are shown as a percentage of the M_{max} (Baldissera et al. 2000, Zehr and Stein 1999, Zehr et al. 2001). The M_{max} represents the excitation of all the motoneurons and gives a standard to which the response of the H reflex can be compared, for example, an H reflex equivalent to 25% of the M_{max} can be assumed to represent activity in 25% of the motoneurons of the muscle (Hugon 1973). Reporting the maximum H wave amplitude (H_{max}) with respect to the M_{max} (H_{max}/M_{max} ratio) allows comparison of measurements of different absolute values on the basis of their relative values (Hugon 1973, Pierrot-Deseilligny and Mazevet 2000).

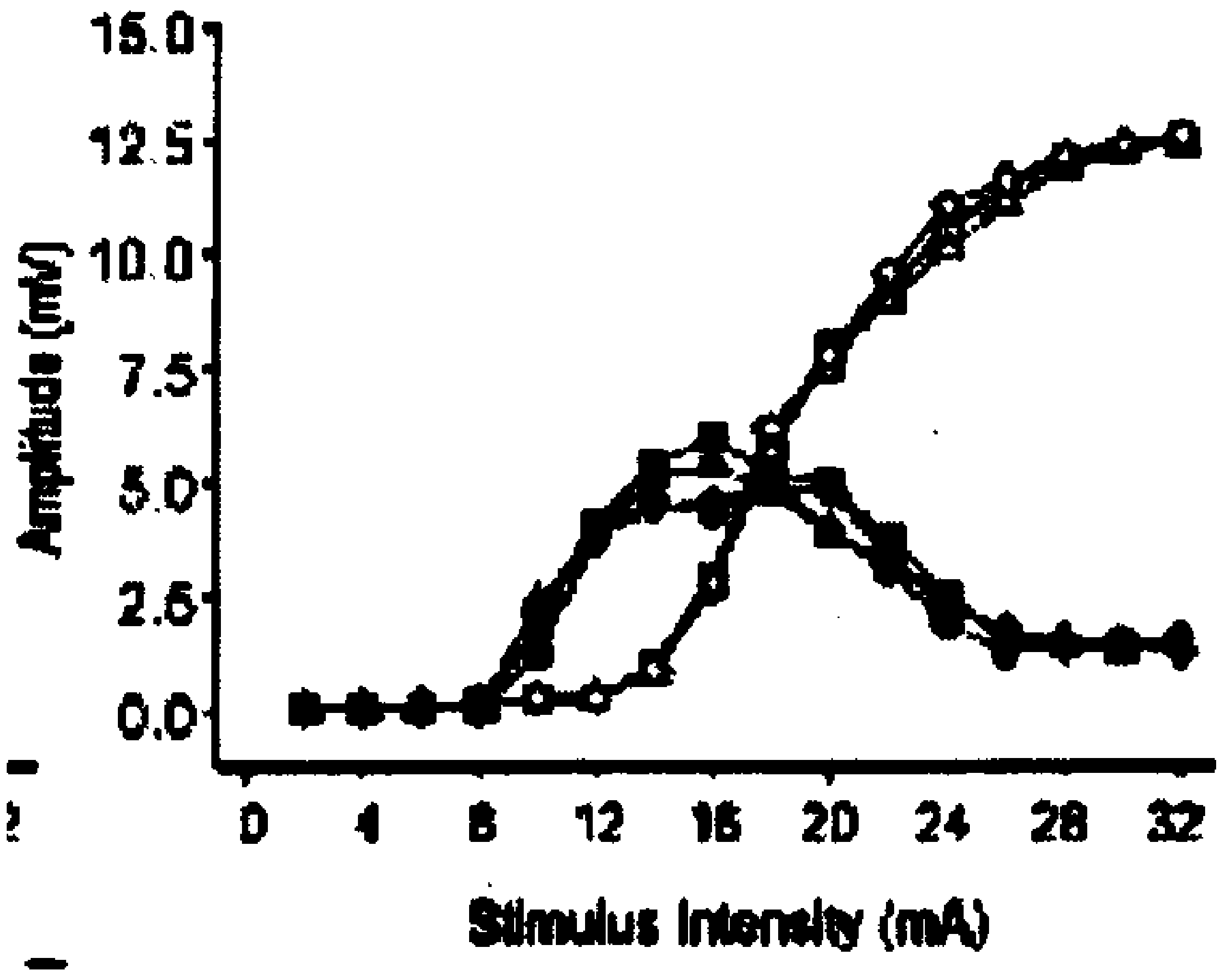

Figure 2.2. H and M wave recruitment curve (adapted from Pinniger et al. 2001)

The H reflex has been used in investigating the response of the nervous system in neurological pathologies (Braddom and Johnson 1974, Fisher 1992), musculoskeletal injuries (Hall et al. 1999, Hoffmann and Koceja 2000, Hopkins et al. 2001, Spencer et al. 1984), application of therapeutic modalities (Bell and Lehmann 1987, Krause et al. 2000, Oksa et al. 2000), pain (Leroux et al. 1995) exercise training (Maffiuletti et al. 2001, Trimble and Koceja, 1994) and performance of motor tasks (Capaday 1997, Capaday and Stein 1986, Hoffmann and Koceja 1995). The majority of the research has been done on the soleus muscle, due to the easy accessibility of the posterior tibial nerve (Hugon 1973), however, the H reflex can be obtained from virtually any muscle where the nerve is available for stimulation (Pierrot- Deseilligny and Mazevet 2000).

The H reflex is commonly considered a monosynaptic reflex as it was initially thought to involve only one synapse (Magladery et al. 1951). Later research, however, discovered the possibility of oligosynaptic and even polysynaptic pathways. Animal experiments have demonstrated that Ia afferents impinge both directly onto alpha motoneurons and also indirectly through interneurons (Fetz et al. 1979, Hultborn et al. 1975). Therefore, the H reflex response might not be altered by a change in alpha motoneuronal excitability per se, but by other mechanisms which alter the responsiveness of the pool during periods of active sensory influence. Mechanisms involving presynaptic inhibition (either centrally or peripherally mediated), homosynaptic post activation depression, reciprocal inhibition from antagonist activation, Ib afferents, group II afferents and cutaneous mechanoreceptors have all been highlighted in modulating reflex response (Pinniger et al. 2001). Presynaptic inhibition has been considered the most common candidate for modulation of the amplitude of the H reflex (Stein 1995). Presynaptic inhibition and facilitation are important because they highlight that Ia afferents do not function solely as sensory relays, but that these neurons may also function as filters, the properties of which may be controlled either centrally or volitionally by inputs to the Ia terminals (Eccles et al. 1962, Schmidt 1971).

Extraneous factors such as head movements, foot positioning, pressure of plate and position of foot plate (Knikou and Conway 2001, Hiraoka 2003), joint angle (Hwang

2002) as well as cognitive factors such as arousal and attention (Paillard 1955) have been shown to affect the H reflex excitability so that cross-study comparisons can sometimes be difficult. The H reflex has shown good intersession and intrasession reliability when these factors are well controlled (Hopkins et al. 2000, McIlroy and Brooke 1987, Williams et al. 1992). The correct methodology for evoking and recording an H reflex in the soleus is outlined in detail by Hugon (1973).

SECTION 2b: THE H REFLEX AND AGEING

The stretch reflex circuit is an important mechanism in the detection and correction of a stretched muscle. Degradation of the neuromuscular system is a known consequence of the ageing process, with changes at each component of the reflex circuit occurring. These changes, for instance, operate initially at the level of the peripheral nervous system, and consist of: 1) a reduced sensitivity and reduced number of muscle spindles (Swash and Fox 1972); 2) both the afferent and efferent nerves are affected by degeneration of the myelin sheath, decreasing the axon integrity (Adinolfi et al. 1991, Lascelles and Thomas 1966); 3) finally, an increase in the innervation ratio of the motorunits will reduce the accuracy of the reflex output (Brown 1972). The assessment of the stretch reflex system using EMG via mechanical lengthening of the muscle gives a global view of the stretch reflex system, whereas the assessment of the H reflex, via electrical stimulation of the Ia fibres, gives a clearer picture of the effects on ageing on the central component of the circuit. Changes in the spinal reflex circuit with ageing have been continually demonstrated. The H_{max} has been consistently shown to decrease with increasing age (Chalmers and Knutzen 2000, deVries et al. 1985, Sabbahi and Sedgwick 1982, Scaglioni et al. 2002, 2003, Vandervoort and Hayes 1989), with a decrease of up to 68% being reported in older adults at a mean age of 73 years when compared to young adults (Scaglioni et al. 2003). Maximum motor response amplitude (M_{max}) has been also been reported to decrease with age (deVries et al. 1985, Scaglioni et al. 2002, Vandervoort and Hayes 1989). When the H_{max} is normalised against the M_{max}, (H_{max}/M_{max}) (Hugon 1973), the findings are inconsistent, with studies showing either a decrease (Koceja et al. 1995, Sabbahi and Sedgwick 1982, Scaglioni et al. 2002), or no change (deVries et al. 1985, Scaglioni et al. 2003, Vandervoort and Hayes 1989). The decrease in the H_{max} and the M_{max} can be explained by the impaired transmission of the signals as demyelination of the afferent and efferent nerves not only reduces the diameter of the axon but increases the area of the axon membrane in contact with the extracellular matrix (Mynark and Koceja 2001). The reduced H_{max}/M_{max} ratio reflects a decrease in the proportion of the available motor units reflexively recruited (Scaglioni et al. 2002).

Changes at the presynaptic or postsynaptic site as a consequence of ageing will also alter the H_{max}/M_{max} ratio (Rudomin and Schmidt 1999, Stein 1995). Using the methods introduced by Hultborn et al. (1987), which have permitted the investigations of presynaptic inhibition in humans, decreased heteronymous Ia facilitation has been demonstrated in older subjects compared to young subjects, suggesting increased tonic levels of presynaptic inhibition in older individuals (Koceja and Mynark 2000, Morita et al. 1995). The functional significance of the increased levels of presynaptic inhibition is not known. Suggestions are that it may be an aspect of the deterioration process that parallels motor disabilities or, on the hand, it may serve to adapt the spinal system to the ageing process of the peripheral neuromuscular system (Morita et al. 1995). Earles et al. (2001), on the other hand, used peroneal conditioning, as opposed to conditioning at the femoral nerve, to estimate tonic presynaptic inhibition and reported that young subjects demonstrated greater heteronymous inhibition than older subjects.

While the ability to modulate the H_{max}/M_{max} ratio in response to a task or perturbation is evident in young individuals (see section 2a), it has becoming apparent that older individuals have a reduced ability to respond to such perturbations. Modulation in spinal reflex excitability has been observed when young subjects change body positions, for example, a decreased spinal reflex excitability is observed when moving from a supine to a standing position (Koceja et al. 1993). Older individuals, in contrast, have been shown not to demonstrate such changes with altered body position (Angulo- Kinzler et al. 1998, Chalmers and Knutzen, 2002, Koceja et al. 1995, Mynark and Koceja, 2002). In young individuals, H reflex amplitude has been shown to be facilitated from the Jendrássik manoeuvre, which consists in upper extremity muscle contraction, through regulation of presynaptic inhibition levels (Delwaide and Toulouse 1980, Zehr and Stein 1999). This facilitation, however, has been shown to be reduced with increasing age (Burke et al. 1996, Tsuruike et al. 2003). Similarly, while voluntary contraction is known to increase spinal reflex excitability through reduced levels of presynaptic inhibition, possibly through supraspinal and segmental mechanisms (Hultborn et al. 1987), this is not as apparent in older subjects. Earles et al. (2001) demonstrated that in young subjects presynaptic inhibition is modulated at low voluntary contractions levels, whereas older individuals failed to modulate the level of presynaptic inhibition until 20% of maximal voluntary contraction (MVC).

Nerve conduction velocity, of both sensory and motor nerves, decreases by between 10 and 20% with increasing age in humans as a consequence of the degeneration of the axon properties (Bouche et al. 1993, Dorfman and Bosley 1979, Drechler 1975). A consequence of the reduced nerve conduction velocity with ageing is a delay in the H reflex onset latency. A 21% increase in H_{max} onset latency was reported by Sabbahi and Sedgwick (1982), while Scaglioni et al. (2002) reported a more modest increase of 10% with increasing age. Interestingly, this decrease in nerve conduction velocity, and consequently, increase in H_{max} onset latency, appears to occur up until the age of 60 years, as subsequent to 60 years no correlation between H_{max} onset latency and age has been demonstrated (deVries et al. 1985, Falco et al. 1994). M_{max} onset latency would be expected to increase with increasing age due to the decrease in nerve conduction velocity of the motor nerves. An increase in M_{max} onset latency of 16% was reported in older adults (Sabbahi and Sedgwick 1982). However, findings of no significant increase in M_{max} onset latency have also been reported (Scaglioni et al. 2002).

Of interest is whether the reduced integrity of the H reflex response with ageing is through physical deconditioning or through degeneration. Studies have shown a difference in the H_{max}/M_{max} ratio between athletes and non athletes and between power and endurance trained athletes (Almeida- Silveira et al. 1996, Casabona et al. 1990, Maffiuletti et al. 2001, Perot et al. 1991). The relationship between physical activity levels and the monosynaptic stretch reflex system with ageing has been studied in both males and females with no significant difference being found between physically active older individuals and sedentary individuals (Clarkson 1978, Hart 1986). Similarly, a 16 week strength training program in older individuals was found to have no effect on either the latency of the H reflex response or the H_{max}/M_{max} ratio, suggesting that the reduced integrity of the H reflex observed in older individuals is not due to physical deconditioning but simply to the ageing process (Scaglioni et al. 2002).

SECTION 2c: H REFLEX AND TEMPERATURE

Despite a lack of standardisation in temperature manipulation procedures and the limited research available, it appears that an increase in the H_{max} amplitude occurs as a result of limb or joint cooling (Knutsson and Mattsson 1969, 1970, Krause et al. 2000, Urbscheit and Bishop 1970) and with whole body cooling (Oksa et al. 2000). It was demonstrated that changes temperature of the area near to the nerve, and not core temperature, are responsible for increased soleus H_{max}, as H_{max} increased following whole body cooling at 10 °C, whereas no increase in amplitude was found when the whole body was cooled, but with neutral leg muscle temperature (Oksa et al. 2000). On the other hand, no changes in the H_{max} with limb cooling have also been reported despite a decrease in soleus intramuscle temperature of 12 °C (Bell and Lehmann 1987). Even fewer papers have been written on the effects of increased temperature on the H_{max}. Only one study was found whereby the body temperature of the cat was increased to hyperthermic levels of 40- 41 °C which resulted in a decrease in the H_{max} (Bhattacharya et al. 1981).

Only two of the studies referenced above report the corresponding changes in M_{max} following cooling, with Oksa et al. (2000) reporting an increased M_{max},while Bell and Lehmann (1987) reporting a decreased M_{max}. In studies whereby H reflex was not measured, the M_{max} is consistently shown to increase with warming and decrease with cooling (Falck and Lang 1986, Rutkove 2000, Rutkove et al. 1997). When comparing changes in the H_{max}/M_{max} ratio following either cooling or warming, an increased H_{max}/M_{max} ratio following whole body cooling has been reported (Oksa et al. 2000), Bell and Lehmann (1987), however, reported no change in the ratio. In the decerebrate cat, cooling the muscle temperature was seen to facilitate the motoneuronal excitability (Chapman et al. 1979).

The increased in the amplitude of the M_{max} and to a certain extent the H_{max} with cooling is primarily due to the previously described changes in the muscle fibre membrane with temperature, which increases the action potential amplitude with cooling and decrease the amplitude with warming (see section 1c).

These changes in the membrane function with temperature do not, however, explain the change in the H_{max}/M_{max} ratio. The level of inhibition either at the presynaptic or post synaptic site can be influenced by inputs from other afferents. An increase in afferent discharge of the sensory endings of muscle spindles has been reported following cooling (Lippold et al. 1960, Michalski and Séguin 1975). Although this would not have a direct influence on the H_{max}/M_{max} ratio, studies on relaxed muscle of the cat have demonstrated that while there was no response to cooling in the Ia primary endings, discharge frequency of the secondary afferents was increased, producing autogenic as well as synergistic facilitation of motoneuronal excitability (Chapman et al. 1979, Michalski and Séguin 1975). Little or no Golgi tendon organ activity was demonstrated in the cooled muscle (Michalski and Séguin 1975). Similarly, cutaneus receptors may influence the level of inhibition/ excitation at the synapse. Nociceptors respond to noxious low temperatures (<20 °C) (Campero et al. 1996) and data from both animal and human experiments reveal a convergence of nociceptive inputs onto spinal reflex pathways via common spinal interneurons (Ellrich and Treede 1998, Steffens and Schomburg 1993).

Similar to the effect of temperature on the muscle fibre membrane, temperature affects the nerve fibre membrane conduction and consequently the latency of the reflex response. A decrease in temperature slows down the opening and closing of the Na^+ channel, reducing the nerve conduction velocity (Hodgkin and Katz 1949), with warming having the opposite effect (Stegeman and De Weerd 1982). From the very early studies of nerve conduction velocity a relatively linear relationship has been shown between the nerve conduction velocity and nerve or near nerve temperature (Edelwejn 1964, Gasser and Trojaborg, 1964, Henrikson, 1956). Changes of between 1.5- 2.4 m/s/°C have been reported on various nerves (reviewed in Rutkove 2001). Reports suggest that there are differences between sensory and motor nerve temperature sensitivity, with the sensory nerves being less sensitive than the motor nerves (Bolton et al. 1981, Halar et al. 1981, 1983, Hlavova et al. 1970), Similarly, differences in temperature sensitivity have been noted according to the fibre size, with larger diameter, faster conducting fibres having higher temperature sensitivity (Douglas and Malcolm 1955, Gasser and Grundfest 1939, Goldman and Albus 1968). With respect to the H reflex, a delay in the H reflex response following cooling and a shortened response a result of warming has been reported (Bhattacharya et al. 1981, Oksa et al. 2000).

SECTION 3a: POSTUROGRAPHY

Balance can be defined as equilibrium resulting from matching torques developed by muscles around a joint. The torques can be matched in anticipation of, or as a reaction to the effects of postural disturbance (Balasubramaniam and Wing 2002). The integrity of the postural control system is typically evaluated with tests of static or dynamic posturography. While static posturography evaluates the postural control system in a stationary position and environment, dynamic posturography evaluates the integrity of the postural control system by assessing the response to postural perturbation (Prieto et al. 1996). The experimental protocols associated with dynamic posturography are considerably more hazardous and physically taxing than those involved with static posturography. Thus, static posturography is a much simpler and safer test to perform and administer to older individuals while providing a reproducible method for evaluating the steady state behaviour of the human body during periods of undisturbed stance (Collins and De Luca 1993).

Postural steadiness is most commonly described with reference to the body's centre of pressure (COP). The COP measures the location of the vertical ground reaction vector from the surface of the force platform (Prieto et al. 1996). This measurement should not be confused with the movement of the body's centre of gravity (COG). While the COG is the parameter being controlled by the postural systems, the movement of this is not directly accessible, whereas the movement of the COP can be directly measured and easily quantified. Increases in displacement of COP reflect consistent increases in those of the COG, suggesting that under static conditions the COP parameters can be used to approximate those of the COG (Murray et al. 1967, Hasan et al. 1996).

Previous studies have used a range of methodologies, acquisition settings and outcome measures when assessing posture, leaving little common ground for comparison between studies (for summary see Schmid et al. 2002). Recent studies have attempted to establish standardised protocols for use of posturography, i.e. standardised acquisition settings (Schmid et al. 2002) and sampling duration (Carpenter et al. 2001, Le Clair and Riach 1996). The various COP parameters that have been reported can be classified into: 1) time domain measures of distance, area and velocity; 2) time domain hybrid measures and frequency domain measures of spectral magnitude and distribution (Prieto et al. 1993). The most frequently reported measures of postural sway include sway area, sway velocity, mean amplitude and mean frequency. The sway area is the total area circumscribed by the COP within the sampling duration; the mean amplitude is the mean distance between sampling points and the arithmetic mean point; the mean frequency is the frequency of a circular motion with a radius equal to mean amplitude and the total length of the sway path;

sway velocity represents the total distance travelled by the COP over time, i.e the amount of regulatory activity associated with the level of stability achieved (Hufschmidt et al. 1980, Schmid et al. 2002). The physiological meaning of the sway velocity is unclear; however it is thought that an increase in velocity represents a decreased ability to control posture and vice versa (Baloh et al. 1998b, Ekdahl et al. 1989, Le Clair and Riach 1996).

During a postural task the human postural system receives information from the visual, vestibular and proprioceptive systems. Afferent signals from these systems are believed to continually modify the activity of the musculature during quiet standing (Collins and De Luca 1993). Collins and De Luca (1993) question the continuity of the feedback systems and suggest that an open loop/closed loop strategy is in place whereby mechanical fluctuations in the joint and their associated drift effects are left unchecked by the postural control system until they exceed some systematic threshold. Only then the efferent signals from the corrective feedback are transmitted to the postural muscles.

The role of the visual system is estimated by removing vision during a postural task. The ratio of the eyes closed measure to the eyes open measure is referred to as the Romberg quotient (Dornan et al. 1978, Prieto et al. 1993). The removal of proprioceptive information by way of ischemic blocking of afferent fibres combined with the removal of visual input has allowed researchers to report the optimal working frequency of the different systems. It has been found that the visual system has an optimal working frequency of below 1 Hz (Dichgans and Brandt 1973, Diener et al. 1983), while the afferents arising from muscle spindle have an optimal working range above 1 Hz (Diener et al. 1984, Mauritz and Dietz 1980). From this it appears that during quiet standing it is mostly the visual system and not the proprioceptive system that is working, as quiet stance has a predominantly low frequency content (Nardone et al. 1997). Consistent with this finding, the postural control of patients with complete loss of large Ia afferent fibres has been reported to be no worse than subjects with fully functioning Ia afferent fibres. However, patients with Ia afferent deficit showed a greater reliance on vision than normal subjects and while the sway area was not significantly different, the difference between the groups was reported as being 22% (Nardone et al. 2000).

SECTION 3b: POSTUROGRAPHY AND AGEING

It has been consistently shown that stability decreases with age (for review see Maki and McIlroy 1996). Cross study comparisons are difficult, however, as the methods and calculations of sway measurements vary from study to study. It appears that sway velocity as opposed to sway amplitude is the best descriptor of instability with ageing, since sway amplitude is not always shown to differ between young and older adults (Baloh et al. 1994, Hufschmidt et al. 1980, Maki et al. 1990). The speed of the displacement of the centre of pressure represents the amount of activity required to maintain stability rather than stability per se (Maki et al. 1994). When 72 subjects aged 79-81 years were followed over a three year period significant increases were found in the sway velocity of the COP (Baloh et al. 1998a).

While it can be argued that spontaneous sway assessments reflect only the integrity of the corrective postural mechanisms rather than the likelihood of experiencing perturbations, little difference between spontaneous sway measures and induced sway measures was reported in the prediction of future falls (Maki et al. 1994). It is unclear whether sway area or sway velocity during a spontaneous sway assessment is the best determinant of the likelihood of falling in the elderly, with studies showing conflicting findings. Fernie et al. (1982) and Maki et al. (1990) reported sway velocity as being the best determinant, whereas others have reported sway area and not sway velocity as being the single best parameter of predicting future falls (Baloh et al. 1994, Maki et al. 1994, Overstall 1980).

When vision was removed the older subjects increased their postural sway velocity and amplitude to a greater extent than younger subjects, whereas when proprioceptive information was removed using tendon vibration, the stability of both the young and older were similarly affected (Hay et al. 1996). It is possible that the explanation for this is simply that the relative importance of proprioceptive information is similar for both the young and older individuals, with the older also relying more on visual inputs. It could, however, be interpreted as the older people being more dependent on vision to substitute for other weakened sensory cues (Hay et al. 1996).

The exact mechanisms for the decreased postural sway with age have not, as yet, been specifically identified. This decline may, however, be connected with changes in both the central and peripheral nervous system, which could affect either or both of the sensory or motor components of balance (Nardone et al. 1995, Stelmach and Worringham 1985). A decreased efficiency of the stretch reflex and specifically the monosynaptic reflex has been demonstrated with increasing age (for review see section 2b). This would affect the prioprioceptive response of the ankle joint when attempting to maintain and correct stability. The latency and amplitude of the monosynaptic stretch reflex and H reflex have been consistently shown to increase and decline, respectively, with age, due to factors such as degenerated muscle spindles (Swash and Fox 1972), decreased nerve conduction velocity (Boxer et al. 1988), impaired sensory- motor synapses (Morita et al. 1995) and changes in the motor unit organisation (for review see Vandervoort 2002). This leads to a less prompt and insufficient feedback muscle action, which may increase the displacement of the COP.

Using a dynamic force platform to induce sway, the association between EMG response, postural sway and age has been studied. These studies, however, give confusing results as to which parameters are correlated. During upward tilt of the platform, a correlation has been reported between the sway area and sway path and the latency of the short latency response (SLR) of the soleus, despite no correlations being reported for the EMG response from the tibialis anterior. During the downward tilt, again a correlation was reported for the sway parameters and the EMG response of the soleus, but this time the correlation was with the long latency response (LLR), as with the upward tilt no correlations were reported with the EMG response of the tibialis anterior. The correlations were stronger for all responses with the eyes closed rather than eyes open (Nardone et al. 1995). Differing findings have been reported whereby, during upward tilt, both the latency and the area under the tibialis anterior medium latency response (MLR) and LLR correlate well with postural sway, whereas no correlation was found between the latency of the SLR (Allum et al. 1993).

SECTION 3c: POSTUROGRAPHY AND TEMPERATURE

Little literature is available on the effects of temperature on postural control. The only study available, published following the study in the thesis, reports that whole body cooling increases sway path, sway velocity and sway area (Makinen et al. 2005). The authors gave very little explanation as to why this occurs, however, they highlight shivering, a result of reduced core temperature, as being a possible determinant.

SECTION 4a: FORCE FLUCTUATIONS DURING FINE MOTOR CONTROL

When an individual is asked to perform a steady constant force muscle contraction, the force output is not constant but instead fluctuates around the target force. The amount of fluctuation is affected by many factors including age, temperature and contraction level (Danion and Gallea 2004, Galganski et al. 1993, Lakie et al. 1994). Force fluctuation is normally defined as the variation in the force output, and it is quantified either as the absolute (standard deviation of the mean, SD) or the normalised (coefficient of variation, CofV) fluctuation. When comparing two groups or conditions at a contraction level relative to the maximal strength of the subject, the CofV of the fluctuation is preferred as this takes into account differences in the absolute target force levels.

During an isometric contraction the CofV varies as a function of the contraction level (% maximal voluntary contraction (MVC)); however, the exact nature of this relationship is unclear. A U shaped relationship has been reported to exist, whereby the force fluctuation is greatest at the lowest contraction levels, reducing as the contraction level increases until the force fluctuation is lowest at an optimal contraction level of around 20-30% MVC; after this level it has been reported that the force fluctuation increases again (Danion and Gallea 2004, Taylor et al. 2003). This relationship is thought to exists because at and around the optimal force level, the force output can be adjusted either by varying the number of active motor units or by modulating the discharge frequency, while above or below this a single strategy is adopted (Danion and Gallea 2004). Other authors have, however, reported a plateau after around 20% MVC (Burnett et al. 2000, Christou et al. 2002, Galganski et al. 1993, Laidlaw et al. 1999, 2000, Moritz et al. 2005, Tracy and Enoka 2002).

Aside from the well recognised fixed passive factors affecting force production (angles of pennation, length-tension relationships, insertion distances), the active control of force within a single muscle group is generally believed to be modulated by two main factors: the recruitment and derecruitment of motor units within the active muscle and changes of the discharge characteristics of the active motor units

(Binder and Mendell 1990). Research on the origins of force fluctuations during an isometric contraction has focused mainly on the discharge characteristics of the active motor units. Moritz et al. (2005), using a combination of experimental observations and computer simulation techniques, identified that discharge rate variability (expressed as CofV of the discharge rate) was the major contributor to the force fluctuation over the working range of the considered muscles. This discharge rate variability was shown to be greatest at the low force levels (2-5% MVC). The discharge rate, however, was reported to have only a minor influence on the force fluctuation.

As with the discharge rate variability, computer simulations have demonstrated that motor unit synchronisation, a measure of the near simultaneous discharge of action potentials of two motor units (Semmler et al. 2000), can affect force fluctuation (Yao et al. 2000). Despite modelling studies showing that fluctuations in force do exist even when there is no motor unit synchronisation (Christakos 1982), it appears that an increased level of motor unit synchronisation increases the variation of the force fluctuation, with the effect being greatest at low contraction levels (Yao et al. 2000). In experimental conditions a positive association has been demonstrated between the motor unit synchronisation and force fluctuation in the FDI muscle during isometric contractions below 10% MVC (Semmler et al. 2000). A relationship has been reported to exist between motor control training, motor unit synchronisation and force fluctuation. Musicians, trained in fine motor control, have lower levels of motor unit synchronisation, and low levels of force fluctuation, while strength trained athletes, trained in gross motor control, have greater levels of motor unit synchronisation and higher force fluctuation when compared to control subjects performing a low level isometric task (Semmler and Nordstrom 1998).

During an isometric contraction, the muscle spindles have been reported to respond to small force fluctuations, consequently facilitating the activation of motor units (Lippold 1970). Work by Marsden (1978) suggests that the short latency stretch reflex creates oscillation at a frequency around 10 Hz, while the long latency stretch reflex oscillates at around 7 Hz. Similarly, using the theory that temperature will alter the delay in the stretch reflex circuit and therefore changes the frequency of oscillation, Lippold (1970) also comes to the conclusion that tremor in the 8-12 Hz band is due to the oscillations in the stretch reflex servo loop. Not all researchers, however, are in agreement as to the contribution of the stretch reflex during isometric contraction. Durbaba et al. (2005), for example, suggest that there is no clear stretch reflex contribution at low level isometric contraction (30%) as they reported no obvious peaks in the frequency band between 8-12 Hz. In an isometric contraction muscle- length changes are minimised and consequently the loop gain is greatly reduced, although Durbaba et al. (2005) acknowledge that the stretch reflex is still present.

SECTION 4b: FORCE FLUCTUATION AND AGEING

One of the consequences of increasing age is the reduced ability to perform simple tasks such as exerting a constant force during a submaximal contraction. Studies are consistently showing that older individuals display more fluctuation during isometric contractions than their younger counterparts (e.g. Bazzucchi et al. 2004, Tracy and

Enoka 2002, Vaillancourt et al. 2003). The difference between the age groups is related to the force level, with the differences being greatest at the lowest and highest intensity and the difference between the groups being lowest or disappearing at a contraction level of around 30-40% MVC (Galganski et al. 1993, Tracy and Enoka 2002, Vaillancourt and Newell 2003). Force steadiness of the knee extensors has been highlighted by Seynnes et al. (2005) as a strong indicator of functional ability of the lower limbs in healthy elderly females. A strong correlation was demonstrated between force steadiness, measured at 50% MVC, and chair rise time and stair climb power (Seynnes et al. 2005).

The origins of the force fluctuation in young individuals have yet to be fully understood, making the research into the causes of increased force fluctuation with ageing difficult. Recent studies have pointed towards at least 4 features of motor output that could contribute to differences in steadiness between young and older adults. These include the average force produced by the motor unit, the amount of motor unit synchronisation and the discharge behaviour of motor units and the pattern of coactivation by the antagonist muscle.

At very low forces (<10% MVC), in which the difference between young and older adults appears to be greatest (Galganski et al. 1993, Tracy and Enoka 2002, Vaillancourt and Newell 2003), the relative contribution of single motor units to the net force is greatest due to the relatively low number of recruited fibres (Fuglevand et al. 1993). As a result of the increased innervation ratio of the low threshold motor units with ageing, the twitch forces of the low threshold motor units are greater in older adults compared to young adults (Galganski et al. 1993, Semmler et al. 2000), leading researchers to hypothesise that at low level isometric contractions, recruitment of these larger motor units would contribute to the increased force fluctuations in the older group compared to the young group. Computer simulation studies, however, have indicated that increasing in the motor unit twitch force by 40% has negligible effects on force fluctuations during isometric contractions (Taylor et al. 2002). Similarly, following several weeks of strength training older individuals, which resulted in the removal of the differences in steadiness between young and older subjects, no difference in the motor unit force or the time course of the twitch was reported in the older individuals (Keen et al. 1994).

As reported previously, motor unit synchronisation has been identified as one of the causes of force fluctuation during isometric contractions (Yao et al. 2000), however, it appears that a change in the amount of motor unit synchronisation is not a consequence of ageing (Semmler et al. 2000, Kamen and Roy 2000). Similar mean motor-unit synchronisation was reported for young and older adults during low level isometric contractions, despite older individuals having greater force fluctuations than the young subjects (Semmler et al. 2000).

The discharge characteristics of the single motor unit, do not appear to be affected by ageing at low level contractions as the majority of investigations have reported no difference in the discharge rate or discharge rate variability between young and older adults at isometric force levels ranging from 2.5 to 50% MVC (Galganski et al. 1993, Laidlaw et al. 2000, Semmler et al. 2000, Vaillancourt et al. 2003). However, a decrease in the discharge rate of the single motor units in the older individual when compared to the younger individual has been reported (Connelly et al. 1999, Kamen and Roy 2000). Conversely, both an increase and decrease in discharge variability have been reported (Laidlaw et al. 2000, Semmler et al. 2000).

Investigations into the role of the antagonist coactivation appear to dismiss this as a factor for the differences between young and older individuals. Burnett et al. (2000) and Laidlaw et al. (2002), report that the increase in force fluctuation seen in the index finger of older individuals was not associated with either the level or the activation pattern of the coactivation of the antagonist muscle in either young or older subjects.

The stretch reflex loop is highlighted as a potential cause of the force fluctuations in young subjects. As changes occur at each level of the stretch reflex loop, from the periphery to the spinal level (reviewed in detail in section 2b), it may be hypothesised that these changes will affect the force fluctuations, potentially changing the frequency of the fluctuations due to the known slowing of the reflex loop with ageing. No work has yet, however, been done to support this speculation.

SECTION 4c: FORCE FLUCTUATION AND TEMPERATURE

There have been few comprehensive studies on the effects of temperature on force fluctuation. Prior research has focused more on tremor at rest and the effects of temperature on manual dexterity tasks. The findings are conflicting with no indications of the physiological mechanisms responsible for changes occurring as a result of altered temperature. For instance, Lakie et al (1994) and Feys et al. (2005) reported improvements in a fine manual dexterity task and tremor amplitude in healthy individuals and patients with essential tremor and multiple sclerosis following a period of arm cooling, whereas Havenith et al. (1995) and Cheung et al. (2003) found opposing findings, whereby healthy subjects showed an impairment in manual dexterity tests with cooling. Findings from Cooper at al. (2000) suggest that the outcome of temperature manipulation on tremor may be population specific as they found that patients with essential tremor benefited from cooling, whereas Parkinson disease patients benefited from warming when completing dexterity tests.

Farina et al. (2005) investigated the effects of the discharge characteristics of single motor units while young subjects performed a low intensity contraction and were asked to maintain a minimum discharge frequency of a target motor unit. After warming, the minimal discharge rate remained constant when compared to control, similarly the recruitment threshold of the target motor unit was constant and the discharge variability, thought to be one of the major causes of the force fluctuation (Moritz et al. 2005), was unaltered. Bigland-Ritchie et al. (1992) showed no change in motor unit discharge rate during a maximal voluntary contraction following cooling of the hand muscles when compared to control conditions. These findings suggest that an alteration to the motor unit discharge characteristics was not the cause of the change in the ability to perform a fine manual task following temperature manipulation. Similarly, a change in the synchronisation of the motor unit firings can be disregarded as cause of change in force fluctuation with temperature, as both cooling and warming have been found to have no effect on the motor unit synchronisation (Bertram et al. 1995, Farina et al. 2005, Gydikov et al. 1979).

As previously described, temperature affects the membrane properties of the motor unit, consequently influencing the twitch properties, including the twitch duration and twitch force. Cooling increasing the duration and twitch force, while warming decreases the duration and twitch force (Bigland-Ritchie et al. 1992, Davies et al. 1982, Geurts et al. 2004, Ranatunga et al. 1987). The effect of this change in twitch properties on force fluctuations is not known, however, computer simulation studies have found only negligible effects of twitch force on force fluctuation (Taylor et al. 2000).

Changes occur at each level of the stretch reflex loop, from the periphery to the spinal level following both warming and cooling (reviewed in detail in section 2c). Therefore, it may be hypothesised that these changes will affect the force fluctuations, potentially changing the frequency of the fluctuations due to the known slowing of the reflex loop with cooling and the quickening with warming. The only work to investigate this was early research by Lippold et al. (1957, 1970), who found that following cooling, there was a reduction in frequency and a reduction in amplitude of the force fluctuations, while warming raised the frequency with no mention of the effects on amplitude of force fluctuations.

SUMMARY OF LITERATURE AND HYPOTHESES

Ageing affects all aspects of the neuromuscular system and consequently motor control. The main effects of ageing include: shrinking and loss of motor units and muscle fibres, changes in the characteristics of the motor units to more slow twitch units (for review see Roos et al. 1997, Vandervoort 2002), changes in the efferent nerves supplying the muscle fibres with information and the afferent nerves providing information to central nervous system from the periphery, changes to the nerve include demylination of the fibres which in turn slows the conduction velocity of the signal (Adinolfi et al. 1991, Lascelles and Thompson 1966). At the periphery the sensory mechanisms including the muscle spindles are reduced in number and have a reduced sensitivity (Swash and Fox 1972). Consequences of these changes in the neuromuscular system to motor control include a loss of strength and power (Macaluso and De Vito 2003), poorer balance (Maki and McIlroy 1996), a slowing of the reflex response (Sabbahi and Sedwick 1982, Scaglioni et al. 2002) and worsening of fine motor control (Tracy and Enoka 2002, Vaillancourt et al. 2003).

A change in muscle temperature in young individuals, either warming or cooling, is known to affect many parts of the neuromuscular system which are affected by ageing. Cooling, for instance, has been found to slow the conduction of the signal along the nerve and across the muscle fibre (Hodgkin and Katz 1949, Bolton et al.1981), increasing the discharge of the muscle spindle (Lippold et al. 1960, Michalski and Séguin 1975) and shifting the force velocity curve of a muscular contraction to the left (Sargeant 1987). Cooling has been also shown to decrease strength and power during dynamic contractions (Davies and Young 1983, Oksa et al. 1997, Sargeant 1987) as well as slowing down the velocity of a reflex response

(Oksa et al. 2000). In contrast, warming has been shown to increase the conduction velocity of the nerve and muscle fibres (Stegeman and De Weerd 1982, Gray et al. 2006) and shift the force velocity curve of a muscular contraction to the right (Sargeant 1987). These changes have been seen to increase strength and power during dynamic contractions (Gray et al. 2006, Sargeant 1987, Stewart et al. 2003) and increase the velocity of a reflex response (Bhattacharya et al. 1981). What has not, as yet, been established is the effects of either cooling or warming on postural control and fine motor control in both healthy young and older subjects.

All studies investigating the effects of temperature on the neuromuscular system have been reporting on young healthy individuals (predominantly fit, healthy males) however, it is not known if the findings from these studies can be transferred to a sedentary female population or, more importantly, an older female population. Hypothesising what may happen when the aged muscle is cooled or warmed is difficult, as it is not known whether the deteriorated muscle, nerve and peripheral sensory mechanisms have the ability to adapt to the modified temperature. As it has been seen that the older individual has a less responsive thermoregulatory system to whole body warming and cooling, including reduced vasoconstriction/dilation, metabolic heat production and cardiovascular function (for review see Florez-Duquet and McDonald 1998, Kenny and Munce 2003), it is possible that one of the consequences of ageing is a lack of adaptability to changes in the external environment. This lack of adaptation is highlighted in section 2b (H reflex and ageing) whereby changes in body position, muscle contraction level and the Jendrássik manoeuvre which alters the level of spinal reflex excitability and, therefore, the amount of excitable motor units in young subjects has no effect on the spinal reflex excitability in older individuals. On the other hand, should the neuromuscular system of the older subjects have a retained ability to respond to altered temperature and respond in a similar manner to younger subjects then this could potentially affect greatly the older individuals ability to successfully perform motor tasks.

Taking this into consideration, the research hypothesises for experimental chapter are outlined below.

Chapter 3:

It is hypothesised that young subjects will increase the strength output during the isokinetic contractions but not during isometric contractions as this has previously been shown not to be affected by either warming nor cooling (Bergh and Ekblom 1979, Stewart et al. 2003, Thornley et al. 2003). With respect to the EMG parameters, it is thought that this will be affected by both warming and cooling due to the change in velocity of the muscle fibre membrane potential, with warming increasing the velocity, hence decreasing the RMS, while increasing the MFCV and the MNF; while cooling will decrease the velocity therefore increasing the RMS while decreasing the MFCV and the MNF. In the older individuals a lower strength output during both isokinetic and isometric contractions when compared to the young subjects is expected along with a lower RMS, MFCV and MNF. With respect to temperature two hypothesises are possible: 1) temperature (both warming and cooling) will have no effect on either the strength or the EMG parameters due to the degenerated neuromuscular system preventing the modifications seen in the young individuals, or 2) it is possible that the older group will respond in a similar manner to the younger subjects, possibly even to a greater extent than the young due to the contraction velocities adopted in the present study being closer to their optimal contraction velocity, whereby the greatest effects of temperature are seen to occur.

Chapter 4:

In the second study, it is hypothesised that in the young subjects the spinal reflex excitability (Hmax/ Mmax ratio) will increase will cooling and decrease with warming and that reflex onset latency will increase with cooling and decrease with warming. In the older individuals, a lower spinal reflex excitability is expected with a slower reflex response latency in comparison to young subjects. With respect to temperature, as the spinal reflex excitability has been shown to be less adaptable to changes in the external environment it is, therefore, hypothesised that the spinal reflex excitability will not be changed with either warming or cooling. It is unclear however, whether the onset latency will be affected by temperature in similar manner to the younger subjects as a consequence of the changes in the nerve structure with ageing.

Chapter 5:

In the third study, as postural stability is partially dependent on the proprioceptive reflex response to detect and respond to postural sway, it is thought that cooling will slow the delivery of the signal from the receptors along the afferent nerves to the central nervous system and slow the corrective response through the efferent nerves to the muscle (as hypothesised in chapter 4), therefore, this delay in reflex response will worsen the postural control of the younger individual. On the other hand, warming will increase the velocity of the corrective response and improve postural control. It is expected that the older individuals will have a poorer postural control compared to the young irrespective of temperature; however, it is not clear whether the older group will be as affected by temperature as the younger subjects. In the present study, we will test both eyes open and eyes closed conditions, as it is possible that the effects of temperature will be more evident when vision is removed and the subjects are more reliant on proprioceptive feedback. It is expected that the removal of vision will impair the older subjects to a greater extent than the young, as it is hypothesised that older subjects will be more reliant on vision to compensate for their impaired proprioception, irrespective of temperature condition.

Chapter 6:

The effect on temperature on fine motor control is unclear even in young individuals, with previous studies being inconclusive in their findings (section 4c). As temperature alters the muscle fibre membrane properties it is hypothesised that the discharge characteristics of the motor unit will be altered, for example, a slowing of the MFCV with cooling may reduce the discharge frequency of the motor units, whereas warming will have the opposite effect of quickening the MFCV and therefore, may increase the discharge frequency. It is expected that any change in the discharge characteristics may have a consequent effect on the force fluctuation. The stretch reflex loop is known to be active during low level isometric contractions and as hypothesised in chapter 4, the onset latency of the response will be slowed with cooling and quickened with warming, which, in turn, will cause a delay in the response with cooling and a quickened response with warming, consequently worsening fine control and improving fine control respectively. The frequency content of the fluctuation is a tool used to indirectly assess the contribution of both motor unit firing and the stretch reflex; therefore, it is hypothesised that any changes in either system will be reflected in changes in the frequency content of the fluctuation. Previous studies have reported poorer fine motor control in older subjects, many reasons have been suggested for this, however, in this study we will look at the contribution of the discharge characteristics of the motor units, with older individuals hypothesised to have a reduced motor unit discharge variability, additionally, indirect assessment of the contribution of the stretch reflex loop to the force fluctuation will test the hypothesis that less of the force fluctuation will consist of corrections from the stretch reflex loop due to the older individuals having a reduced sensitivity of the muscle spindles.

CHAPTER 3

Muscle temperature affects the toque and surface electromyographic properties of knee extensors in young but not older women

ABSTRACT

The purpose of this study was to investigate the effect of altered local temperature on torque and EMG parameters in 15 young women (21.5 ± 2.2 years; mean ± SD) and 12 older women (73.6 ± 3.2 years). Subjects completed maximal voluntary isometric contractions (MVC) and isokinetic knee extensions (30, 60, 90, 120 and 240 °/s) at three muscle temperatures: control (~34 °C), cold (~30 °C) and warm (~38 °C). Torque was lower in the older compared to young subjects regardless of temperature (comparisons at control temperature, torque at MVC, 30, 60, 90, 120, 240 °/s respectively; young: 138.2 ± 5.1; 142 ± 7.2; 123.6 ± 6.1; 107.0 ± 6.1; 99.3 ± 5.6; 76.4 ± 5.0 Nm; older: 101.0 ± 6.1; 94.7 ± 6.4; 84.0 ± 5.4; 67.8 ± 6.7; 60.4 ± 5.6; 45.3 ± 3.1 Nm; $P<0.001$). Warming had no effect on torque in either group, whilst cooling decreased the torque during the isokinetic contractions in the young group only, by 9.8, 7.3, 5.6, 5.6 % for 30, 60, 90, 240 °/s, respectively, ($P<0.05$). In both groups, muscle fibre conduction velocity (MFCV) was slower with cooling compared to the warm condition (decrease of 15% in the young and 17% in the older subjects; ($P<0.05$). Temperature, however, had no effect on the coactivation levels or the rate of force development in either group. This study suggests that the muscles of the older individuals are less responsive to altered temperature compared to young subjects.

INTRODUCTION

A known consequence of ageing is the reduced strength and power output during a voluntary contraction (Bazzucchi et al. 2004, Macaluso and De Vito 2003, Skelton et al. 1994). It is critical that older individuals are able to generate enough power to perform simple day to day physical tasks such as rising from a chair, climbing stairs or lifting shopping bags to maintain independent living (Harridge et al. 1999b). Age related changes to the neuromuscular system, including a decrease in muscle mass, remodelling of the motor units from the fast type II motor units to the slower type I motor units and changes in the discharge characteristics of the motor units, all contribute to this reduction in muscle function (Macaluso and De Vito 2004, Roos et al. 1997, Vandervoort 2002).

Temperature is known to affect the voluntary muscle contraction of young healthy muscles, with warming enhancing muscle force output (Bergh and Ekblom 1979, Sargeant 1987) and cooling impairing force output (Bergh and Ekblom 1979, Cheung and Sleivert 2004, Comeau et al. 2003, Oksa et al. 1997, Sargeant 1987). This effect is more apparent in dynamic contractions as compared to isometric contractions, as force output during isometric contractions have been shown to be unaffected by temperature (Bergh and Ekblom 1979, Binkhorst et al. 1977, Stewart et al. 2003, Thornley et al. 2003). As the amount of tension produced per cross bridge remains the same at different temperatures and that it is the population shift in the number of cross bridges that gives rise to the change in force production (Zhao and Kawai 1994, Coupland et al. 2001, Wang and Kawai 2001), changes in rate of cross bridge cycling due to changes in the enzymatic processes, including ATPase activity, are more discriminate in dynamic contractions (Bárány 1967). Older individuals have a more sedentary lifestyle during a typical day than their younger counterparts (Davis and Fox 2006), it is likely, therefore, that the limb temperature will be more influenced by environmental temperature in older individuals. Should older individuals display the same response to reduced muscle temperature as healthy young individuals, this could have serious implications to the success of performing tasks if they reside in a below normal room temperature, as cooling may reduce the muscular strength to below the critical level for performing the task. On the contrary, warming may be used to assist the individual in performing a task if, like young individuals, muscle function is enhanced. In contrast, however, it may be that the degenerated neuromuscular system of older individuals may prevent the modifications seen with altered temperature in young healthy muscles.

The aim of the study, therefore, was to investigate the effects of altered muscle temperature on neuromuscular responses in older women in comparison to that of younger women. Women were studied as they are more likely to reach the threshold for an independent life before males (Katz et al. 1983, Skelton et al. 1994).

METHODS

Subjects.

Twenty-seven healthy women (15 young: aged 21.5 ± 2.2 years, body mass 62.7 ± 6.1 kg, stature 1.65 ± 0.05 m and 12 older: aged 73.6 ± 3.2 years, body mass 66.0 ± 11.9 kg, stature 1.60 ± 0.06 m; mean ± SD) participated in the study after giving written informed consent. Subjects had no known neuromuscular disorders and older subjects were selected according to the criteria for being medically stable as proposed by Greig et al. (1994). All women were moderately active participating in non competitive physical activities no more than twice a week. Ethical approval was obtained from the Ethics committee of the University of Strathclyde.

Experimental design

After an initial familiarisation session allowing the subjects to become accustomed to the procedures and exercises, subjects attended the laboratory on one single occasion. Minimal physical activity was performed and no caffeine or alcohol was permitted 24 hours prior to testing. Following preparation subjects performed tests under three muscle temperature conditions, administered in a random order: cold, control and warm. In each testing condition individuals were required to perform a series of tasks: maximal isometric voluntary contraction of the knee extensors (MVC) and knee flexors (MVF) followed by a series of isokinetic knee extensions at 30, 60, 90, 120 and 240 °/s, administered in a random order.

Temperature measurements.

Muscle and skin temperature were measured from the vastus lateralis of the dominant leg. Muscle temperature was measured using a flexible intramuscular probe (Ellab ltd, Norfolk, UK) inserted 1cm below the subcutaneous fat layer (skinfolds x 0.5) at an angle of 45° in the direction of the muscle fibres. The thermistor was inserted through a venflon 18GA cannula (Becton Dickinson, Sweden) and advanced 0.5 cm beyond the end of the cannula into the muscle. Skin temperature was measured using a skin thermistor (Ellab ltd, Norfolk, UK) placed 2 cm above the insertion of the muscle temperature probe. Both skin and muscle thermistors were secured with tape. Temperatures were recorded from a Medical Precision Thermometer (DM 852, Ellab, Copenhagen, Denmark). Core temperature was estimated using an infrared tympanic thermistor (Braun, type 6013, Germany). Muscle temperature was continuously monitored ensuring consistent temperatures during each contraction.

Testing was conducted at muscle temperatures of 30, 34 and 38 °C; this was considered as the cold, control and warm muscle temperature conditions, respectively. Ice bags covering the whole of the quadriceps muscle group were used to cool the muscles and hot water bottles again, covering the whole of the quadriceps muscle group, were used to warm the muscles.

Strength and power measurements

Isometric and isokinetic knee extension torques of the dominant limb were measured with a dynamometer (Biodex System 3, Biodex Medical Systems Inc, New York).

Subjects were seated in the dynamometer with hip and knee angles of 90 °. Straps were secured across the chest and waist. The rotational centre of the lever arm was aligned to the lateral femoral epicondyle of the knee. The lever arm was secured to the lower leg with a resistance pad around the ankle. Visual feedback was provided to the subjects on a computer screen. Subjects were required to produce one MVC followed by one MVF. The MVC and MVF were repeated, with target bands on the screen set 20% higher than previous performance. Subjects followed the force production on the screen and were verbally encouraged to achieve their maximum, with contraction to be maintained for approximately 3 seconds. Prior to every contraction it was emphasised that they were to reach their maximum as fast as possible.

After a rest period of 3 minutes the subjects completed the series of isokinetic knee extensions, with 2 contractions at each velocity. A resting period of one minute was given between all contractions. The movement angle for every contraction was 60 ° (from 90 ° to 150 °, with 180 ° being full knee extension). Again, prior to every contraction emphasis was placed on the importance of reaching the maximum force as fast as possible.

Surface electromyography (EMG) recordings.

EMG recordings were obtained from the distal portion of the vastus lateralis and the biceps femoris using an adhesive linear array of 4 electrodes, 10 mm interelectrode distance (ELSCH 004, SPECS Medica, Salerno, Italy). The optimal electrode position was determined after the most distal innervation zone was located. The electrode was placed distally to this location with the orientation being the position with the best propagation of the signal along the array without a change in shape, determined from visual inspection of the signals. After slight abrading of the skin with abrasive paste (Meditec- Every, Parma, Italy), the electrodes were attached and 20 μL of conductive gel was inserted into the cavities of the electrode to ensure proper skin-electrode contact. Signals were amplified (EMG 16, LISiN- Prima Biomedical & Sport, Treviso, Italy) and band passed filtered (10-500Hz) at a sampling frequency of 2048 Hz.

Data analysis

Data were analysed off line using the Biodex and Labview software for the mechanical and EMG data, respectively. Torque was calculated as the mean value for a 500 ms window centred at the peak force. The rate of force development (RFD) was calculated from the MVC. Force at time points 0, 20, 50, 100 and 200 ms were determined. Time point 0 was taken as being the point whereby force level increased above baseline by 2 Nm. RFD at each stage was calculated by subtracting the force at 0 ms from the force at that time point (Aagaard et al. 2002a). To remove the deceleration phase of the isokinetic movement only values from 90° to 140° were analysed.

The EMG variables calculated for the MVC and the isokinetic contractions were root mean square (RMS), average rectified value (ARV), median frequency (MDF), mean frequency (MNF) (formulas given below) and muscle fibre conduction velocity (MFCV) (detailed below). For the MVF, only RMS and ARV were extracted. RMS, ARV, MDF and MNF were computed from the central single differential signal of the selected triplet using adjacent epochs of 256 ms with an overlap of 128 ms. These values were calculated for the 512 ms window centred at the peak torque (Figure 3.1). The MFCV was estimated according to Merletti and Lo Conte (1995), from the two double differentials of a triplet of adjacent signals using the EMG cross-correlation (CC) function which assumes that the time delay between two similar signals is the amount of time shift that must be applied to one signal to minimize the mean square error with the other and to maximizes the CC between the two signals (Naeije and Zorn 1983). Estimates of MFCV were accepted only if the CC values were higher than 0.8. RMS and ARV of the EMG from the biceps femoris muscle were calculated for the same period during the knee extension to determine the effects of altered agonist muscle temperature on coactivation. This RMS (ARV) value is expressed as the percentage of maximal biceps femoris RMS (ARV) measured during the knee flexion. Similarly, the effect of altered antagonist muscle temperature on coactivation during knee flexion is expressed as a percentage of maximal vastus lateralis RMS (ARV) measured during the knee extension.

ARV= $$\frac{1}{N}\sum_{n=-N/2}^{N/2} | x_n |$$

RMS= $$\sqrt{\frac{1}{N}\sum_{n=-N/2}^{N/2} x_n^2}$$

MDF= $$\tfrac{1}{2}\int_0^{\infty} P(f)df = \tfrac{1}{2}M_0$$

$$\text{MNF}=\int_0^\infty fP(f)df \Big/ \int_0^\infty P(f)df = M_1/M_0$$

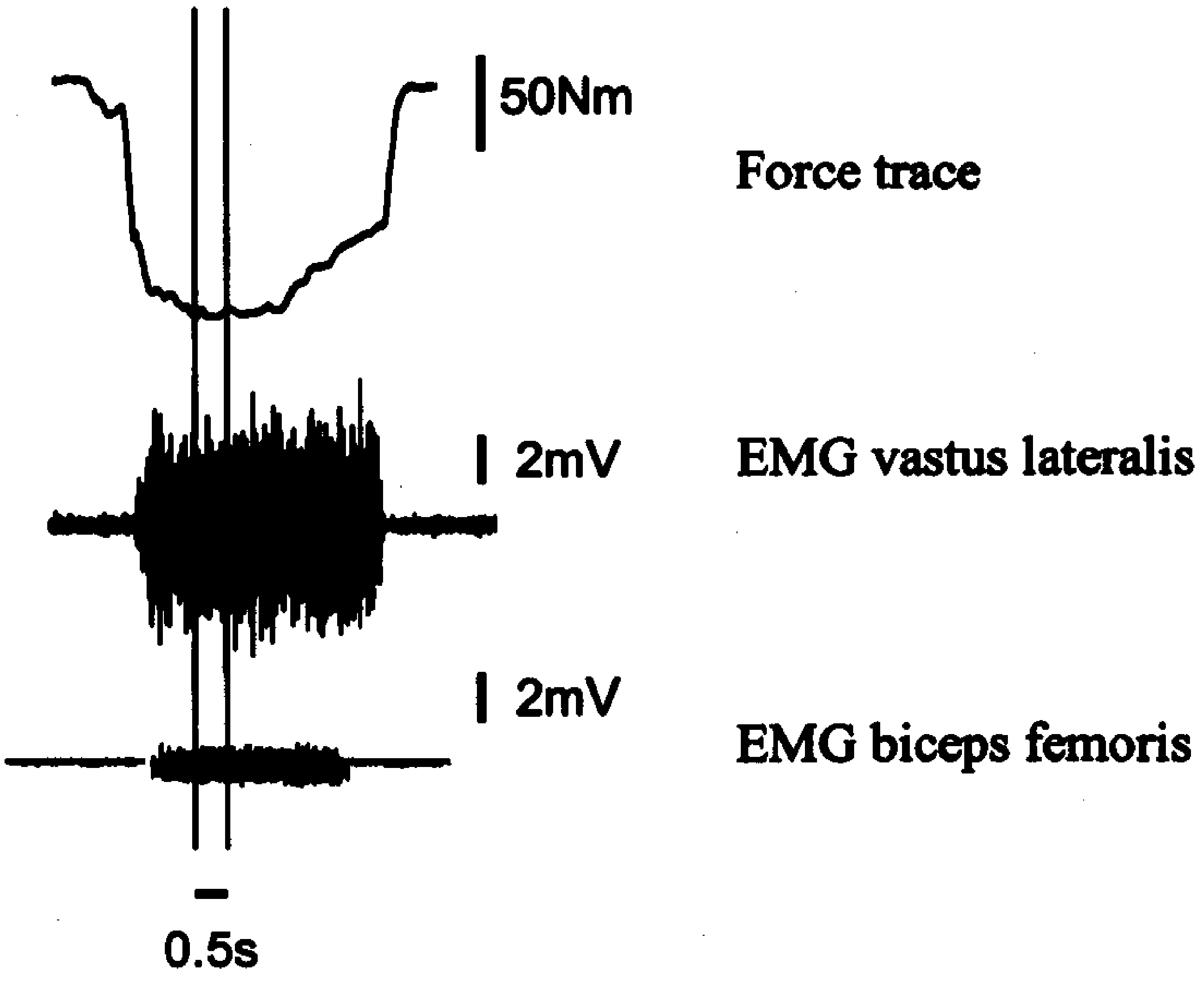

Figure 3.1. Example data of the raw traces of the torque and the EMG during an MVC (knee extension, young subject). The portion of the signal used for analysis is highlighted.

Statistical analysis

All data were normally distributed in terms of skewness and kurtosis. Data were analysed with a three-way repeated measures ANOVA (age × temperature × force level) for data in the torque, RFD and EMG parameters. A two-way repeated measures ANOVA (age x temperature) was used for the muscle, skin and core temperature and coactivation analysis. An alpha level of 0.05 was used for all statistical comparisons and post-hoc comparisons (Student-Newman-Keuls (SNK)) were performed when the ANOVA was significant. Data are given as mean ± standard error (SE) unless otherwise indicated.

RESULTS

Temperature

As seen in table 3.1, cooling the muscles of the knee extensors decreased the muscle temperature of the vastus lateralis by ~ 4°C when compared to control conditions ($P<0.001$), in both groups, while warming increased the muscle temperature by ~4°C ($P<0.001$) compared to control conditions again in both groups. Similarly, in both young and older subjects, skin temperature of the vastus lateralis was decreased and increased following cooling and warming respectively ($P<0.001$). The estimated core temperatures (tympanic temperature) were the same for both groups and for all temperature conditions.

		Cold	Control	Warm
T_m (°C)	Y	29.7 ± 0.2*	34.1 ± 0.1	38.1 ± 0.1*
	O	29.1 ± 0.2*	33.9 ± 0.1	37.9 ± 0.1*
T_{sk} (°C)	Y	24.6 ± 1.0*	31.3 ± 0.3	38.7 ± 0.4*
	O	26.1 ± 2.0*	32.8 ± 0.7	38.6 ± 1.2*
T_t (°C)	Y	36.7 ± 0.1	36.8 ± 0.1	36.8 ± 0.1
	O	36.4 ± 0.1	36.4 ± 0.1	36.4 ± 0.1

Data are means ± SE; n =15 in young and 12 in older group; * denotes difference from control condition ($P<0.01$). T_m= muscle temperature, T_{sk}= skin temperature, T_t= tympanic temperature

Table 3.1. Temperature values for the young (Y) and older (O) groups during cold, control and warm temperature conditions.

Torque

The torque was greater in the young subjects than the older subjects for the MVC and MVF and at all angular velocities (ANOVA: $P<0.001$) (Figure 3.2). For the MVC under control conditions, older subjects reported a torque of only 73% of that attained by the young subjects. With respect to the effects of temperature on the torque production, there was a general effect of temperature in the young subjects, with the torque following cooling being significantly lower than the torque at control temperature (SNK: $P<0.05$). Warming was not different to control (Figure 3.2A). There was no significant effect of temperature on the older subjects. When the interaction action between velocity and temperature was analysed further in the younger subjects, a reduction in torque with cooling resulted for all angular velocities excluding 120 °/s, but not the MVC (0 °/s). When the torques are normalised to the torque value during the MVC at control temperature, the significant effects of cooling on the torque in the young subjects disappears, however the trend is similar with cooling being lower than control. Neither cooling nor warming affects the normalised torque in either the young or older subjects (Figure 3.2B).

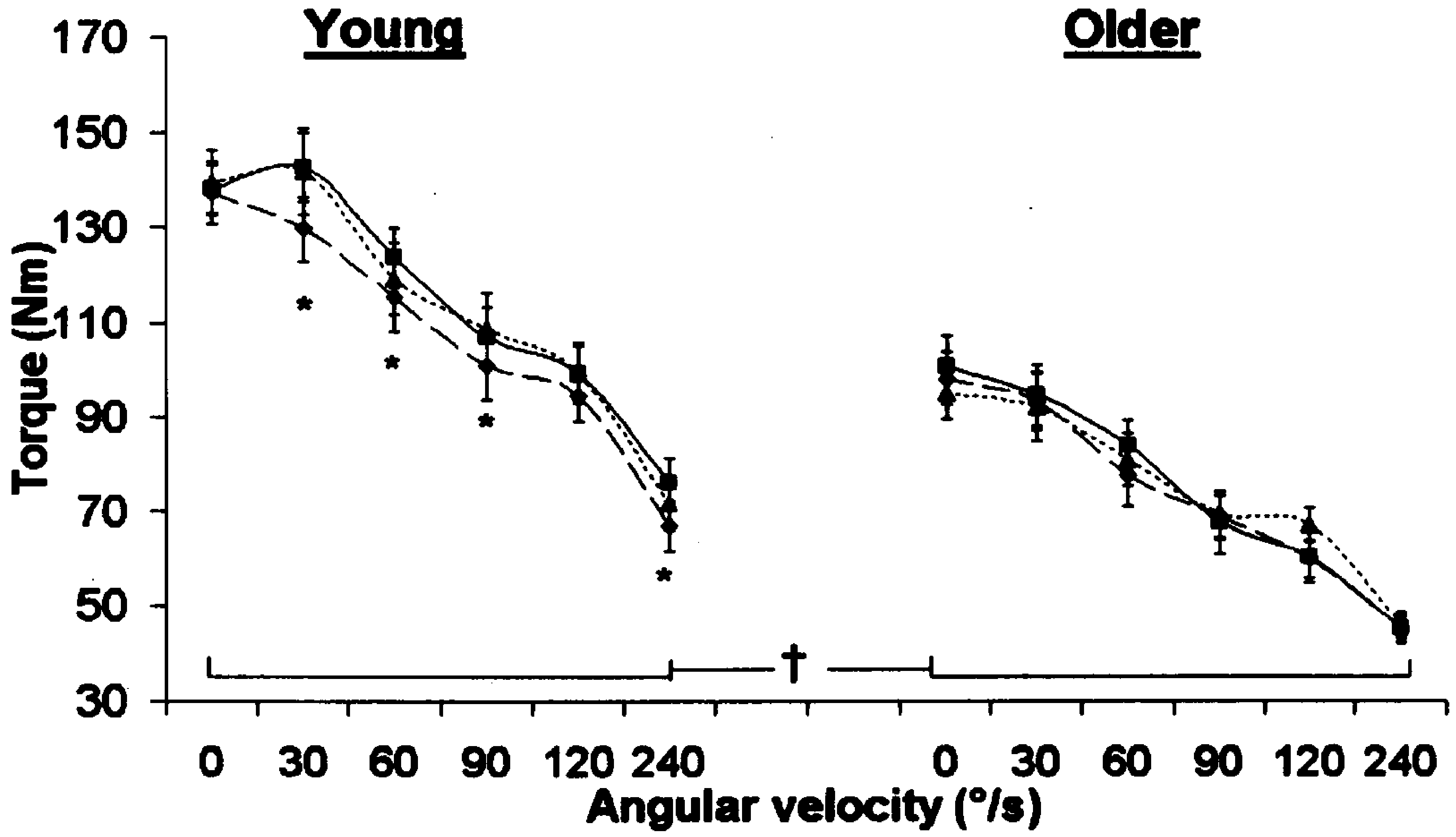

Figure 3.2A. Torque (Nm) (mean ± SE) during knee extension for the young (left side, *n* =15) and older subjects (right side, *n* =12) for the cold --♦--, control —■— and warm ···▲··· conditions. Torque is given for angular velocities of 0 (MVC), 30, 60, 90, 120 and 240 °/s. * denotes significant differences between cold and control; † denotes significant difference between young and older subjects.

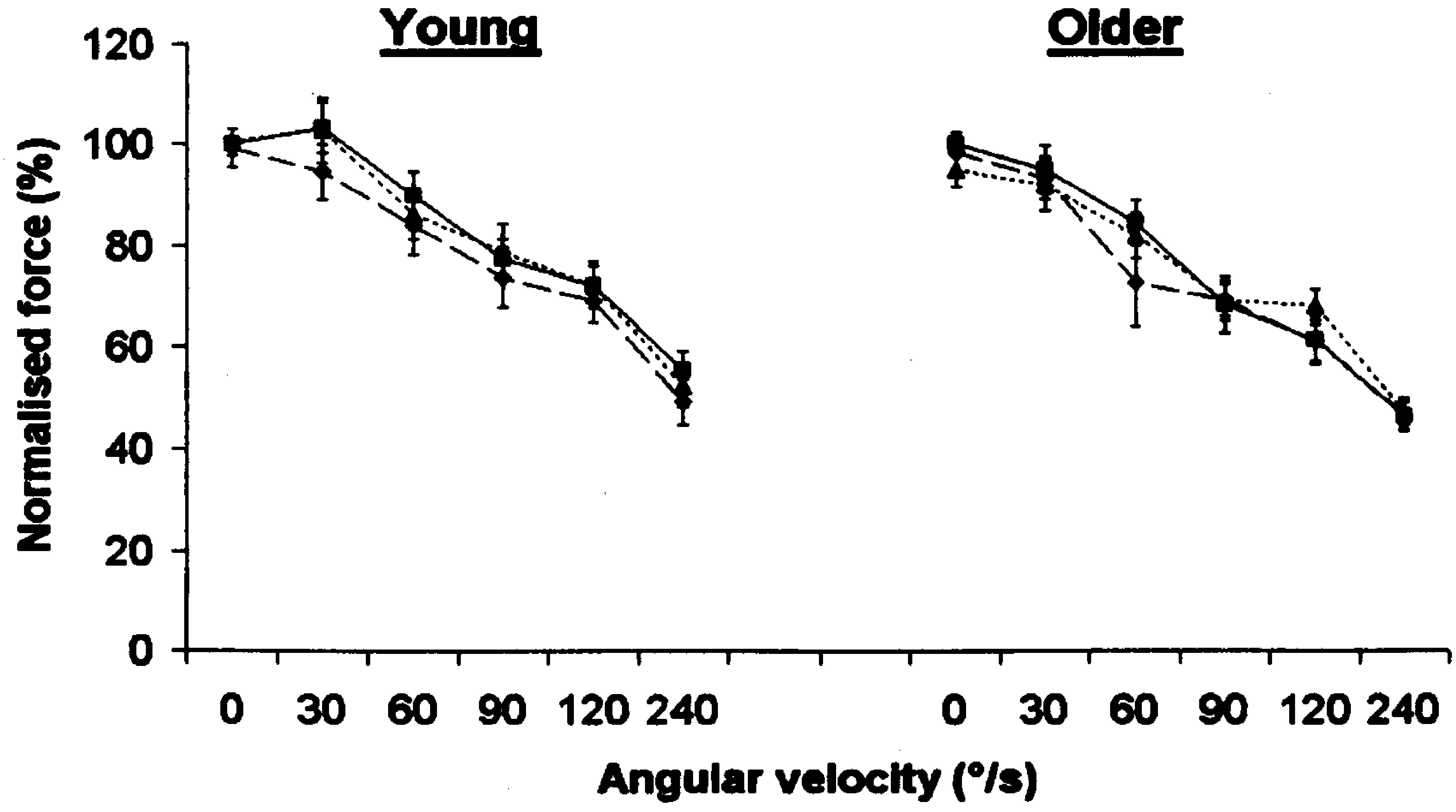

Figure 3.2B. Normalised torque (%) (mean ± SE) during knee extension for the young (left side, *n* =15) and older subjects (right side, *n* =12) for the cold --♦--, control —■— and warm ···▲··· conditions. Torque is given for angular velocities of 0 (MVC), 30, 60, 90, 120 and 240 °/s. All values are normalised against the torque at MVC during the control temperature condition.

EMG

RMS and ARV yielded similar results and the MNF and MDF yielded similar results, therefore, for the sake of simplicity and clarity, only RMS and MNF will be displayed and discussed.

The RMS was significantly greater in the young subjects than the older subjects (ANOVA: $P<0.01$) (Figure 3.3A). With respect to temperature, there was a general effect of temperature on RMS (ANOVA: $P<0.01$) but this is seen only in the young subjects where, in contrast to the torque results, it is warming that significantly affects the RMS, with RMS being lower following warming compared to the control condition (SNK: $P<0.01$), with no effect of cooling compared to control condition (Figure 3.3A). When the RMS is normalised to the RMS recorded during the MVC at control temperature the same effects of temperature exists whereby warming decreases the RMS compared to control condition in the young subjects only (Figure 3.3B).

There was no significant difference in the MNF between the young and older group (Figure 3.4A). There was an effect of temperature (ANOVA: $P<0.05$), which post hoc analysis revealed was in the young subjects only, which, consistent with torque, was significantly decreased with cooling compared to control condition (SNK: $P<0.05$), with no change in the MNF following warming (Figure 3.4A). Normalising the MNF value does not change the findings of the absolute MNF (Figure 3.4B). For both the absolute and the normalised data attention should be drawn to the large variability within both the young and older subjects which may mask any effects of temperature, specifically in the older group.

There was no difference in MFCV between the groups (Figure 3.5A). With respect to temperature, the ANOVA showed a significant effect ($P<0.05$), however, the differences were only between the cold and warm conditions (SNK: $P<0.05$) with no difference between the cold and control conditions or the warm and control conditions. There was no interaction between age and temperature, with both groups showing the same difference between the cold and warm conditions. Normalising the MFCV does not change the findings of the absolute MFCV (Figure 3.5B). Similar to the MNF data, large variability was seen specifically within the older subjects for both the absolute and normalised data, which may mask further effects of temperature.

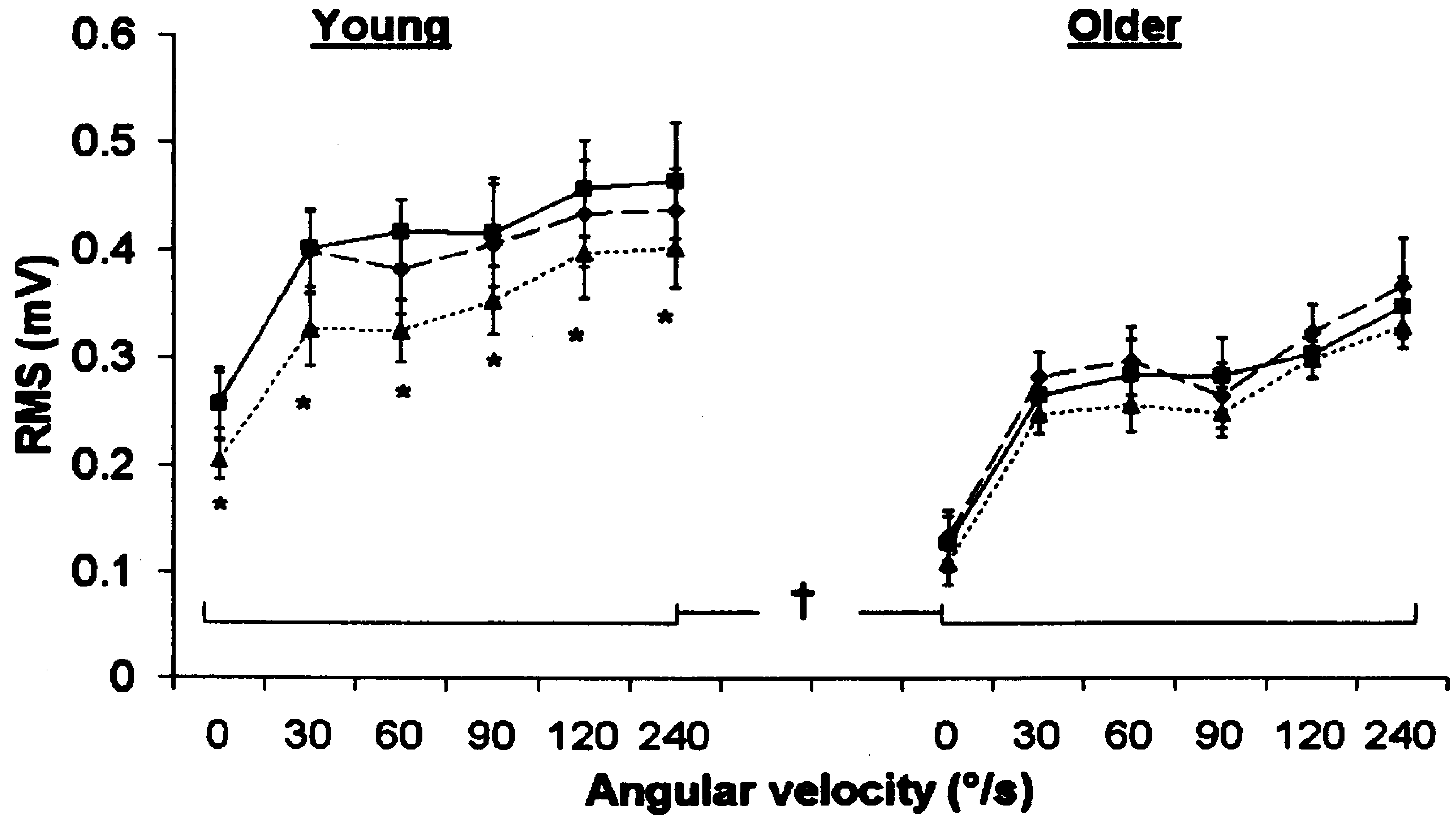

Figure 3.3A. RMS (mV) of the EMG around the peak torque value (mean ± SE) for the young (left side, n=15) and older subjects (right side, n =12) for the cold –♦–, control –■– and warm ···▲··· conditions. RMS is given for angular velocities of 0 (MVC), 30, 60, 90, 120 and 240 °/s. * denotes

significant differences between warm and control; † denotes significant difference between young and older subjects.

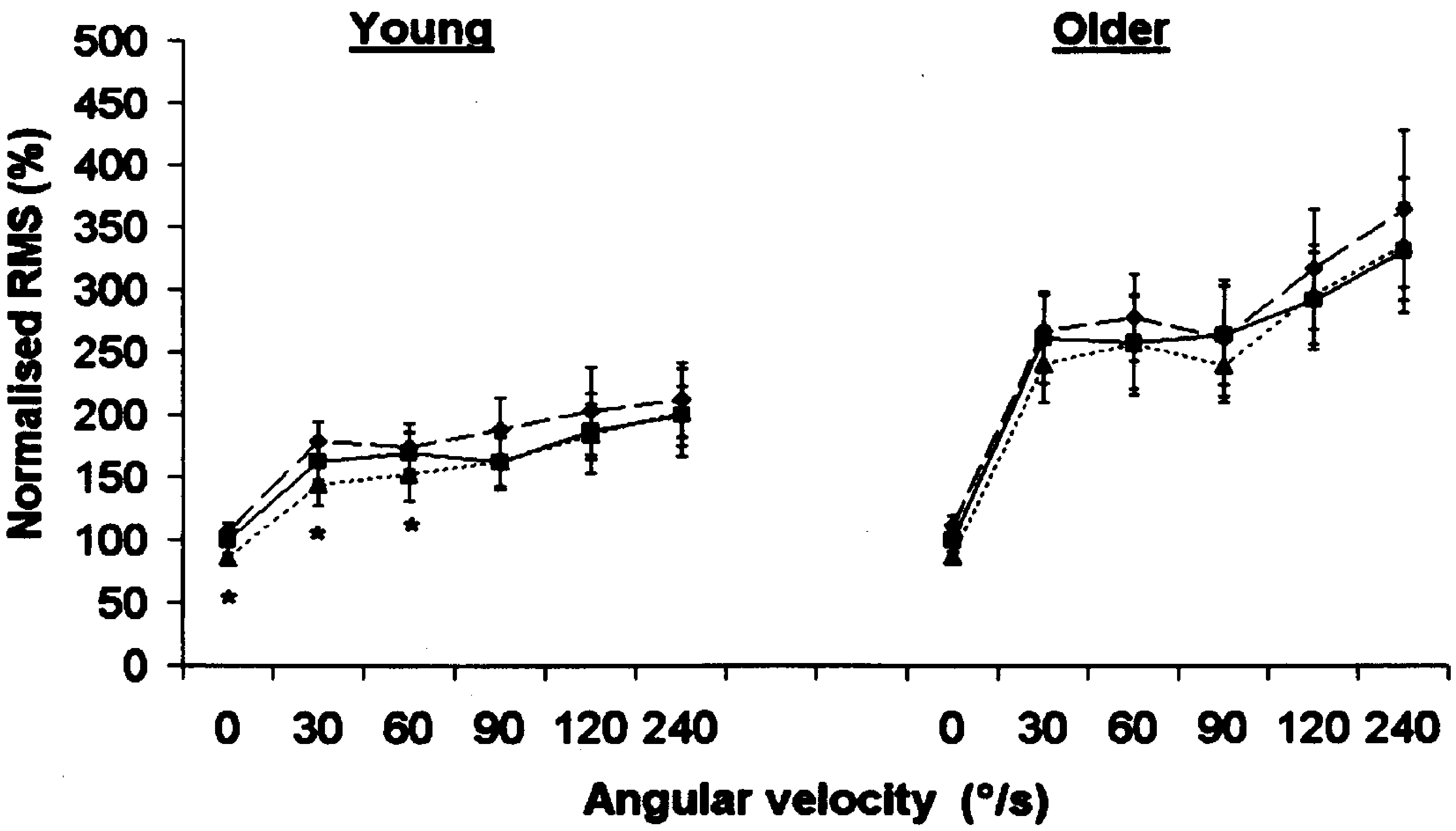

Figure 3.3B. Normalised RMS (%) of the EMG around the peak torque value (mean ± SE) for the young (left side, n=15) and older subjects (right side, n =12) for the cold --♦--, control —■— and warm ···▲··· conditions. RMS is given for angular velocities of 0 (MVC), 30, 60, 90, 120 and 240 °/s. * denotes significant differences between warm and control. All values are normalised against the EMG RMS at MVC during the control temperature condition.

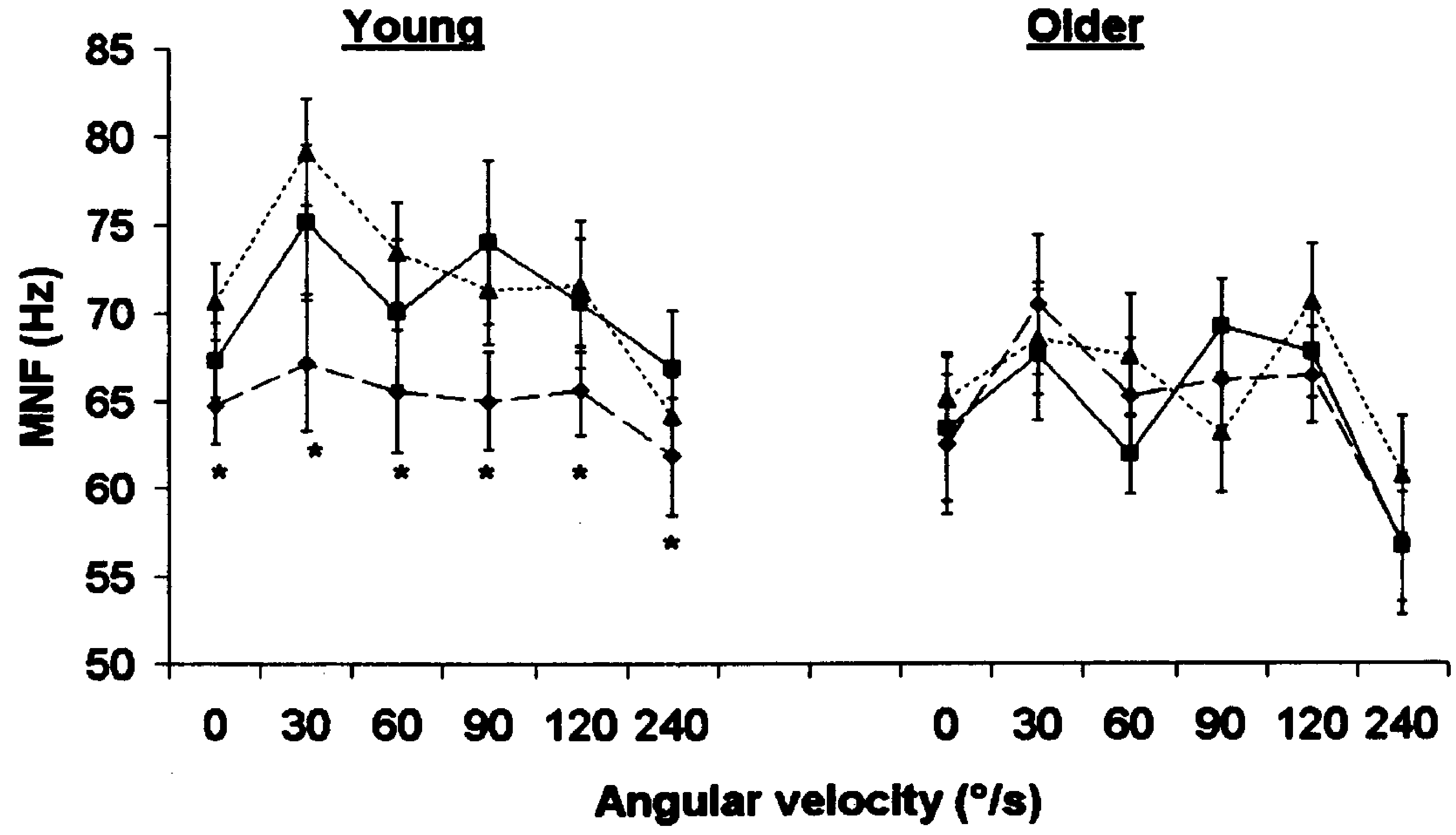

Figure 3.4A. MNF (Hz) of the EMG around the peak torque value (mean ± SE) for the young (left side, *n* =15) and older subjects (right side, *n* =12) for the cold --♦--, control —■— and warm ···▲··· conditions. MNF is given for angular velocities of 0 (MVC), 30, 60, 90, 120 and 240 °/s. * denotes significant differences between cold and control.

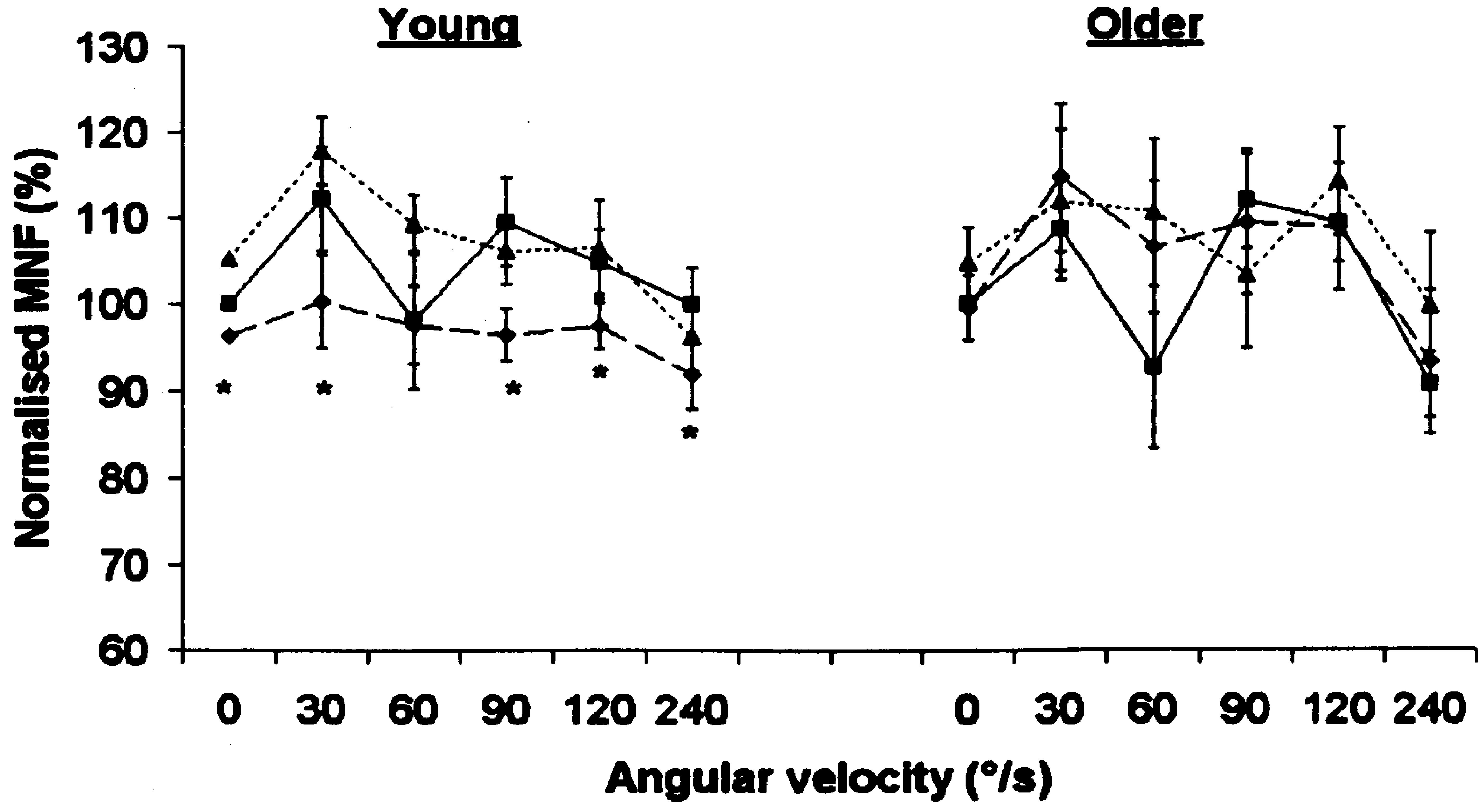

Figure 3.4B. Normalised MNF (%) of the EMG around the peak torque value (mean ± SE) for the young (left side, *n* =15) and older subjects (right side, *n* =12) for the cold --♦--, control —■— and warm ···▲··· conditions. MNF is given for angular velocities of 0 (MVC), 30, 60, 90, 120 and 240 °/s. *

denotes significant differences between cold and control. All values are normalised against the EMG MNF at MVC during the control temperature condition.

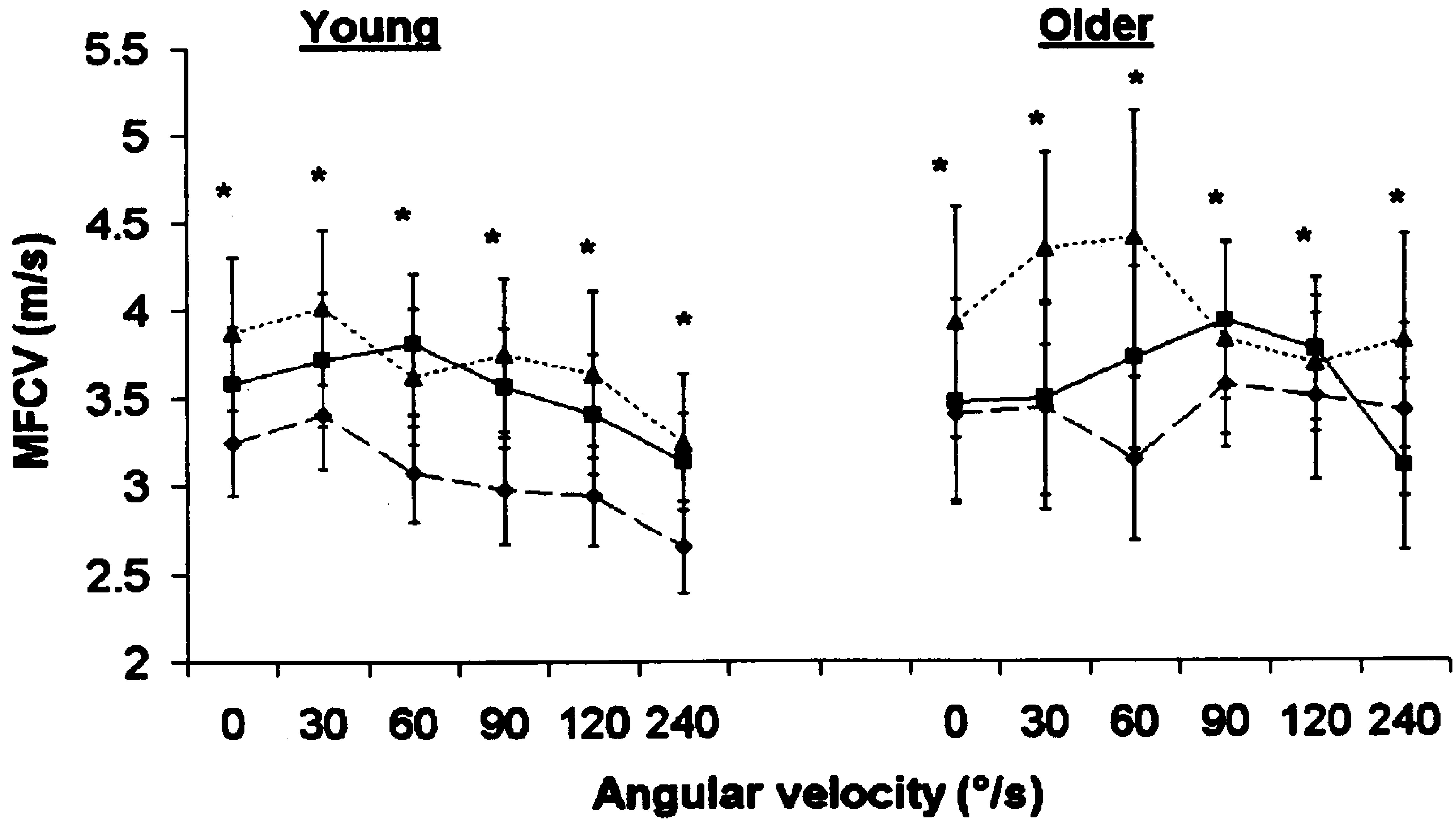

Figure 3.5A. MFCV (m/s) (mean ± SE) for the young (left side, n =15) and older subjects (right side, n =10) for the cold --◆--, control —■— and warm ···▲··· conditions. MFCV is given for angular velocities of 0 (MVC), 30, 60, 90, 120 and 240 °/s. * denotes significant difference between cold and warm trials.

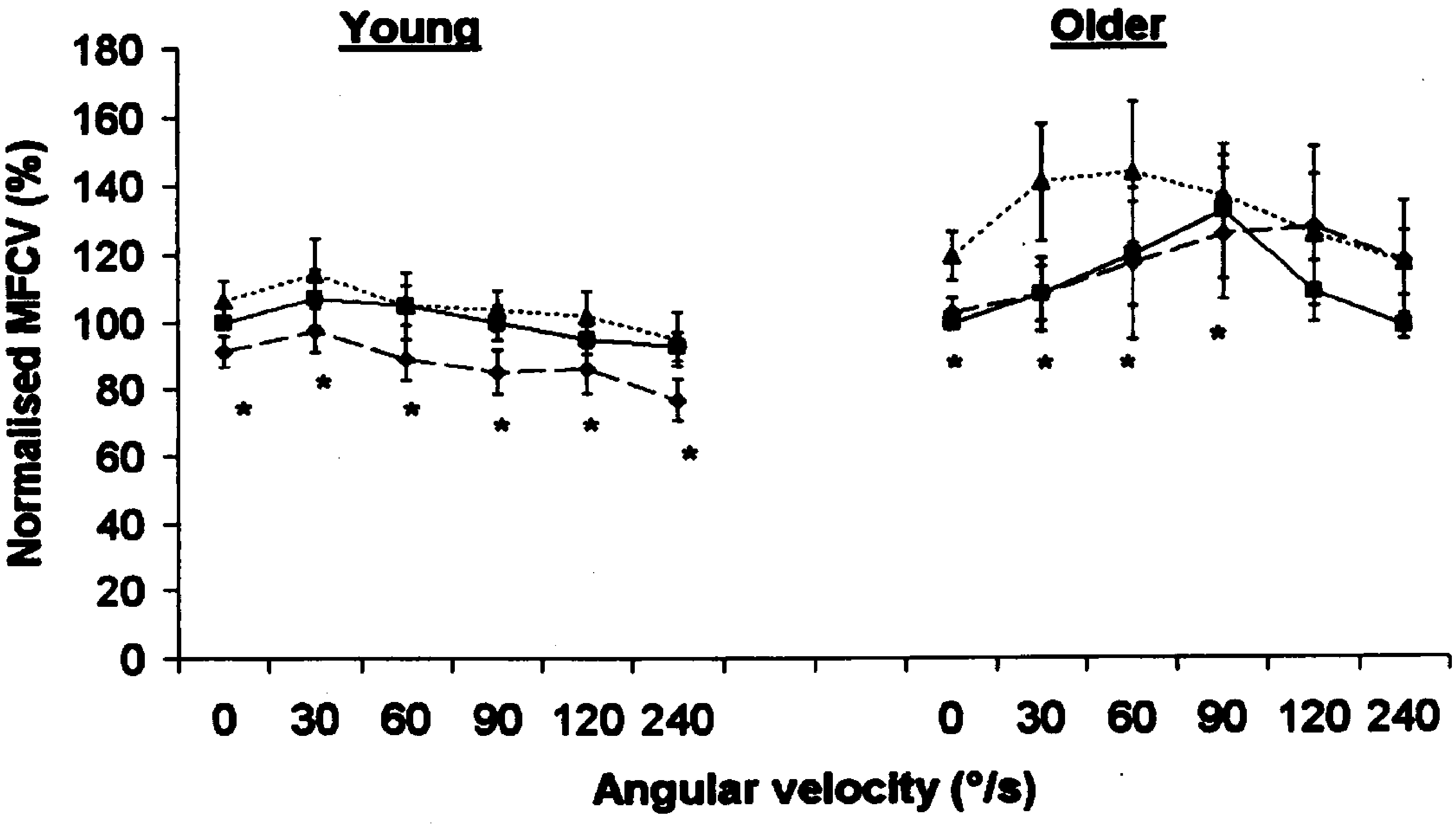

Figure 3.5B. Normalised MFCV (%) (mean ± SE) for the young (left side, n =15) and older subjects

(right side, *n* =10) for the cold --◆--, control —■— and warm ···▲··· conditions. MFCV is given for angular velocities of 0 (MVC), 30, 60, 90, 120 and 240 °/s. * denotes significant difference between cold and warm trials. All values are normalised against the MFCV at MVC during the control temperature condition

Coactivation

Coactivation was higher in older subjects than the young during the knee flexion (P<0.05) but not during knee extension. Neither cooling nor warming of the knee extensors affected the level of coactivation during either maximum knee extension or knee flexion (Figure 3.6).

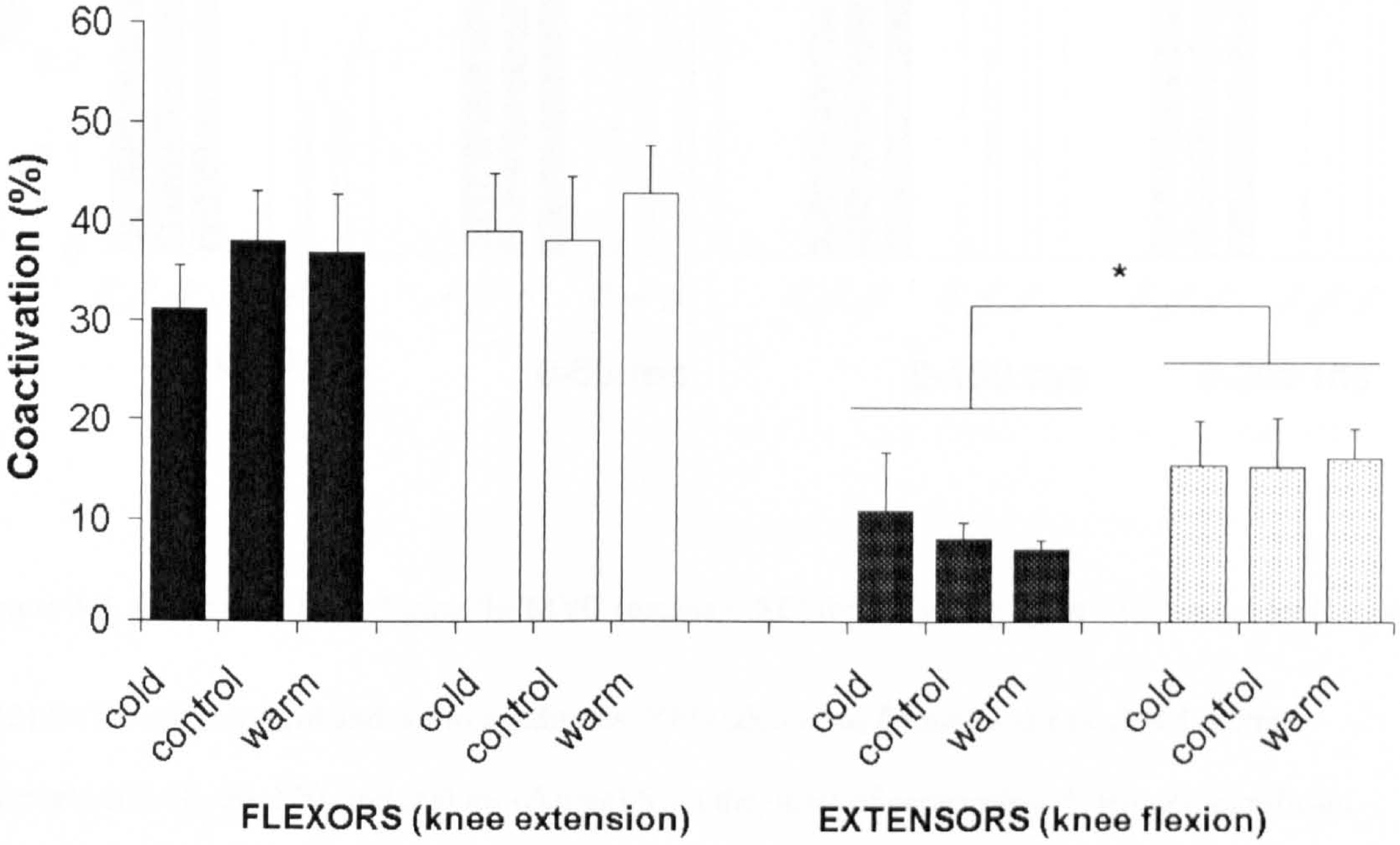

Figure 3.6. Coactivation of the antagonistic muscle for the young (*n* =15) and older (*n* =12) subjects during the knee extension and knee flexion. Coactivation of the biceps femoris during the knee extension is expressed as a percentage of the maximal biceps femoris RMS value while coactivation of the vastus lateralis muscle during knee flexion is expressed as a percentage of the maximal vastus lateralis RMS value. Young coactivation during knee extension ■; older coactivation during knee extension □; young contraction during knee flexion ▦; older coactivation during knee flexion ░.

RFD

RFD was greater in young compared to older subjects for each time interval calculated (ANOVA: $P< 0.01$). Neither cooling nor warming had an effect on the RFD in either group for any of the time intervals (Figure 3.7).

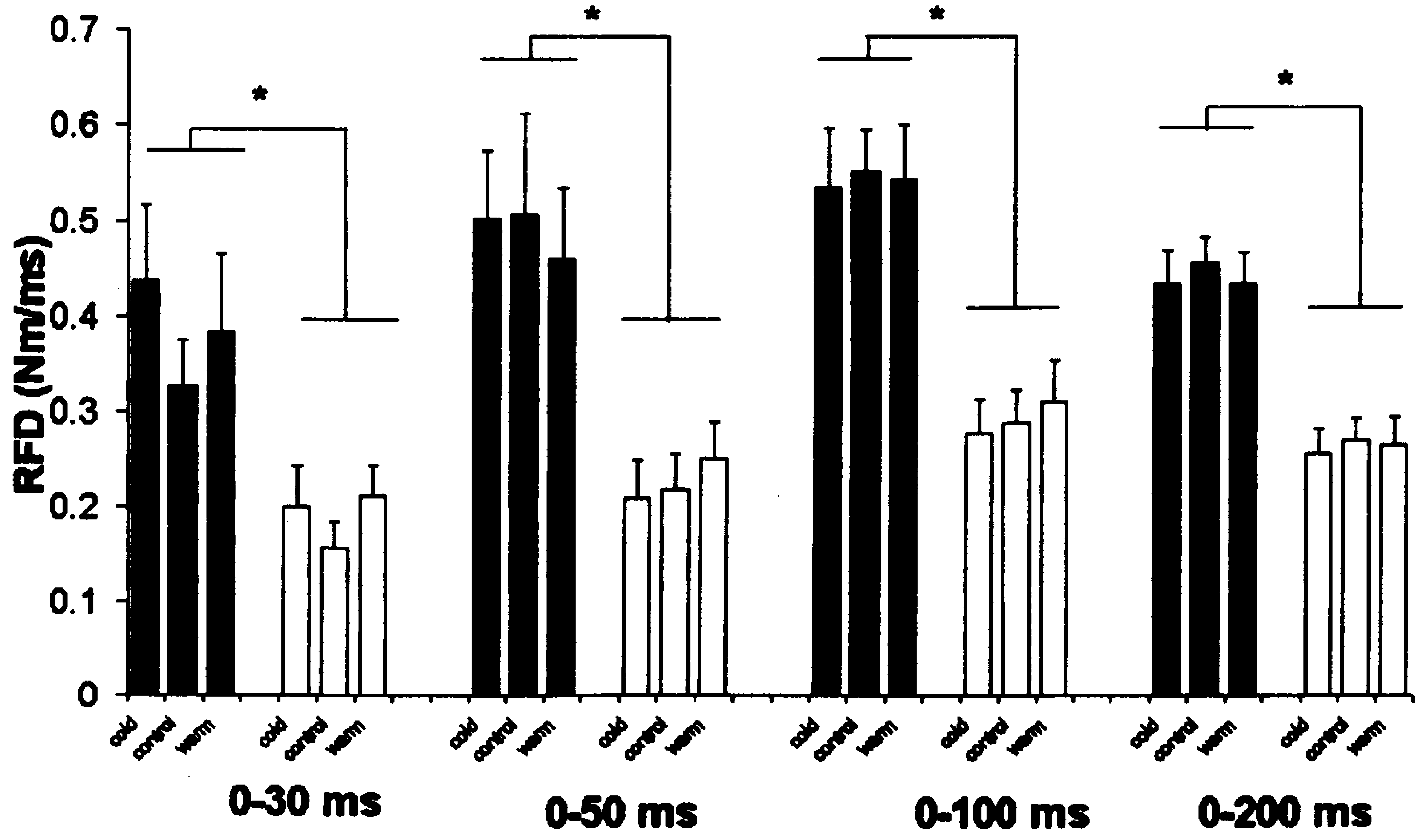

Figure 3.7. Contractile RFD during the MVC (means ± SE) for the young (■, n =15) and older (□, n =12) for the cold, control and warm conditions. RFD (Δ torque/Δtime) was calculated in time intervals of 0-30, 50, 100, and 200 ms (Δtime) from the onset of contraction. * denotes significant difference between young and older subjects.

DISCUSSION

The main finding of the present study was the difference in the response of the torque output between young and older women following cooling. Whilst warming of the knee extensors had no effect on the torque in either group, the effect of cooling was to lower the torque during isokinetic contractions in the young but not older subjects. This difference in response between groups was not seen in the MFCV as, in both groups, the MFCV was slower with cooling compared with warming.

Torque, EMG and age

The lower force level observed during both MVC and isokinetic contractions in the older females compared with the young females is consistent with previous findings (Bazzucchi et al. 2004, Macaluso and De Vito 2003, Skelton et al. 1994). The reduction in torque is explained by the well documented changes in motor unit structure and number seen with increasing age (for review see: Macaluso and De Vito 2004, Roos et al. 1997, Vandervoort 2002). In addition to reducing the force output, the age related changes in muscle were reflected in the RMS of the EMG. Like previously reported data in other studies, RMS was lower in the older subjects compared to the young, which is thought to be due to the reduction in the number of motor units in older individuals and to the reduced discharge rate of the firing motor units in older individuals (Esposito et al. 1996, Merletti et al. 2002).

Surprisingly, neither MNF nor MFCV were different between the young and older groups. This is in contrast to previous studies which have reported a lower MNF and MFCV with ageing (Bazzucchi et al. 2004, Esposito et al. 1996, Yamada et al. 2002).

Interestingly, Esposito et al. (1996) showed reduced MNF in older males but not older females when compared to their younger counterparts. A lower MNF and MFCV was expected as both reflect the conduction of the action potentials along the muscle fibres (Arendt- Nielsen and Mills 1985, Stulen and De Luca 1978) and older subjects are known to experience selective atrophy of the fast conducting type II fibres (Lexell et al. 1988, Merletti et al. 1992, Thompson 1994). Other studies have, however, also reported no difference in the MFCV between young and older individuals (Bazzucchi et al. 2004, Merletti et al. 2002). One of the pitfalls of the technique used in the present study to record MFCV is that the large motor unit action potentials (MUAP) can mask the MUAP of the smaller units. As described by Merletti et al. (2002), the MUAPs identified by the surface electrodes may have a similar MFCV and their numbers not sufficient to discriminate between the age groups. Additionally, young and older muscles have a different distribution of fast and slow fibres (Lexell et al. 1983), which compromises the comparison of the MFCV when recorded from the surface EMG between young and older subjects.

The subcutaneous fat layer between the skin and the muscle acts as a low pass filter for the EMG signal which greatly affects the amplitude of the surface EMG and to a lesser extent the spectral frequencies (Basmajian and De Luca 1985, Farina and Rainoldi 1999). Older subjects have been previously reported as having higher skinfold thickness than young subjects both above the vastus lateralis and the biceps femoris muscles (Macaluso et al. 2002). In the present study, however, the skinfold thickness of the EMG site was similar for both groups, discarding this as a potential reason for the differences in the RMS between the groups (vastus lateralis: 23.3 ± 1.0

and 22.4 ± 2.1 mm; biceps femoris: 24.0 ± 1.0 and 25.4 ± 2.1 mm for the young and older groups, respectively). Difference in the dryness of the skin between the groups, however, cannot be disregarded, as this was not measured in the present study.

Torque, EMG and temperature

The response of the young subjects to muscle cooling was a reduction in the torque during the isokinetic contractions, but not in the MVC. This significant difference does not exist, however, when the values are normalised to the control temperature MVC, however the trend remains similar. The temperature independence of the MVC has been reported previously (Bergh and Ekblom 1979, Binkhorst et al. 1977, Stewart et al. 2003, Thornley et al. 2003). A relationship exists between the muscle temperature and the rate of the enzymatic processes, including ATPase activity (Bárány 1967, Gray et al. 2006). This relationship, however, applies only to dynamic contractions, as during isometric contractions the rate of ATP hydrolysis is greater than necessary (Rall and Woledge 1990). While the MVC is used to measure the maximum strength of an individual (Hill 1938), the use of the isokinetic assessment is more applicable to functional tasks, which are dynamic in nature. It has been suggested that that the effect of temperature on muscle force and power output is most evident at high velocity contractions (Sargeant 1987), for example during sprint cycling (Ball et al. 1999, Davies and Young 1983, Gray et al. 2006, Sargeant 1987) or during vertical jumping (Davies and Young 1983, Ferretti et al. 1992, Stewart et al. 2003). In the present study, however, the relatively low velocity movements were enough to yield a reduction in torque with cooling in the young subjects, which supports previous reports which have described a temperature effect on torque at velocities within the range used in the present study (Bergh and Ekblom 1979, Cheung and Sleivert 2004, Comeau et al. 2003). As most movements in a day to day environment involve low velocity movements it was felt that the controlled, relatively low velocity contractions performed on a dynamometer were of greater relevance for understanding the effects of temperature on movements that will be replicated day to day by older individuals.

Under control conditions, the EMG time and frequency domain analysis is known to provide data on the degree of activation of the motor unit pool (Basmajian and De Luca 1985). With respect to the response to altered muscle temperature on the EMG, the membrane properties of the muscle fibre are altered, thereby changing the shape of the action potentials (Rutkove 2001). This change in the membrane properties may mask any effects that a change in activation of the muscle may have on the RMS and the MNF, however, cooling has been shown not to affect the discharge frequency of the motor units during an MVC (Bigland- Ritchie et al. 1992). As recruitment and discharge characteristics of individual motor units were not measured in the present study, it was assumed, therefore, that any changes in the RMS and the MNF were the result of the changes in the action potential characteristics as a result of temperature changes on the membrane. In the young subjects warming reduced the RMS amplitude. While we cannot explain why cooling affected the torque but not the RMS, the reduction in RMS with warming can be explained by the quickening of the opening and closing of the ion channels with warming, meaning less ions can enter the cell, inducing a smaller action potential amplitude (Rutkove 2001).

MFCV has been shown to have a positive linear relationship with temperature (Farina et al. 2005, Gray et al. 2006, Morimoto et al. 1980). While figure 3.4 shows, for both groups, a clear trend for the MFCV to decrease with cooling and increase with warming, the only significant difference lay between the cold and warm condition with neither being different from control condition. This change in MFCV reflects the changes in the muscle fibre membrane, with cooling slowing the opening and closing of the ion channels and, therefore, the conduction speed of the action potential along the muscle fibre. The opposite occurs with warming increasing the conduction speed (Rutkove 2001).

Difference in torque response between young and older groups with cooling

While both young and older subjects showed no torque changes following warming, only young subjects showed a decrease in torque following cooling. Both groups displayed the same response to temperature for the MFCV, suggesting that even with the deleterious changes in motor unit structure, the muscle fibre membrane in the older subjects shows the same modulation response as that of young subjects to altered temperature. This was not reflected, however, in the RMS whereby only young subjects showed a decrease with warming. One possible explanation for the difference in torque response to cooling in the two groups may be that while temperature alters the twitch characteristics in the young, this does not happen in the older subjects.

Cocontraction

Force output is the net value of the force produced by the agonists minus the opposing force produced by the antagonists. The effects of both ageing and temperature on the torque production, therefore, depend not only on what happens within the agonist but also on changes in the antagonist. In the present study ageing was seen to increase the level of coactivation during knee flexion, but not the knee extension. An increase in the antagonist activation in older subjects has been shown previously (Bazzucchi et al. 2004, Izquierdo et al. 1999b, Klein et al. 2001, Macaluso et al. 2002, Valkeinen et al. 2002) and is thought to be a strategy adopted by older individuals to increase joint stiffness and stabilise motor output (Hortobágyi and DeVita 2006).

By changing the muscle temperature of the knee extensors, it was hypothesised that this may affect the level of coactivation during both knee extension and knee flexion, this hypothesis was proved incorrect, however, as neither warming nor cooling affected the level of coactivation during both knee extension and knee flexion in either the young or the older subjects.

RFD

The RFD is an important measure to assess the ability of an individual to rapidly reach peak force, which is of great relevance especially in older individuals. For example, an older individual when recovering from loss of balance needs to produce fast and forceful muscle contractions to prevent falling. The present study used a variety of time intervals (0-50 to 0-200 ms) to assess the RFD and found that, regardless of the time interval, young subjects had a greater RFD than the older subjects, which is in agreement to previous studies (Clarkson et al. 1981, Hakkinen et al. 1995, Izuierdo et al. 1999, Thelen et al. 1996, Vandervoort and McComas 1986). The physiological factors that can affect the RFD include muscle fibre type (Harridge et al. 1996), muscle cross sectional area (Aagaard and Thorslensson 2003), maximal muscle strength (Schmidtbleicher 1992), visco-elastic properties of the muscle-tendon complex (Bojsen-Moller et al. 2005), and neural drive to the muscle (Aagaard et al. 2002a). As ageing affects all of these parameters it is not surprising that older individuals have a lower RFD.

With respect to altered temperature, it was hypothesised that cooling would reduce the RFD, while warming would increase the RFD due to a slowing of both the conduction of the neural drive to the muscle and the conduction of the action potential along the fibres with cooling, and vice versa with warming. This hypothesis was found not to be the case, however, with neither warming nor cooling affecting the RFD in either young or older subjects. The RFD has been shown to increase with warming and decrease with cooling in stimulated contractions (De Ruiter and De Hann 2000; Ranatunga and Wylie 1983, Ranatunga 1984), however, in support of the present results, Ranatunga et al. (1987) reported that the RFD during a voluntary contraction did not show a clear dependence on temperature. Ranatunga et al. (1987) speculated that this temperature independence during a voluntary contraction was due to a possible change in the motor unit recruitment order following temperature manipulation. In other words, instead of the recruitment order being slow to fast motor units as described by the size principle (Henneman et al. 1965), cooling, for example, may alter the recruitment sequence, changing it to fast to slow motor units. On the other hand, using animal experiments, Rome (1990) demonstrated that following cooling the recruitment of the fibre types was similar to that under the control temperature, going from slow to fast, however, a more condensed recruitment curve was reported, whereby more muscle fibres and faster fibre types were recruited earlier.

Clinical perspectives.

The results of the present study show that, unlike young individuals, the outcome of performing a maximal dynamic task is not temperature dependent in older individuals. From an applied perspective this is both advantageous and disadvantageous to the older individual. Had the older individuals responded similarly to the younger subjects in the present study to cooling, whereby peak torque is decreased during a dynamic contraction, then this would put an older individual, who may struggle to successfully perform day to day tasks involving muscle strength under normal environmental conditions, at risk of being unable to achieve the desired outcome of a task due to a further lowering of the torque output when in an cold environment. On the other hand, it was expected that young individuals would increase the force output with warming, which in the case of the present study did not happen, however it was originally hypothesized that should the older subjects respond in a similar manner as that expected of the young subjects and increased the torque output, then this could be used as a method to increase the functional ability of the older subjects.

Conclusions

In response to cooling of the knee extensors, young individuals displayed a reduced knee extension torque during isokinetic contractions, whereas older individuals demonstrated no change in torque. Warming had no effect on the torque in either the young or the older group. This result suggests that older individuals will not be further impaired when performing functional tasks requiring high intensity contractions in a cold condition than in a normal or warm conditions.

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CHAPTER 4

Temperature dependence of soleus H reflex and M wave in young and older women

Data presented in this chapter are presented in the following article:

Dewhurst S, Riches P E, Nimmo M A, De Vito G. Temperature dependence of soleus H-reflex and M wave in young and older women, Eur J Appl Physiol. 2005; 94: 491-499.

Data from this chapter was presented at the following conference

The Physiological Society; March 2004, Glasgow, UK. Effects of altered localised temperature on spinal reflex excitability in young and older women.

ABSTRACT

The purpose of this study was to investigate the effect of altered local temperature on Soleus H reflex and compound muscle action potential (M wave) in young and older women. H reflex and M wave responses were elicited in 10 young (22.3 ± 3.3 years) and 10 older (72.5 ± 3.2 years) women at 3 muscle temperatures: control (34.2 ± 0.3 °C), cold (31.3 ± 0.5 °C) and warm (37.1 ± 0.2 °C). H reflex output, expressed as the ratio between maximal H reflex and maximal M wave (H_{max}/M_{max}), was lower in the older compared to the young group, regardless of temperature. In control temperature conditions, for example, the H_{max}/M_{max} ratio was 36.8 ± 24% in the young and 25.4 ± 20% in the older ($P<0.05$). Warming had no effect on the H reflex output in either group, whilst cooling increased H reflex output only in the younger group (+28 %). In both groups, cooling increased (+5.3 %), and warming decreased (-5.5 %) the H reflex latency. This study confirms that older individuals experience a reduced ability to modulate the reflex output in response to a perturbation. In a cold environment, for example, the lack of facilitation in the reflex output, along with a delayed reflex response could be critical to an older individual in responding to postural perturbations thus potentially compromising both static and dynamic balance.

INTRODUCTION

The ability of the central nervous system to respond to perturbations through modulation of spinal reflex excitability is an important mechanism in controlling motor behaviour. In humans, the investigation on spinal circuitry and its reflex output has traditionally been conducted through the evaluation of the Hoffmann reflex (H reflex). A commonly adopted index of spinal reflex excitability is the H reflex output, which is the ratio between maximum H reflex (H_{max}) and the maximum compound muscle action potential (M_{max}) (H_{max}/M_{max} ratio) (Schieppati 1987).

It is well established that modulation of H reflex output can occur in certain physiological conditions. For example, a depression in H reflex output has been demonstrated when moving from a supine to a standing position (Capaday and Stein 1986, Earles et al. 2000, Koceja et al. 1993). However, investigations into this response in older individuals have revealed no such modulation (Chalmers and Knutzen 2002, Koceja et al. 1995, Mynark and Koceja 2002). Similarly, the facilitation of H reflex output in response to upper extremity muscle contraction (e.g. Jendrássik manoeuvre) demonstrated in young subjects is reported to be reduced with increasing age (Burke et al. 1996, Tsuruike et al. 2003). This phenomenon has been generally attributed to an impaired ability to regulate presynaptic inhibition levels of the Ia afferents (Earles et al. 2001, Stein 1995).

Other factors that have been found to affect H reflex output in young subjects include altered temperature, with most of the focus being on reduced temperature. Localised cooling has been shown to facilitate H reflex output as indicated by an increased

H_{max}/M_{max} ratio (Hopkins and Stencil 2002, Oksa et al. 2000). Although whole body warming has been found to increase H_{max} in cats (Bhattacharya et al. 1981), little is known about the effects of increased local temperature on H reflex output in humans.

The modulation of the spinal reflex output in response to altered temperature could be critical to an older individual who already has impaired motor control. For instance, given the importance of lower limb afferent feedback in postural control any temperature dependent alteration in the reflex output could affect postural stability (Mynark and Koceja 2002). This is particularly important for older women who tend to reach levels of neuromuscular function below the thresholds for tasks important for an independent life before men (Katz et al. 1983, Skelton et al. 1994).

The purpose of the present study was, therefore, to investigate the effects of decreased and increased local temperature on the soleus muscle H reflex and M wave response in young and older women.

METHODS

Subjects

Ten young (aged 22 ± 3 years; body mass 58 ± 7 kg; stature 1.63 ± 0.07 m; mean ± SD) and 10 older (aged 73 ± 3 years; body mass 68 ± 10 kg; stature 1.61 ± 0.07 m; mean ± SD) female adults gave written informed consent to participate in the study after being fully informed about the investigation and the possible related risks and discomforts. One young and one older subject failed to display an H reflex response and were excluded from the study. Young subjects were healthy with no known neuromuscular disorders. Older subjects were considered medically stable as proposed by Greig et al. (1994). All subjects were moderately active participating in non-competitive, physical activities no more than twice a week. Ethical approval for the experimental procedures was obtained from the University of Strathclyde Ethics Committee.

Experimental design

After an initial familiarisation session, subjects attended the laboratory on a single occasion during which all tests were performed. For young subjects testing was performed in the follicular phase of the menstrual cycle to control for potential hormonal influences. Minimal physical activity was performed and no caffeine or alcohol was permitted 24 hours prior to the testing session. Following subject preparation subjects performed the control trial first, which was followed by both a warm and cold trial administered in a random order.

Temperature measurements

Muscle and the skin temperatures were measured in the dominant leg. Muscle temperature was measured in the vastus lateralis muscle using a flexible temperature probe (Ellab Ltd, Copenhagen, Denmark) inserted 1cm below the subcutaneous fat layer (skinfold thickness x 0.5; since the skinfold corresponds to about twice the actual fold thickness) at an angle of 45 ° in the direction of the muscle fibers. The thermistor was inserted through a flexible cannula (Venflon 18 GA, Becton Dickinson, Sweden) and advanced ~0.5 cm beyond the end of the cannula into the muscle. Previous unpublished data collected in this laboratory, on both young and older women, have shown a positive correlation between intramuscular temperature of the vastus lateralis and the soleus using the warming and cooling methods employed in the present study. Figure 4.1 shows, for one subject, the typical intra-muscle temperature responses concerning this test.

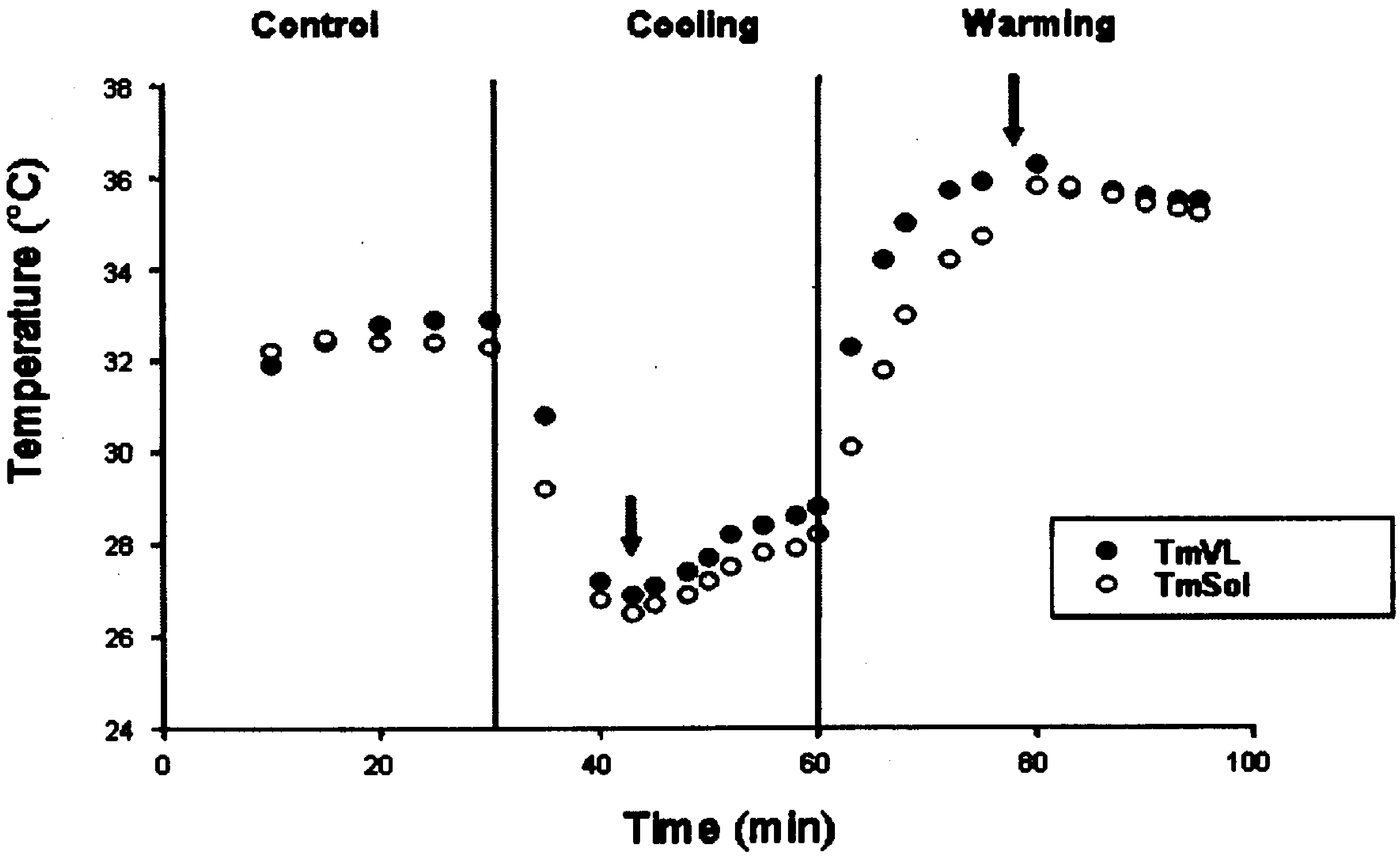


Figure 4.1. Typical intra-muscle temperatures (T_m) recorded simultaneously from the vastus lateralis (VL) and the soleus (Sol) muscles in one representative subject. The two arrows indicate the moment when the cooling and heating blankets were removed from the legs.

Skin temperature was measured using skin thermistors (Grants Instruments Ltd, Cambridge, UK) from 3 sites: the vastus lateralis (1cm proximal to the insertion point of the muscle probe), popliteal fossa (beside the stimulation point on posterior tibial nerve) and the soleus (muscle belly) and were secured with tape and covered with cotton wool and further secured with tape. Muscle and skin temperatures were recorded with a Medical Precision Thermometer (DM 852, Ellab Ltd, Copenhagen, Denmark) and 1000 series 8-bit squirrel data logger (Type 1002, Grants Instruments Ltd., Cambridge, UK), respectively. Core temperature was estimated using an infrared tympanic thermistor (Braun, type 6013, Germany).

The subjects rested in the supine position for 30 min at room temperature (≅ 26 °C) to achieve steady state temperatures. Temperatures recorded immediately after the 30 min rest were considered the control temperatures. Following the H reflex assessment under the control temperature condition, leg temperature was increased using electrically heated blankets or decreased using a specifically made ice blanket consisting of large thick plastic sacks filled with crushed ice. In both temperature conditions blankets covered the whole of both legs from the gluteal furrow to the foot. Warming and cooling proceeded until muscle temperature was increased or decreased by approximately 3 °C with respect to the control muscle temperature. The duration of the cooling and warming periods was not constant but differed among individuals. On average the cooling phase duration ranged between 15 and 20 minutes and the warming between 35 and 45 minutes. Blankets were removed prior to testing to prevent the potential influence that the weight of the blankets could have on the level of presynaptic inhibition via cutaneous afferent input (Wood et al. 1998).

Surface electromyographic (EMG) recordings

Surface EMG activities of the soleus and the tibialis anterior (TA) muscles were recorded. The skin was prepared by rubbing the designated area with fine sand paper before cleansing with an alcohol wipe. Two silver/silver chloride electrodes (Medicotest, Blue sensor, type N-10-A, Cambridge, UK), pre- gelled and self adhesive, were placed below the gastrocnemius bifurcation on the soleus muscle, and on the upper third of the muscle belly for the TA muscle, on the dominant leg. Inter-electrode distance was 20 mm. A ground electrode was placed midpoint between the knee and recording electrodes. EMG signals were pre amplified (x1000) (NeuroLog remote AC preamplifier NL824, Digitimer Ltd, Hertfordshire, UK) and band-pass filtered (NeuroLog filter NL125, Digitimer Ltd, Hertfordshire, UK) and A-D converted (type 1401; Cambridge Electronic Design, Cambridge, UK) at a sampling rate of 2000 Hz and stored using commercially available software (Spike2, version 2.02, Cambridge Electronic Design, Cambridge, UK) for offline analysis.

H reflex assessment

Subjects were seated on an isokinetic dynamometer (Kin-Com, 500H, Chattecx, Chattanooga, TN, USA), adjusted so that the dominant leg was flexed 105 ° at the hip and 120 ° at the knee. The right foot was strapped to a footplate so that the angle formed between the footplate and the lower leg was 90 °. Foot, ankle, thigh and trunk were all secured with straps. Particular care was taken in maintaining subjects' body position and avoiding head movements in order to minimize the potential confounding effects of altered presynaptic or postsynaptic inhibition arising from postural changes (Schieppati 1987). Additionally, subjects were asked to remain relaxed throughout the duration of the test.

H reflexes and M waves were evoked in the soleus muscle by electrical stimulation of the posterior tibial nerve via a cathode ball electrode (0.5 cm in diameter) pressed into the popliteal fossa. The cathode was a specifically made ball ended probe which maintains consistent pressure and direction of the stimulus. A free rotational ball within a wooden block contained the probe. The block was strapped in place around the knee and when the correct position was found the probe was locked in place. The anode was a 4.5 x 4.5 cm square electrode placed proximal to the patella. The stimuli were 1 ms rectangular pulses delivered from a constant current stimulator (DS7A, Digitimer Ltd, Hertfordshire, UK). Stimulus intensity was increased by 0.5 mA increments until the H_{max} and M_{max} amplitudes were determined. At each intensity, five stimuli were delivered with a five second interval between stimuli. From this data the maximum amplitude (peak to peak height of the waves) of the H reflex and the M wave were identified and the H_{max}/M_{max} ratio calculated. H reflex and motor response (M wave) recruitment curves for each subject and for each temperature condition were obtained.

Onset latency of the H_{max} and M_{max} were measured as the time interval between the stimulus artefact and the first deflection of the H or the M wave respectively. Background EMG of the soleus was monitored from a 1 second recording prior to the stimulation. Additionally, corresponding EMG activity of the TA muscle was recorded, and represented as the area of the rectified waveform corresponding to the latency of the soleus H_{max}.

Statistical Analysis

Data are presented as mean ± SE, unless otherwise indicated. To assess the effect of age and temperature condition data were analysed using a two-factor (age x condition) repeated measures analysis of variance (ANOVA). Where a significant effect was observed differences were located with *post hoc* multiple paired Student's *t*-tests adopting a Bonferroni correction to the selected alpha level ($P<0.05$; 0.05/2). All statistical tests were performed with the commercially available software (SPSS version 12, SPSS Inc Chicago, IL)

RESULTS

Temperature

Both warming and cooling significantly decreased and increased muscle temperature and skin temperature respectively (*t*-tests: P<0.001), without any differences between the two groups (Table 4.1). Despite the changes in muscle and skin temperature, tympanic temperature was unchanged with either warming or cooling for both groups.

		Cold	Control	Warm
T_m (°C)	Y	31.7 ± 0.5*	34.7 ± 0.2	37.3 ± 0.2*
	O	30.9 ± 0.4*	33.7 ± 0.4	36.8 ± 0.2*
T_{sk} V.L(°C)	Y	26.5 ± 1.0*	32.6 ± 0.4	38.0 ± 2.1*
	O	25.2 ± 1.1*	31.5 ± 0.5	33.5 ± 2.9*
T_{sk} P.F.(°C)	Y	23.8 ± 1.4*	32.1 ± 0.3	38.1 ± 0.8*
	O	23.8 ± 0.9*	31.9 ± 0.6	36.6 ± 1.0*
T_{sk} Sol.(°C)	Y	20.0 ± 1.4*	31.9 ± 0.4	36.9 ± 2.0*
	O	19.7 ± 2.6*	31.6 ± 0.5	36.2 ± 1.4*
T_t (°C)	Y	36.8 ± 0.1	36.9 ± 0.7	36.8 ± 1.5
	O	36.3 ± 0.1	36.6 ± 0.1	36.7 ± 0.1

Data are means ± SE; *n* =9 in both groups; * denotes difference from control condition (P<0.025). T_m= muscle temperature, T_{sk}= skin temperature, V.L.= vastus lateralis, P.F.= popliteal fossa, Sol.= soleus, T_t= tympanic temperature

Table 4.1. Temperature values for the young (Y) and older (O) groups, during cold, control and warm temperature conditions.

Background EMG

EMG activity from soleus prior to the onset of the stimulation was the same for both the young and the older groups and did not differ between the temperature conditions. As subjects were at rest, this minimal activity is assumed to be noise not muscular activity. Similarly, the area of the EMG waveform of the TA for the corresponding duration of the H_{max} was the same for both groups and was unchanged between the temperature conditions.

H_{max} and M_{max}

Figure 4.2 shows the EMG traces recorded from the soleus muscle during the H_{max} elicitation in two representative subjects one young and one older.

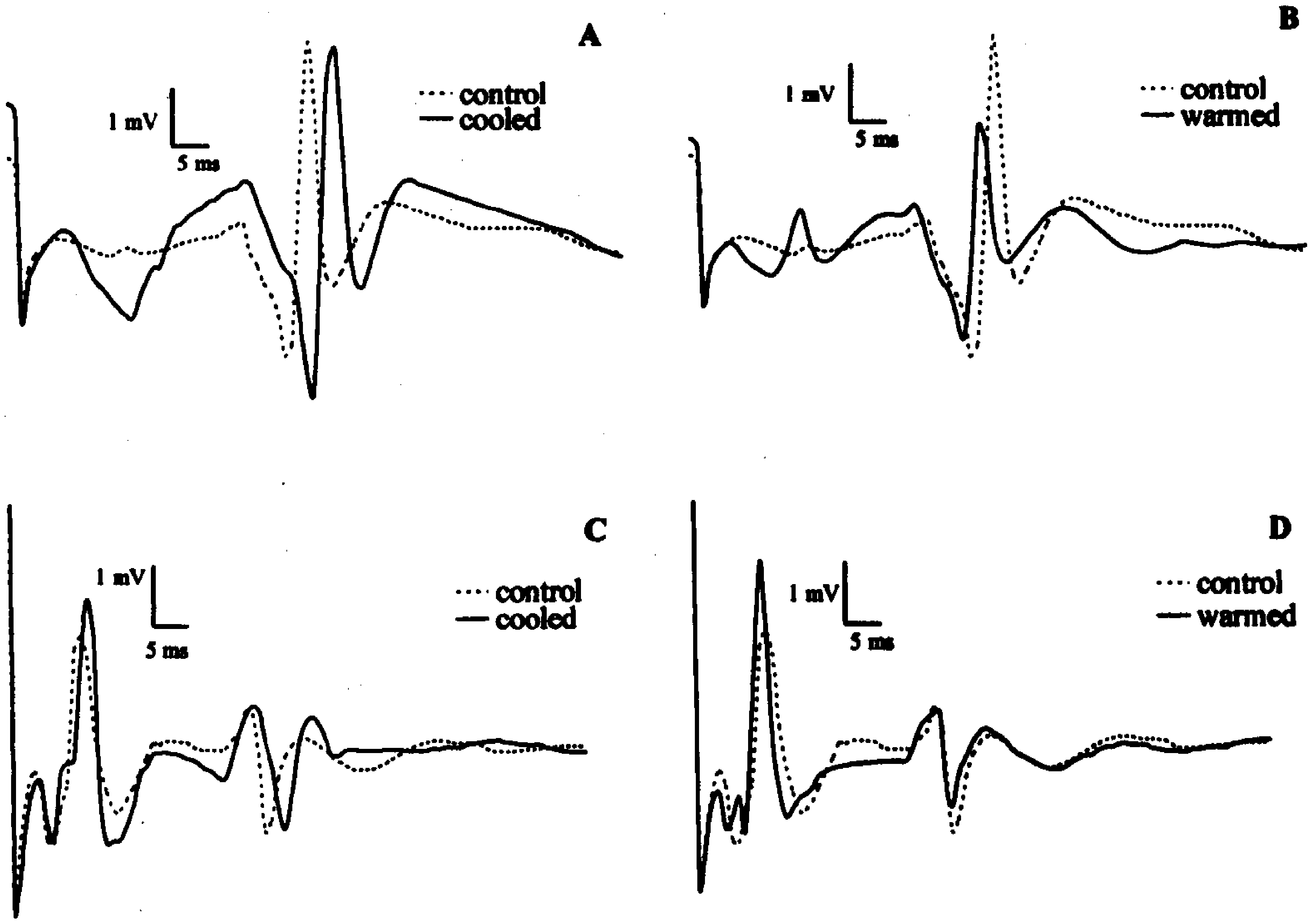


Figure 4.2. EMG recorded from the soleus muscle during the H_{max} elicitation. Data are from one young and one older subject, whose data best represent the group data. Young subject: (A) control condition vs. cold condition; (B) control condition vs. warm condition. Older subject: (C) control condition vs. cold condition; (D) control condition vs. warm condition.

The amplitude of the H_{max} was higher in young than older individuals (ANOVA: P<0.01; Figure 4.3A) regardless of temperature condition, with older displaying a 50 % lower mean H_{max} than young in the control condition. The M_{max} amplitude was not statistically different for the young and older group, regardless of temperature, despite the amplitude being about 20-30 % lower in the older subjects compared to the young group across the 3 temperature conditions (Figure 4.3B).

In the young group H_{max} decreased with warming (19 %, *t*-tests: P<0.01; Figure 4.3A) and increased with cooling (28 %; *t*-tests: P<0.01) when compared to control condition, whereas in the older subjects H_{max} was the same for all temperature conditions (Figure 4.3A) despite an apparent decrease in H_{max} with warming, compared to both control and cooling, which was found to be non significant. Temperature had a similar effect on M_{max} in both groups (Figure 4.3B). When compared to the control condition, warming decreased M_{max} by 12 % (*t*-tests: P<0.01), while cooling increased M_{max} by 15 % (*t*-tests: P<0.01).

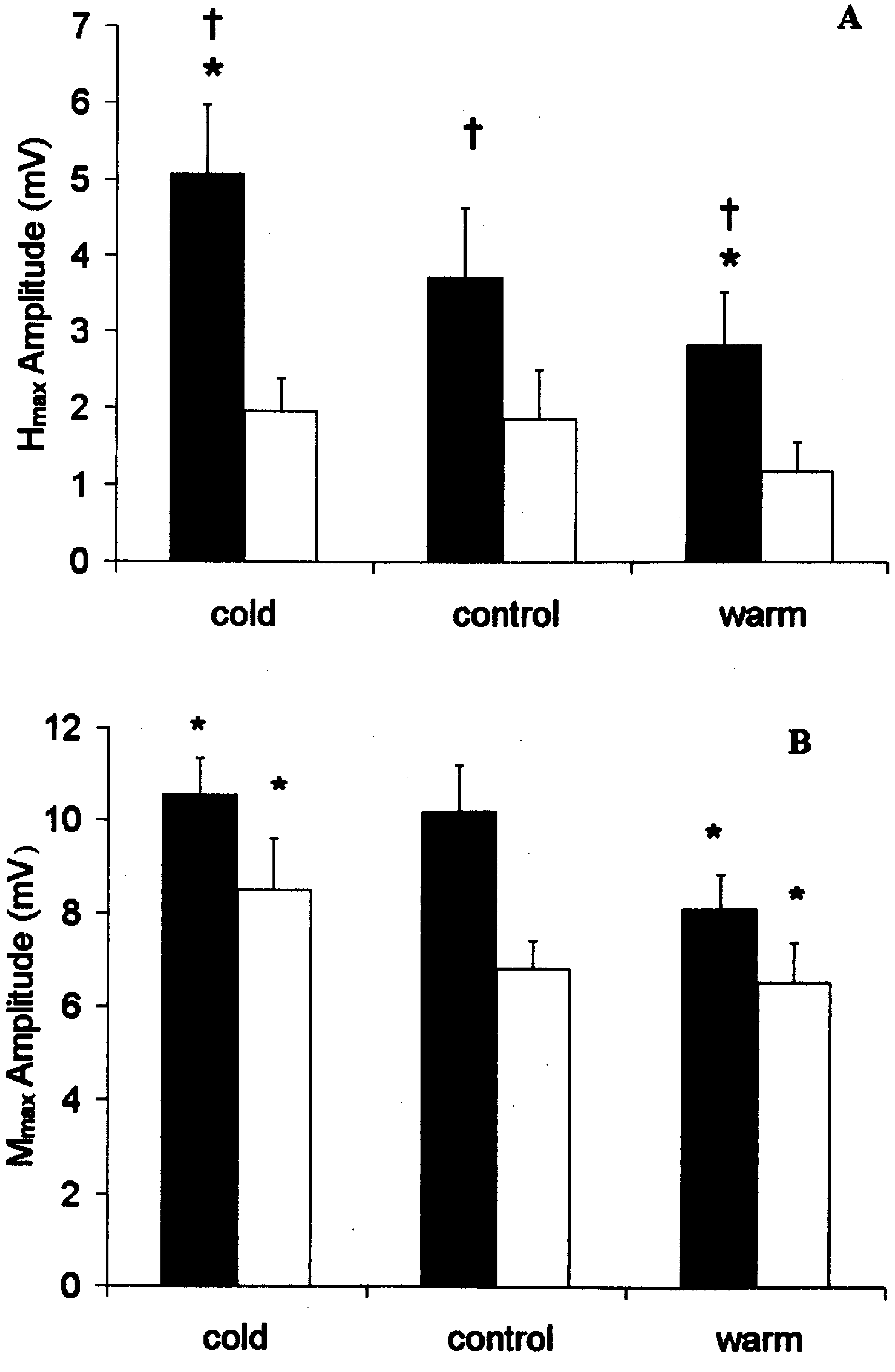


Figure 4.3. Maximum H (A) and M (B) wave amplitudes measured in the young (■, n=9) and older (□, n=9) groups in cold, control, and warm temperature conditions. † denotes significant difference (main effect) between young and older. * denotes significant difference from the control condition. Data are presented as means ± SE.

H_{max}/M_{max} ratio

An example of the difference in the H reflex/ M wave recruitment curves between the groups and with temperature are given below (Figure 4.4). Note the difference in the amplitude of the M wave at H_{max} being lower in the young subjects compared the older subjects. This is also reflected in the EMG trace in figure 4.2 above.

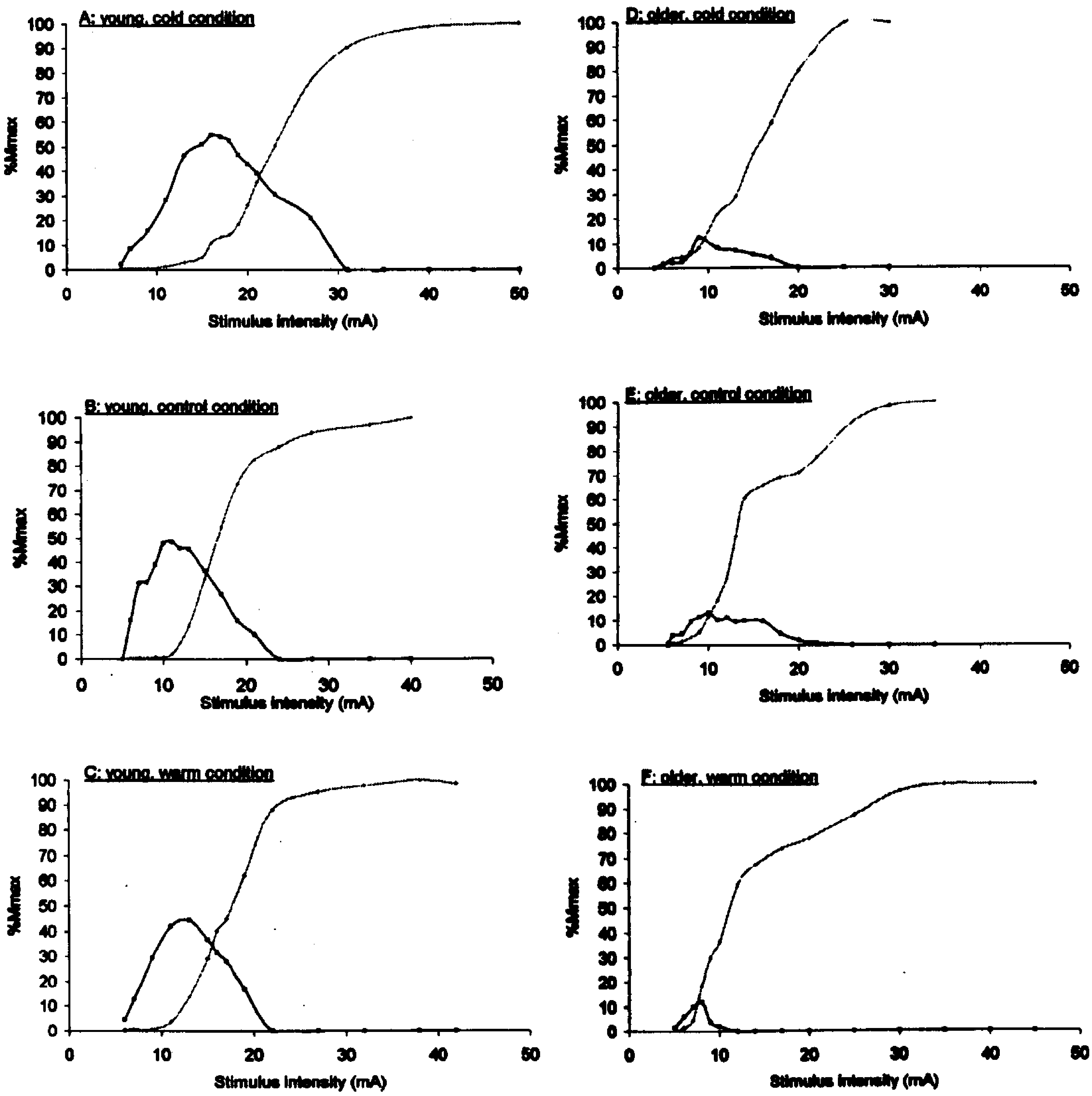


Figure 4.4A, B, C, D, E, F. A representative H reflex / M wave recruitment curve from one young and one older subjects, the curves are presented as a percentage of M_{max}. H reflex is presented by the black line and M wave represented by the grey line. A: young subject, cold condition; B: young subject, control condition; C: young subjects, warm condition; D: older subject, cold condition; E: older subject, control condition; F: older subject, warm condition.

The lower amplitude of the H_{max} in the older group compared to the young group and the maintained amplitude of the M_{max} was reflected in a lower H_{max}/M_{max} ratio in the older compared to the young group (ANOVA: P<0.01; Figure 4.5).

The H_{max}/M_{max} ratio did not vary with warming in either age group. With cooling, however, H_{max}/M_{max} ratio was increased in the young subjects (28 %, *t*-tests : P<0.01; Figure 4.5), but not in the older subjects. These differences are highlighted in figure 4.6 where the spread of the individual changes of the H_{max}/M_{max} ratio with cooling and warming are displayed.

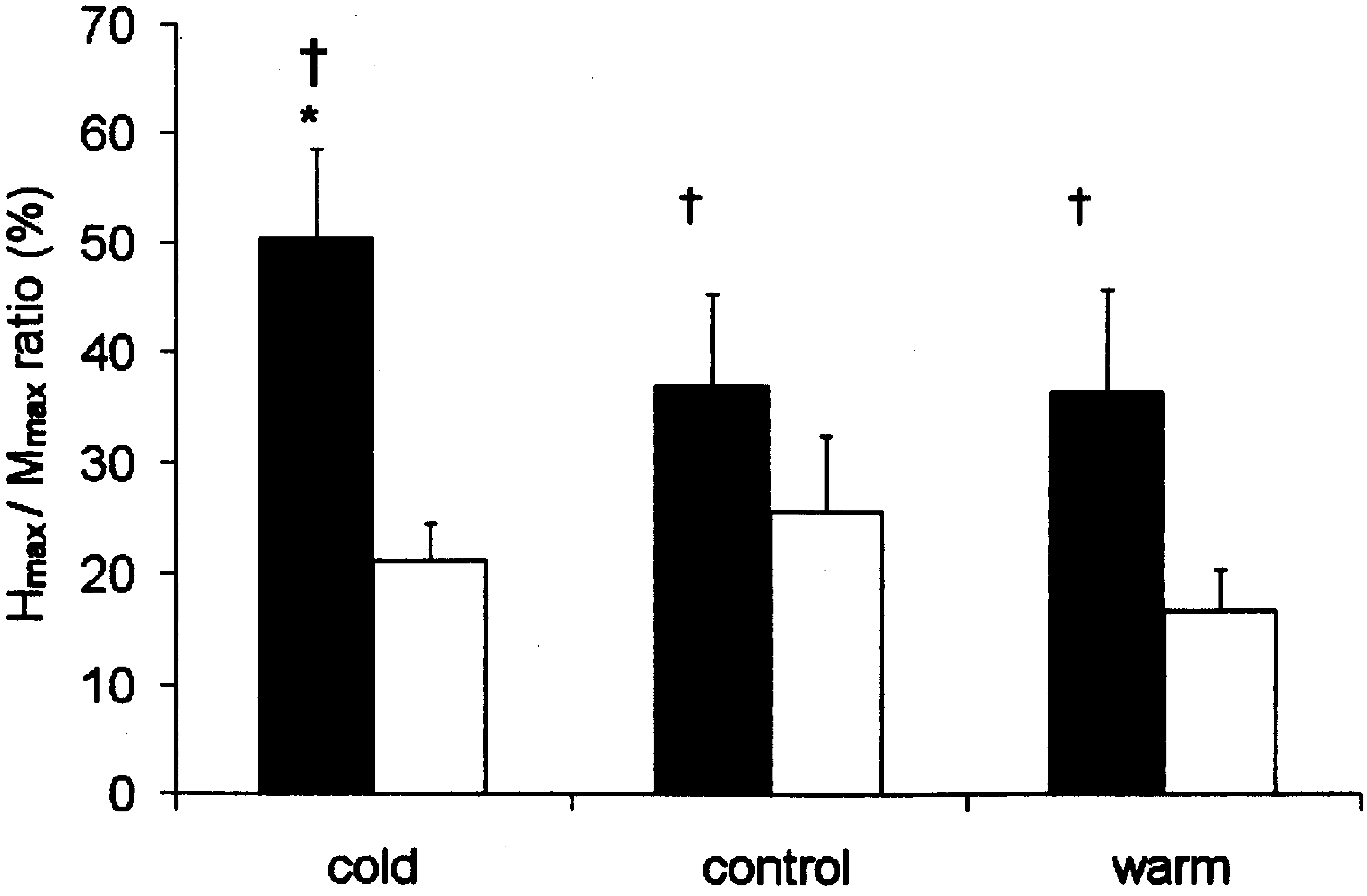


Figure 4.5. H_{max}/M_{max} ratio for the young (■, *n*=9) and older (□, *n*=9) groups in cold, control, and warm conditions. † denotes significant difference (main effect) between young and older. * denotes significant difference from the control condition. Data are presented as means ± SE.

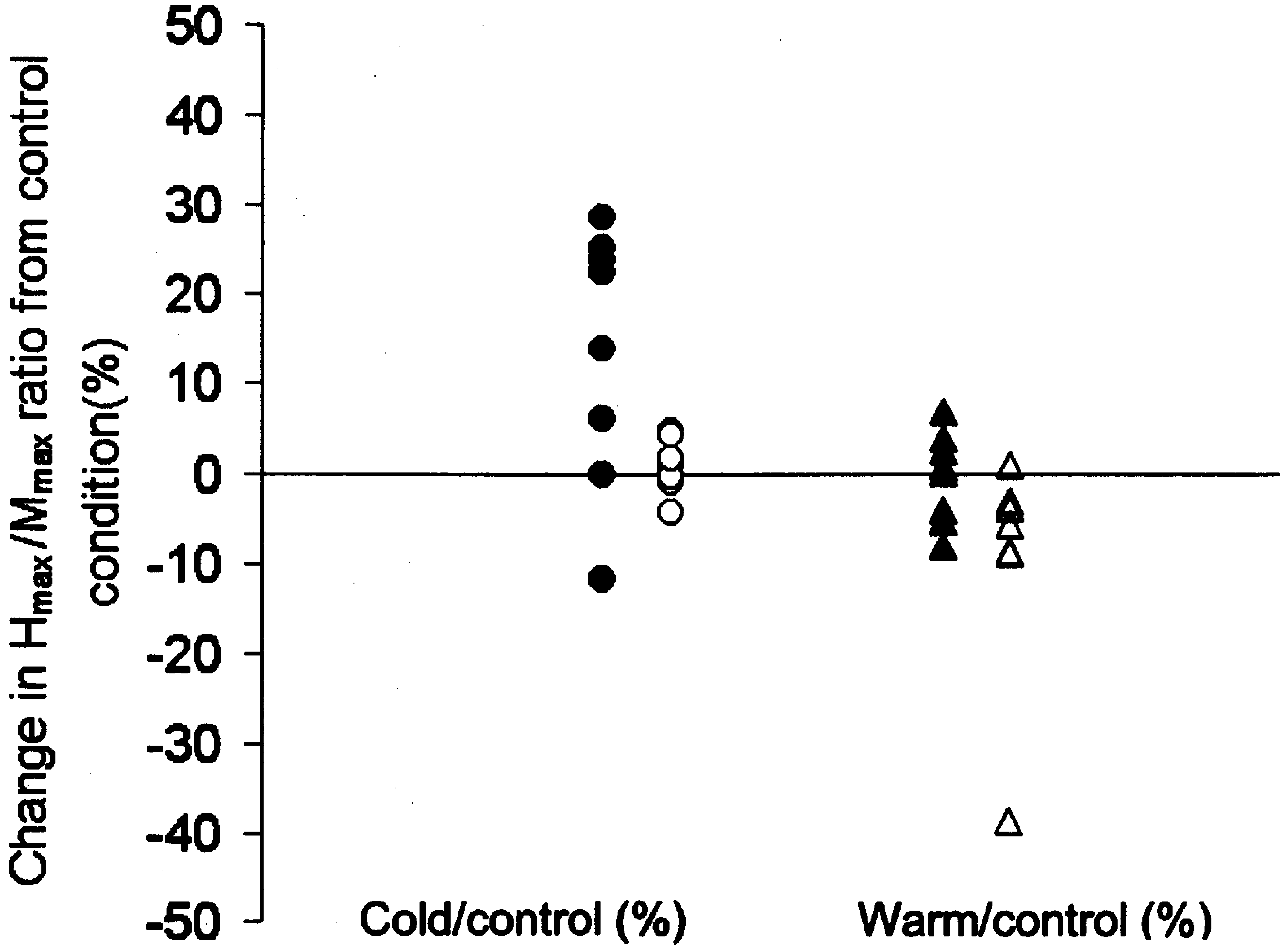


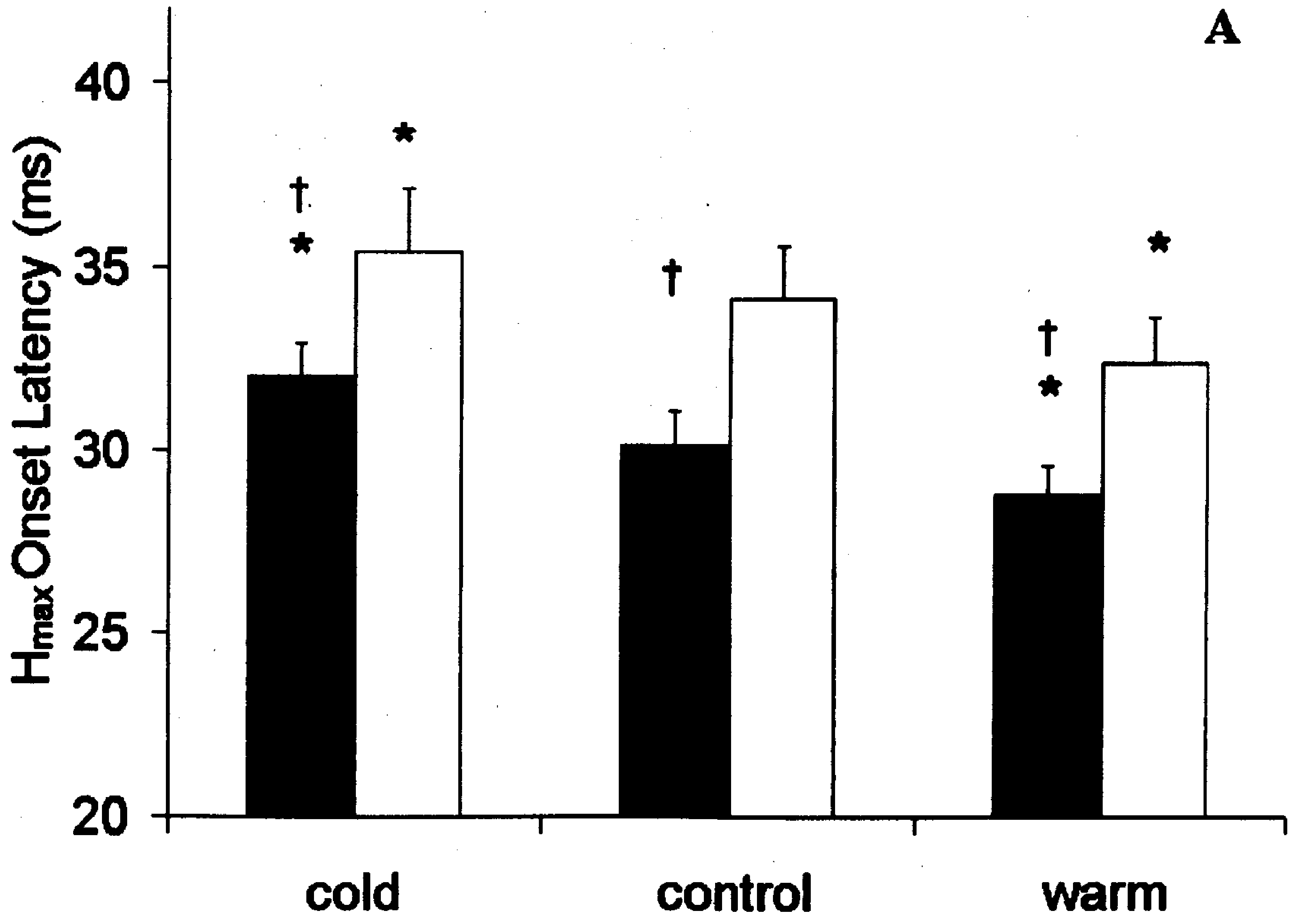
Figure 4.6. Individual absolute changes (compared to control condition) in H_{max}/M_{max} ratio with cooling and warming. Cold/control condition young (●), cold/control condition older (○), warm/control condition young (▲), warm/control condition older (△).

Latency of H_{max} and M_{max} response.

In control conditions, the older subjects had a longer H_{max} onset latency than the young group (ANOVA: $P<0.01$, Figure 4.7A). In contrast M_{max} onset latency was the same for both groups (Figure 4.7B).

Temperature had a similar effect on H_{max} onset latency in both the young and older group (Figure 4.7A). Compared to control conditions, cooling increased (*t*-tests: $P<0.01$) the H_{max} onset latency by 1.61 ± 0.6 ms, while warming decreased (*t*-tests:

P<0.01) onset latency by 1.51 ± 0.5 ms, respectively. M_{max} onset latency in young subjects was increased with cooling (*t*-tests: P<0.01), while warming had no effect in this group. By contrast, when compared to the control condition, the M_{max} onset latency of the older group was decreased with warming (*t*-tests: P<0.01), with cooling having no effect.



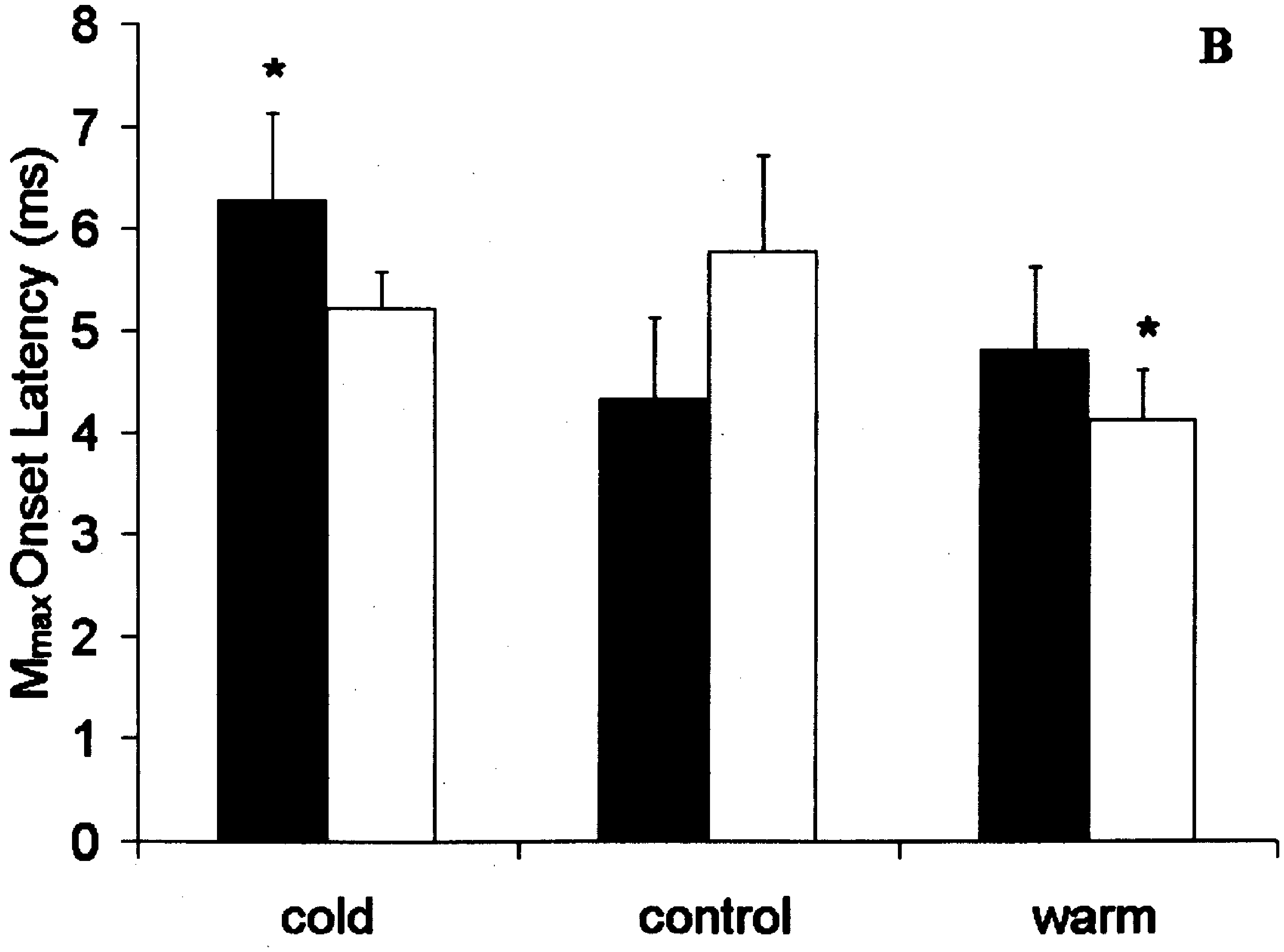


Figure 4.7. Maximum H (A) and M (B) wave onset latencies for young (■, n =9) and older (□, n =9) subjects in cold, control, and warm temperature conditions. † denotes significant difference (main effect) between young and older groups. * denotes significant difference from the control condition. Data are presented as means ± SE.

DISCUSSION

The main finding of the present study was the difference in the modulation response of H reflex output between the young and older females with cooling. Whilst localised warming had no effect on spinal reflex excitability in either group, the effect of cooling was to facilitate H reflex output in the young but not the older group. Furthermore, in both groups, warming shortened and cooling delayed the onset latency.

H reflex, M wave and age

The reduced H reflex output observed in the older women suggests a reduced efficiency of the Ia afferent and α- motoneuron synapse. This is consistent with previous findings (Kido et al. 2004, Koceja et al. 1995, Mynark and Koceja 2002, Scaglioni et al. 2002) but in contradiction with others (Kawashima et al. 2004) who did not report any difference in the H reflex output between young and older individuals. In the present study, the lower H_{max}/M_{max} ratio observed in older subjects is mainly a consequence of the lower H_{max} exhibited by older in comparison to young subjects. The lower H_{max} in the older group may be explained by the structural changes seen in both the sensory and motor nerves with aging. Several age-related changes in the Ia afferent fibers and the α- motoneurons have been reported, with degeneration of the myelin sheath being the most noteworthy (Adinolfi et al. 1991, Lascelles and Thomas 1966). Demyelination not only reduces the diameter of the axon, but increases the area of the axon membrane in contact with the extracellular matrix, reducing the integrity of the axonal transmission. While these changes occur at a slower rate in the α- motoneuron axons than in the Ia afferent (Lee and Oh

1994), a decrease in M_{max} would nevertheless be expected as a result not only of the demyelination of the motoneurons, but also of the well documented changes in the motor unit structure and number shown with increasing age (Macaluso and De Vito 2004, Vandervoort 2002). In addition to the structural changes that contribute to the lower H reflex output in older individuals, a higher level of tonic presynaptic inhibition has been previously demonstrated in this population, reducing the transmission of the signal across the synapse (Koceja and Mynark 2000, Morita et al. 1995).

An increased neural homogeneity between the sensory and motor nerves has been speculated by Scaglioni et al. (2003). It is suggested that a decrease in the diameter of the sensory fibres shown by Ochoa and Mair (1969) and Rao and Krinke (1983) consequently increases the similarity between the excitability threshold of the afferent and efferent axons. This homogeneity can be seen in Figure 4.4 with the amplitude of the M wave at H_{max} and the amplitude of the H_{max} being similar in the older subjects.

H reflex modulation with cooling

The mechanism responsible for the facilitation of H reflex output with cooling exhibited in the young subjects is not fully understood. First described by Hodgkin and Katz (1949), a change in temperature alters the opening and closing time of the Na^+ voltage-gated channels along the nerve axon. This finding can be extrapolated to the muscle fibre membrane whereby cooling slows down the depolarization time, consequently allowing more Na^+ to enter the cell hence increasing the depolarization amplitude, while warming has the opposite effect (Rutkove 2001). In young subjects, it is speculated that this phenomenon could explain the increased M_{max} with cooling and decreased M_{max} with warming. Similarly, this could be responsible for the trend of an increased H_{max} with cooling and a decreased H_{max} with warming. However, the H_{max}/M_{max} ratio normalizes the effect on the H_{max} to that on the M_{max}, suggesting that H_{max} was increased not only as a consequence of increased depolarization duration but also to a change in H reflex output.

One possible mechanism for the facilitated H reflex output with cooling is the increase in afferent discharge of the sensory endings of muscle spindles (Lippold et al. 1960, Michalski and Séguin 1975). Studies on relaxed muscle of the cat have demonstrated that while there was no response to cooling in the Ia primary endings, discharge frequency of the secondary afferents was increased producing autogenic as well as synergistic facilitation of motoneuronal excitability (Chapman et al. 1979, Michalski and Séguin 1975). Similarly, little or no Golgi tendon organ activity was demonstrated in the cooled muscle (Michalski and Séguin 1975). This could indicate that the facilitation of the motoneuronal excitability observed with cooling by Chapman et al. (1979) was to be ascribed mainly to the muscle spindle secondary endings.

An additional mechanism, to explain the increased excitability level with cooling, is represented by the potential role of the cutaneous thermoreceptors on the facilitation of the reflex. Should the thermoreceptors play a part in the modulation of spinal reflex excitability, this may partially explain the difference in modulation response between warming and cooling observed in the present study. While muscle temperature was increased and decreased to the same degree with warming and cooling (≅ 3 °C), skin temperature was decreased to a greater extent than was increased (Table 4.1). In the present study, mean skin temperature of the soleus dropped below 20 °C in the young subjects with cooling which would potentially trigger a nociceptor response. Nociceptors respond to noxious low temperatures (<20 °C) (Campero et al. 1996) and data from both animal and human experiments reveal a convergence of nociceptive inputs onto spinal reflex pathways via common spinal interneurons (Ellrich and Treede 1998, Steffens and Schomburg 1993).

Consistent background EMG levels of the soleus, recorded prior to stimulation, indicate that a shivering response was not evoked with cooling. A shivering response, increasing motoneuronal pool activation levels of the soleus, would have the potential to increase excitability levels through presynaptic facilitation (Burke et al. 1989, Earles et al. 2001, Schieppati 1987). Similarly, the consistent level of EMG activity of the antagonistic TA in all of the trials, discards the possible contributions of altered levels of reciprocal inhibition from the TA.

Difference in modulation response between young and older groups

While both the young and older group showed no H reflex modulation response to warming, only the younger subjects showed modulation with cooling. This difference in response between young and older individuals is consistent with previous studies investigating the response of older individuals to varying perturbations including changing body position (Koceja et al. 1995), responding to unstable environments (Earles et al. 2000) as well as the response to the Jendrássik maneuver (Burke et al. 1996, Tsuruike et al. 2003), muscle vibration (Burke et la. 1996), and to volitional contractions (Earles et al. 2001). A general consensus is that a reduced ability of the older individuals to modulate presynaptic inhibition levels may be the mediating mechanism for the difference in H reflex output response between the groups. However, the authors of the aforementioned studies do concede that the role of postsynaptic mechanisms cannot be ruled out.

One alternative explanation to explain the different response observed in the two groups could be related to the actual age-related differences in the size of the H reflex. It has been, in fact, previously shown (Crone et al. 1990) that the susceptibility of the H reflex itself to increase or decrease during a conditioning stimulation of the motoneuronal pool varies with the size of the unconditioned reflex. In addition to changes occurring at spinal level with increasing age, changes at the periphery could explain the difference in modulation response between the groups. Structural changes, a decrease in the discharge frequency and a reduction in the number of muscle spindles have been demonstrated with increasing age (Miwa et al. 1995, Swash and Fox 1972). If, as previously mentioned, autogenic excitation from the cooled muscle spindles contribute to the facilitation of the H reflex output in the younger group, the age-related degenerative changes in the muscle spindles may be responsible for the lack of modulation observed in older individuals.

H_{max} and M_{max} onset latency

A longer H_{max} onset latency was demonstrated in the older compared to the younger group. This is in agreement to previous studies (Kido et al. 2004, Sabbahi and Sedgwick 1982, Scaglioni et al. 2002). Nerve conduction velocity has been shown to decrease by over 20 % with increasing age in both sensory and motor nerves as a consequence of degeneration of the axon properties (Boxer et al. 1988, Chase et al. 1985). Furthermore, changes in the delay time at the Ia afferent- α- motoneuron junction or at the neuromuscular junction in older individuals could increase the onset latency (Sabbahi and Sedgwick 1982). It is likely however, that a combination of the above mechanisms will be responsible for the difference in the reflex onset latency between the groups.

Both warming and cooling induced a significant change in the H_{max} onset latency in both the young and the older group. As described previously the changes in the Na^+ voltage gated channel function affect the conduction of the depolarization (Rutkove 2001). A similar effect on the M_{max} onset latency would have been expected, however due to the short distance between the stimulation site and the recording site it is possible that any quickening or slowing of the conduction velocity with warming or cooling would have been very discrete and would be masked by any slight inaccuracy in the measurement of the onset latency.

Prior to temperature manipulation, older subjects presented slower reflex onset latencies than young participants. This is functionally important as the onset latency of the stretch reflex response has been shown to correlate with postural sway parameters (Nardone et al. 1995). An additional, slowing of the H_{max} reflex response with cooling could further impair the ability to maintain upright stance putting the older individual at risk of loss of balance especially under conditions in which subjects have to correct rapid perturbations of the body (Maki and McIlroy 1996, Nardone and Schieppati 2004).

Conclusions

In response to localised cooling, young individuals displayed a facilitated H reflex output, as indicated by an increased H_{max}/M_{max} ratio, whereas older individuals demonstrated no such modulation response. Warming had no effect on H reflex output in either the young or the older group. In a cold environment, the lack of facilitation in the reflex output, along with a further delay to an already impaired reflex response could be critical to an older individual in responding to a potentially hazardous stimulus such as to a loss of balance or simply maintaining a standing posture.

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CHAPTER 5

Moderate alterations in lower limbs muscle temperature do not affect postural stability during quiet standing in both young and older women

Data presented in this chapter are presented in the following article:

Dewhurst S, Riches PE, De Vito G. Moderate alterations in lower limbs muscle temperature do not affect postural stability during quiet standing in both young and older women. J Electromyogr Kinesiol. 2007; 94: 491-499.

Data from this chapter was presented at the following conference:

International Society for Ageing and Physical Activity; August 2004, Ontario, Canada. The effects of altered localised temperature on spinal reflex excitability and postural sway in young and older women.

ABSTRACT

Older adults demonstrate increased amounts of postural sway, which may ultimately lead to falls. Temperature is known to have a profound effect on the performance of the neuromuscular system which could have important implications on motor control. It is, therefore, of interest to investigate if the age-related decline in postural stability could be affected by changes in local limb temperature. The present study investigated the effects of localised warming and cooling on postural sway in nine young (22 ± 3 years; mean ± SD) and nine older (73 ± 3 years) women. Postural sway was assessed, using a force platform, during quiet standing at 3 muscle temperature conditions: control (34.2 ± 0.2 °C), cold (31.3 ± 0.3 °C) and warm (37.0 ± 0.1 °C). Two stances were evaluated, the Romberg (large support base) and modified Tandem (narrow support base), under both eyes-open and eyes-closed conditions. Root mean square (RMS), mean velocity (MV), sway area (SA) and mean power frequency (MPF) were calculated from the centre of pressure (COP) displacement. Neither warming nor cooling significantly affected any of the postural parameters which were, however, all higher ($P<0.05$) in the older group than the young group in all conditions. This study demonstrated that, in quiet standing conditions, a moderate variation (±3°C) in lower limbs temperature does not affect postural steadiness in either young or older women.

INTRODUCTION

Detection and response to sway during standing is vital to the maintenance of successful postural control. Signals from the vestibular, visual and proprioceptive sensory systems are integrated to provide the nervous system with the information necessary in achieving this task (Horak and Macpherson 1996). A known consequence of aging is represented by deleterious changes to the structure and function of the proprioceptive system, which contribute to the increased postural instability and consequently an increased risk of falls in the older population (Maki and McIlroy 1996, Stelmach and Worringham 1985). Indeed, correlations have been reported between the stretch reflex onset latency and postural sway in adults of increasing age, with a slower onset latency resulting in a greater postural sway (Nardone et al. 1995).

In light of these age-related alterations in the mechanisms which maintain postural control it is also of interest to consider external factors which could potentially contribute to alter postural stability (Maki and McIlroy 1996). Temperature is known to have a profound effect on the neuromuscular system (Hodgkin and Katz 1949, Rome 1990); a linear relationship is known to exist between the conduction velocity of a nerve and its local temperature (for review see: Rutkove 2001). Further, the previous investigation has demonstrated a lengthening of the reflex onset latency with cooling and a shortening of the onset latency with warming in both older and young individuals (chapter 4). Older subjects, however, exhibit slower onset latency than young even in normal temperature conditions. Therefore, a further delay induced by cooling could have critical effect on the ability to successfully maintain postural steadiness in an older population.

The aim of the present study was, therefore, to investigate the effects of decreased and increased local temperature on the postural stability in young and older women. The study was conducted on women since, with advanced age, they exhibit higher rate of falls and related injuries than men (Schultz et al. 1997). It has been also shown in a prospective study that in the winter period the observed increase in the rate of falls in the older population was observed in women but not in men (Campbell et al. 1988).

METHODS

Participants

Nine young [aged 22 ± 3 years; body mass 59 ±3 kg; stature 1.64 ± 0.08 m) and nine older [73 ± 3 years; body mass 68 ± 11 kg; stature 1.61 ± 0.07 m) women gave written consent to participate in the study after being fully informed about the investigation and the possible related risks and discomforts. Young subjects were healthy with no known neuromuscular disorders. Older subjects were considered medically stable as proposed by Greig et al. (1994). All subjects were moderately active participating in non-competitive, physical activities no more than twice a week. Ethical approval for the experimental procedures was obtained from the local University Ethics Committee.

Experimental design

After an initial familiarisation session, subjects attended the laboratory on a single occasion during which all tests were performed. Minimal physical activity was performed and no caffeine or alcohol was permitted 24 hours prior to the testing session. Following subject preparation subjects performed the control trial first, which was followed by both a warming and cooling trial administered in a counterbalanced fashion.

Temperature measurements

Muscle and the skin temperatures were measured from the dominant leg, muscle temperature was continually measured from the vastus lateralis muscle using a flexible temperature probe (Ellab Ltd, Copenhagen, Denmark) inserted 1 cm below the subcutaneous fat layer at an angle of 45 ° in the direction of the muscle fibres. The thermistor was inserted through a flexible cannula (Venflon 18 GA, Becton Dickinson, Sweden) and advanced ~0.5 cm beyond the end of the cannula into the muscle. Skin temperature was measured using skin thermistors (Grants Instruments Ltd, Cambridge, UK) from two sites, the vastus lateralis (close to the muscle probe) and the soleus (muscle belly). Muscle and skin temperatures were recorded from Medical Precision Thermometer (DM 852, Ellab Ltd, Copenhagen, Denmark) and 1000 series 8-bit squirrel data logger (Type 1002, Grants Instruments Ltd., Cambridge, UK), respectively. Core temperature was estimated using an infrared tympanic thermistor (Braun, type 6013, Germany).

The subjects rested in the supine position for 30 min at room temperature (≅ 26 °C) to achieve steady state temperatures. Temperatures recorded immediately after the 30 min rest were considered the control temperatures. Following the balance performance assessment under the control temperature condition, temperature of the legs was increased using electrically heated blankets or decreased using a specifically made ice blanket consisting of large thick plastic sacks filled with crushed ice. In both temperature conditions blankets covered the whole of both legs from the gluteal furrow to the foot. Warming and cooling proceeded until muscle temperature was increased or decreased by approximately 3 °C with respect to the control muscle temperature. Muscle temperature was monitored throughout the trial to ensure the desired value was maintained. Blankets were removed during each trial but were applied again during the rest period between trials.

Data acquisition and analysis

Balance performance was assessed during quiet standing in two positions, one with a large support base (the Romberg position) and the other with a narrow support base (modified Tandem position) (figure 5.1). For each trial subjects stood barefoot, centrally aligned on the force plate. The Romberg position involved the subject standing feet together with their arms lying along legs, whilst in the modified Tandem position the subjects took a small step back with their dominant foot so the feet were aligned heel to toes but not directly behind one another, again with the arms lying along legs. Subjects kept the position for 35 seconds, although the initial 5 seconds were not included in the subsequent analysis. Trials for both stance positions were performed under two visual conditions, eyes open and eyes closed administered in a randomized order. Each trial was repeated three times, with two minutes rest between trials. During the open-eyes trials subjects had to focus on a visual target placed two meters in front of the subjects at eye level, spectacles were worn if required. Data were obtained using a piezo-electric force platform (Kistler 9261A, Winterhur, Switzerland) adopting a sampling frequency of 100Hz. Data from the force platform were amplified (Kistler, charge amplifier, 9865B), A/D converted before being transferred to a PC. Data were low-pass filtered using a 4th order Butterworth filter with a 5Hz cut-off frequency. Subsequently, the following centre of pressure (COP) based parameters were calculated using matlab software: root mean square (RMS), which is the value of the resultant distance in the time series and is related to stability achieved by the postural system, and mean velocity (MV) which is the average velocity of the COP using the total excursion and is related to the amount of regulatory activity; as representative of the time domain measures, sway area (SA) as representative of a time domain hybrid measure (Prieto et al. 1996), SA estimated the area enclosed by the COP path per unit of time, and mean power frequency (MPF), for the frequency domain measure which is the mean value of the power spectral density (Schmid et al. 2002) (full equations used are given below). For each of the parameters the Romberg Quotient (RQ) and Tandem Quotient (TQ) were calculated to assess the importance of vision on the COP parameter, which was calculated as the ratio of the eyes closed value to the eyes open value.

Posturographic parameters: definitions of the measures: T= duration the observation, f= frequency, P(f)= power density spectrum, COPr= resultant COP, COPml= COP in medio-lateral direction, COPap= COP in the anterior-posterior direction.

RMS=

$$\sqrt{\frac{1}{T}\int_{0}^{T} COP_{R}^{\,2}(t)dt}$$

Mean Velocity=

$$\frac{1}{T}\int_{0}^{T}\sqrt{\left(\frac{\partial COP_{AP}(t)}{\partial t}\right)^{2}+\left(\frac{\partial COP_{ML}(t)}{\partial t}\right)^{2}}\,dt$$

Sway Area=

$$\int_{0}^{T}\left[\left(\frac{\partial COP_{AP}(t)}{\partial t}\cdot COP_{ML}(t)-\frac{\partial COP_{ML}(t)}{\partial t}\cdot COP_{AP}(t)\right)/2\right]dt$$

Mean Power Frequency=

$$\frac{\int_{0}^{F_c/2} f\cdot P_{COP_{AP}}(f)df}{\int_{0}^{F_c/2} P_{COP_{AP}}(f)df}$$

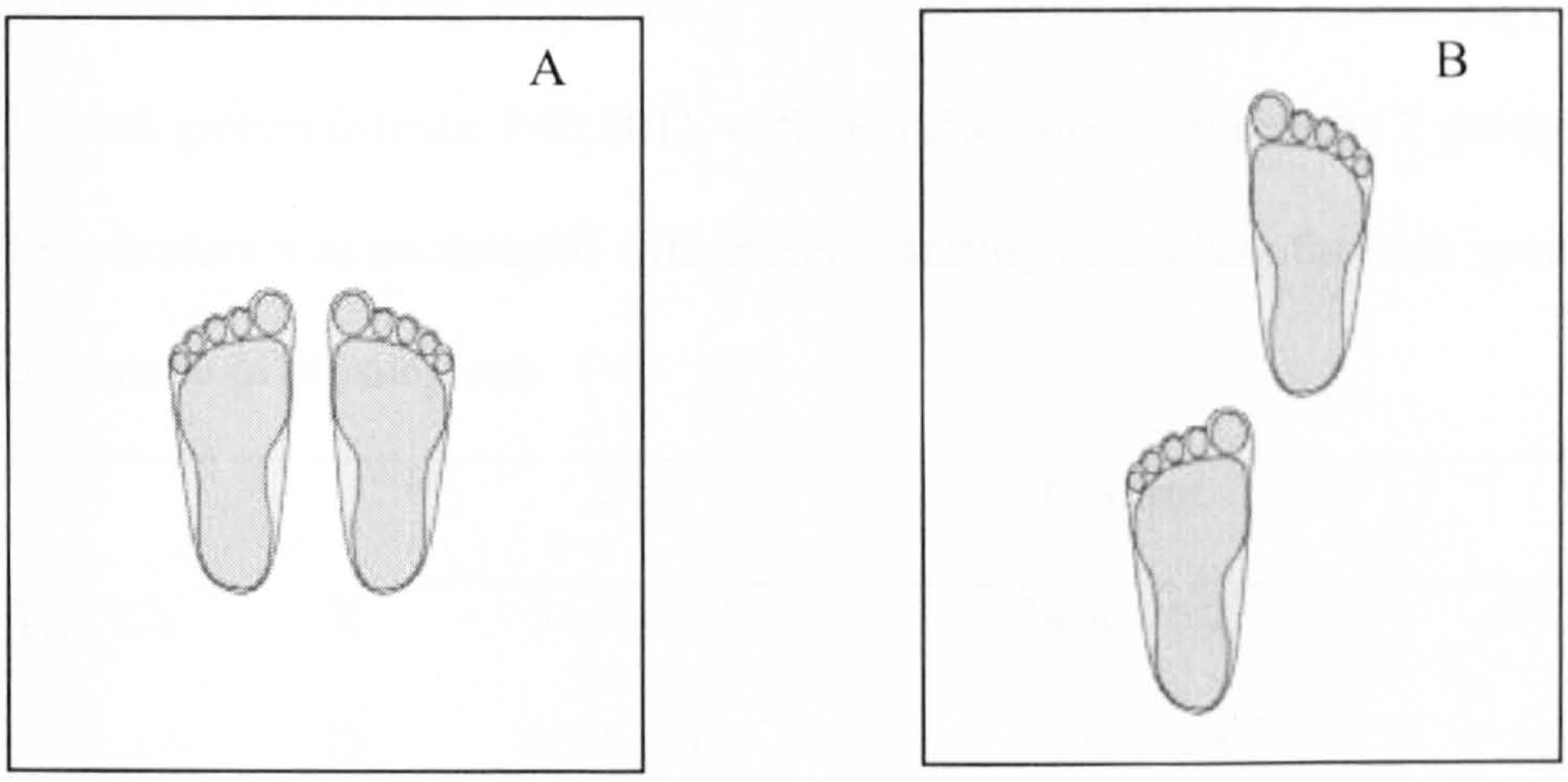


Figure 1. Foot positions on the force platform for the Romberg position (A) and Tandem position (B).

Statistical analysis

To assess the effect of age and temperature condition and the effects vision, data were analysed using a three-way repeated measures analysis of variance (ANOVA) (age x temperature condition x eye condition) for both the Romberg and Tandem stance. Where a significant effect was observed differences were located with *post hoc* multiple paired Student's *t*-tests adopting a Bonferroni correction to the selected alpha level ($P<0.05$; $P<0.05/3$).

RESULTS

Temperature

Warming and cooling significantly decreased and increased T_m and T_{sk} (VL and Sol) in both groups (*t*-tests: $P<0.001$), with no difference between the 2 groups. Tympanic temperature was unchanged with either warming or cooling for both groups (Table 5.1, mean of all subjects).

		Cold	Control	Warm
T_m (°C)	Y	31.8 ±0.4*	34.8 ± 0.2	37.3 ± 0.1*
	O	30.9 ± 0.4*	33.8 ± 0.3	36.7 ± 0.1*
T_{sk} V.L(°C)	Y	26.6 ± 1.0*	32.6 ± 0.3	34.5 ± 1.6*
	O	25.2 ± 1.1*	31.6 ± 0.5	34.0 ± 2.7*
T_{sk} P.F.(°C)	Y	23.8 ± 1.2*	32.0 ± 0.3	37.0 ± 1.7*
	O	23.8 ± 0.9*	32.0 ± 0.5	36.8 ± 0.9*
T_{sk} Sol.(°C)	Y	19.6 ± 1.3*	31.7 ± 0.4	36.9 ± 1.9*
	O	19.7 ± 2.5*	31.8 ± 0.5	36.5 ± 1.3*
T_t (°C)	Y	36.7 ± 0.2	36.8 ± 0.1	36.8 ± 0.1
	O	36.3 ± 0.1	36.6 ± 0.1	36.6 ± 0.1

Data are means ± SE; *n* =10 in both groups; * denotes difference from control condition ($P<0.025$). T_m= muscle temperature, T_{sk}= skin temperature, V.L.= vastus lateralis, P.F.= popliteal fossa, Sol.= soleus, T_t= tympanic temperature.

Table 5.1. Temperature values for the young (Y) and older (O) groups, during cold, control and warm temperature conditions.

Force-plate data

Figure 5.2 gives an example of trace of the centre of pressure for one young and one older subject. As expected for both the Romberg and Tandem assessments there was a significant effect of age on the postural parameters, with RMS, MV, SA and MPF being significantly greater in the older group compared to the young (ANOVA: $P<0.05$; Figure 5.3A, B, C, D and 5.4A, B, C, D).

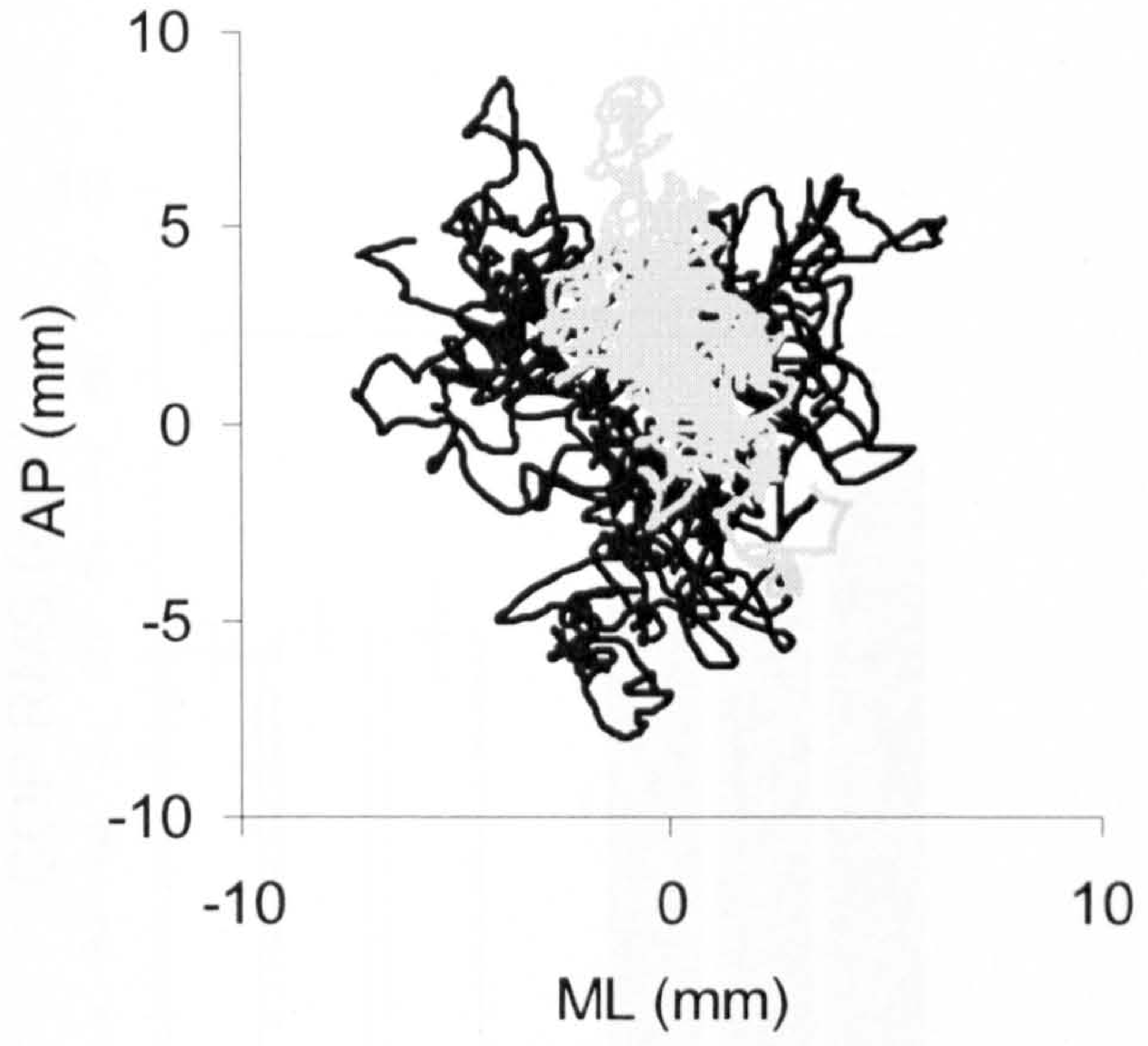
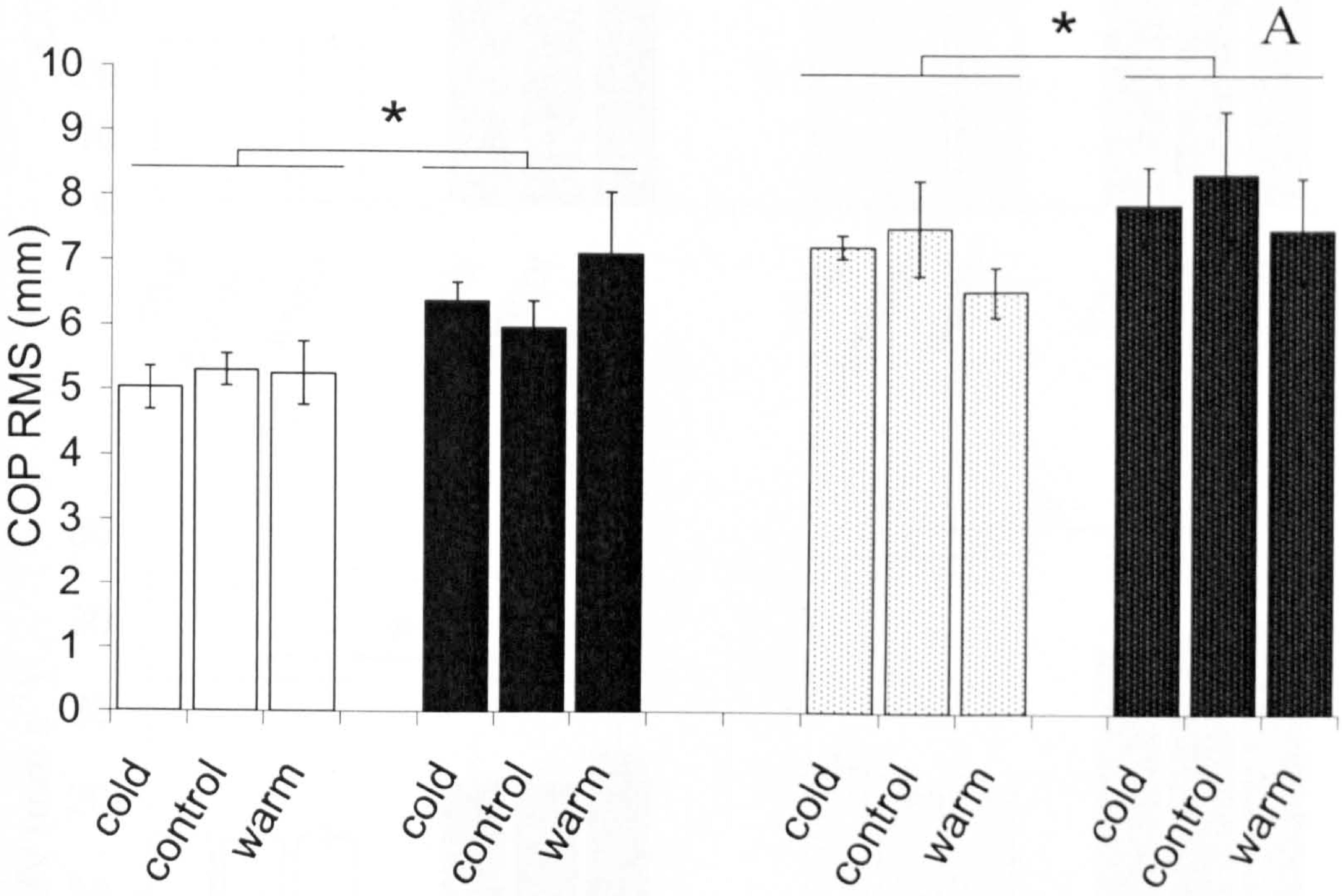
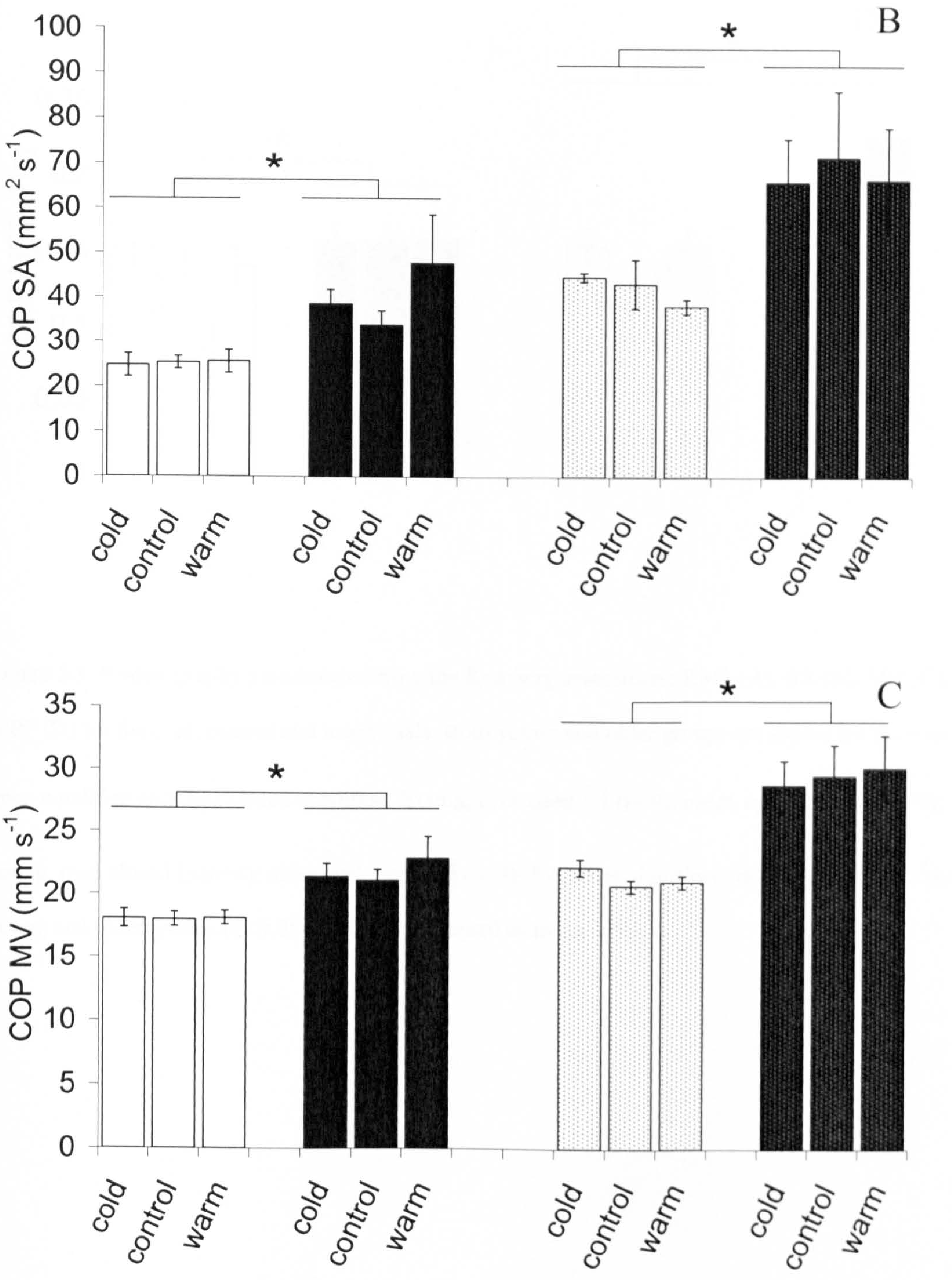


Figure 5.2. Centre of pressure trace for a young (grey trace) and older subject (black trace) for the control temperature Romberg trial with eyes open. AP: anterior- posterior direction, ML: medial-lateral position.

Neither cooling nor warming affected RMS, MV, SA and MPF in either of the postural assessments in both the young and older groups (Figure 5.3A, B, C, D and 5.4A, B, C, D).

Both groups showed a significantly greater RMS, MV and SA values with eyes closed in both the Romberg and Tandem trials compared to eyes open (ANOVA: $P<0.05$). The MPF was greater in the eyes closed trial during the Romberg assessment (*t*-tests: $P<0.05$), whereas in the Tandem trial MPF was the same for both the eyes open and eyes closed condition (Figure 5.3A, B, C, D and 5.4A, B, C, D). Two older subjects were not able to complete the test in the Tandem closed eyes condition.




B
COP SA (mm^2 s^{-1})
100
90
80
70
60
50
40
30
20
10
0
*
*
cold
control
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cold
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COP MV (mm s^{-1})
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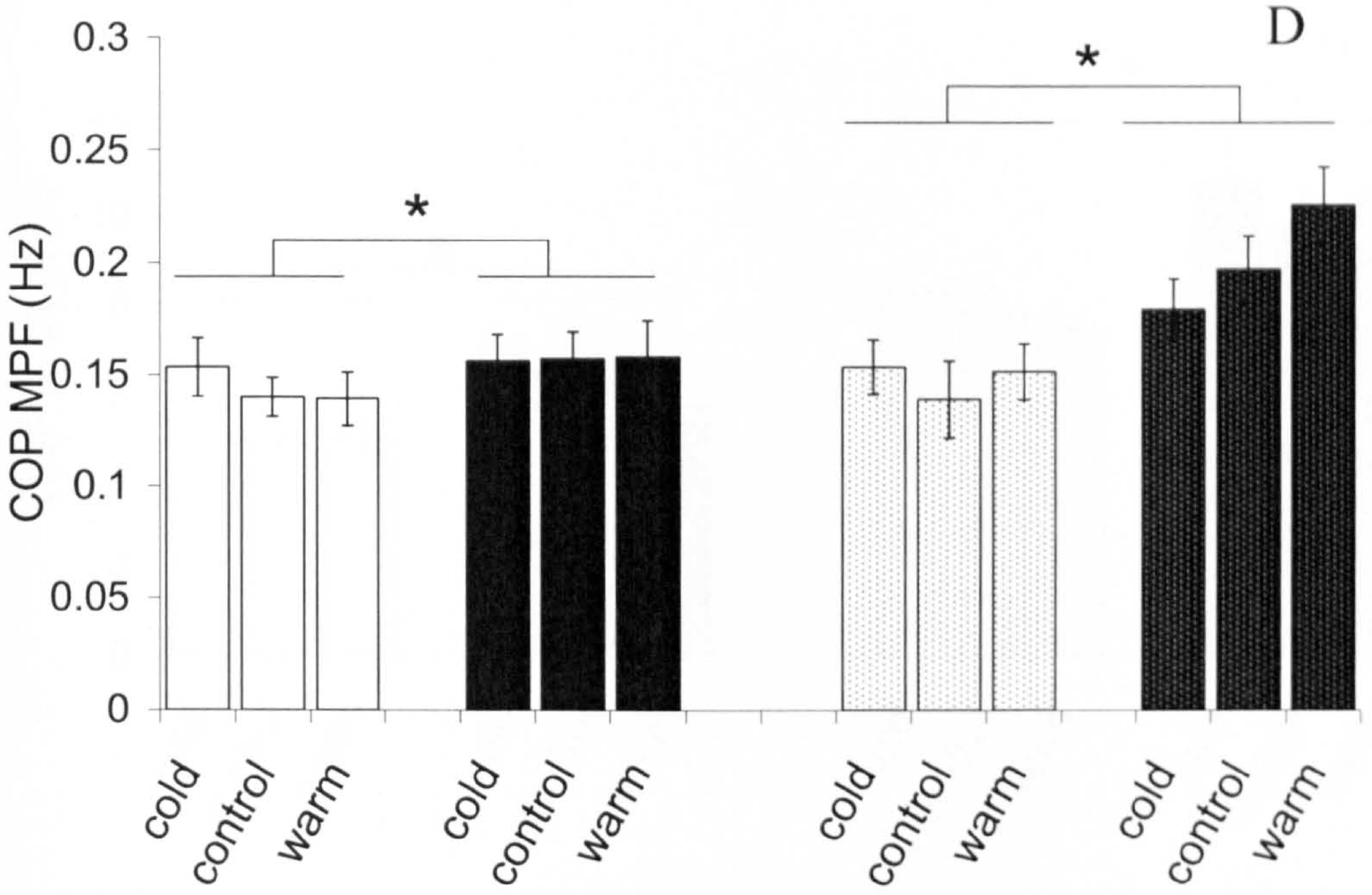
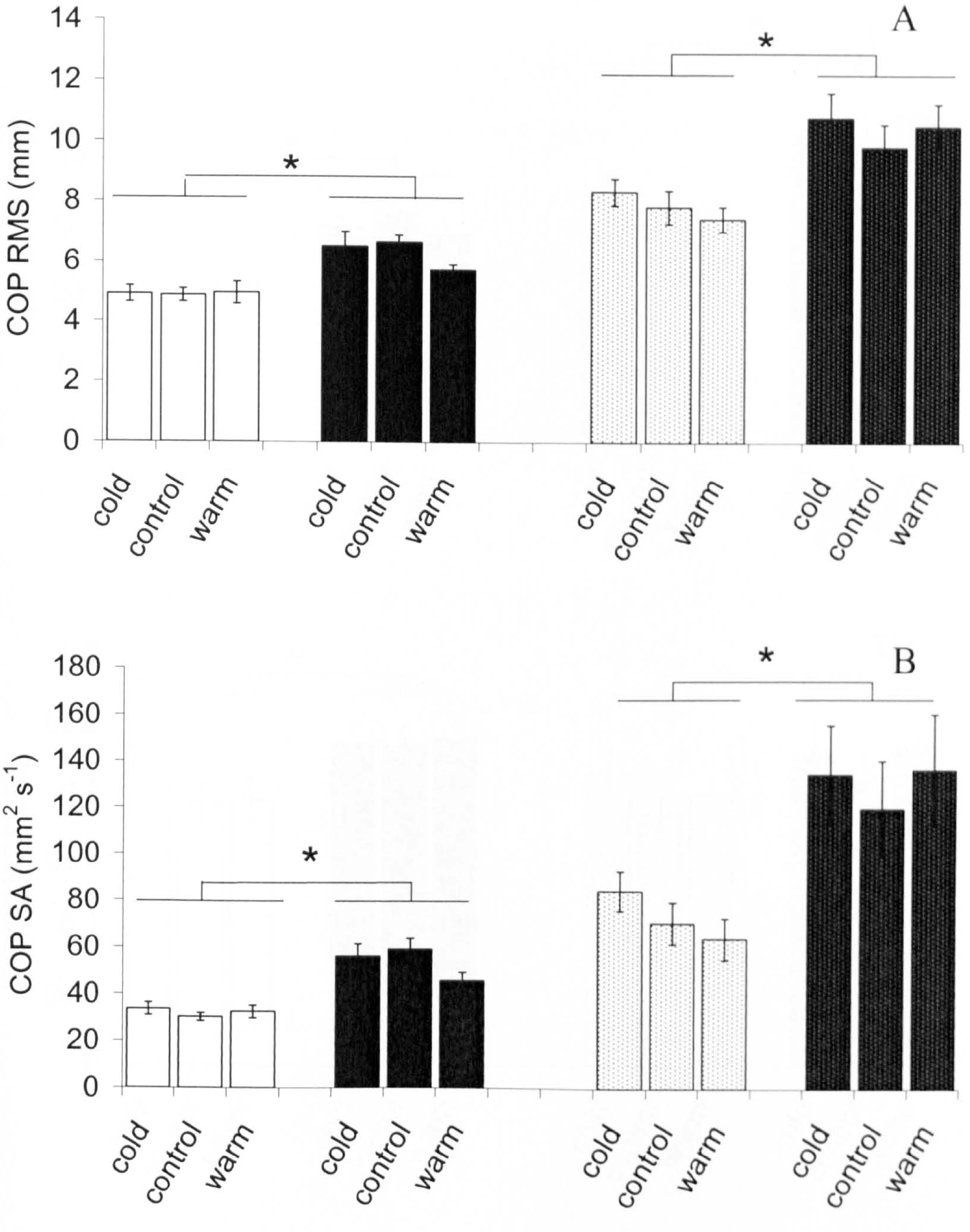


Figure 5.3. Posturography parameters during the Romberg assessment: RMS (A), SA (B), MV (C), MPF (D) for the cold, control and warm trials. Both young and older groups are shown for the eyes open condition and eyes closed condition. Young, eyes open □ (n=9); older, eyes closed ■ (n=9); young, eyes closed ░ (n=9); older eyes closed ▓ (n=9). * denotes significant difference between the young and older groups ($P<0.05$). Data are presented as mean ± SE.


A
COP RMS (mm)
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B
COP SA (mm^2 s^{-1})
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40
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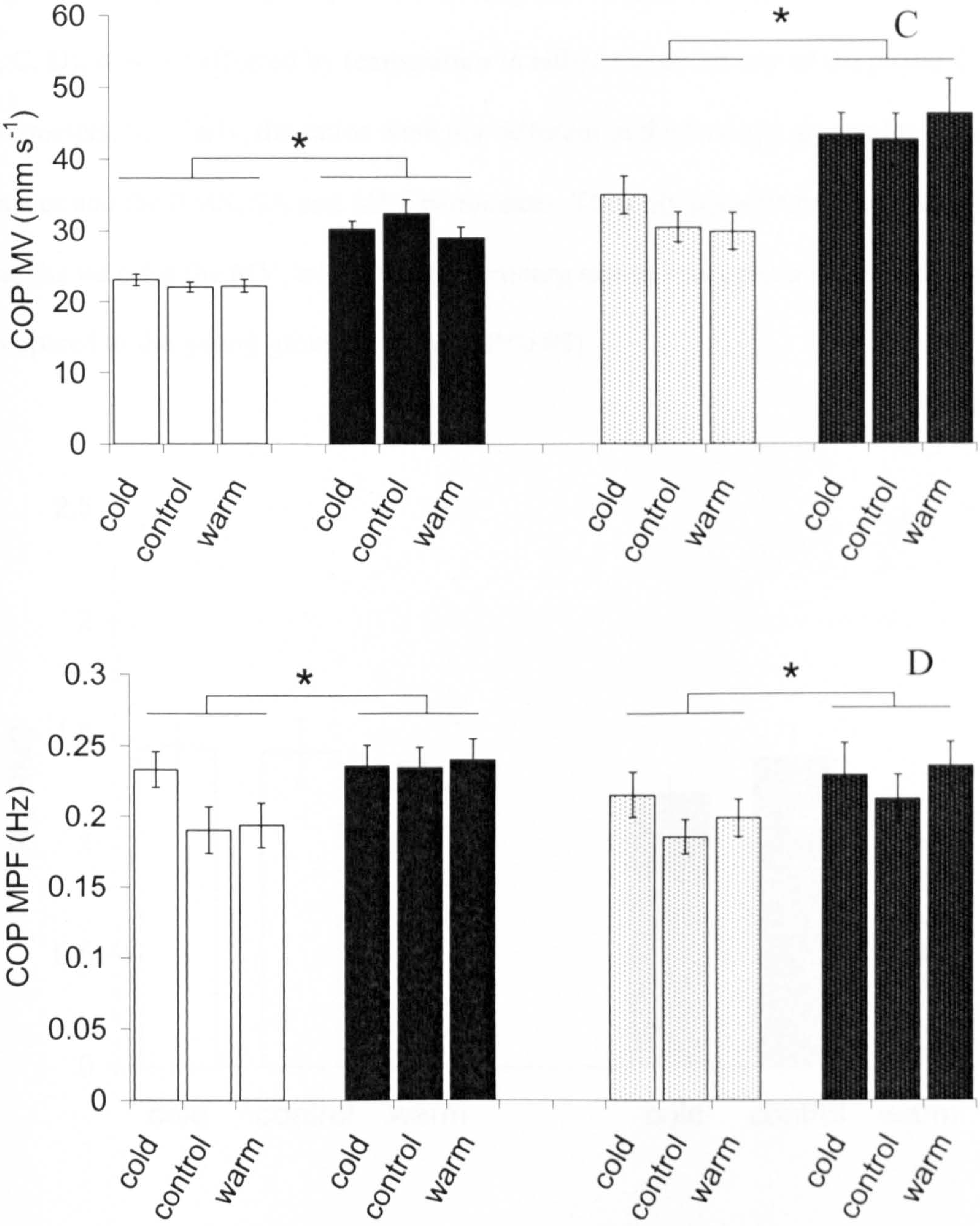
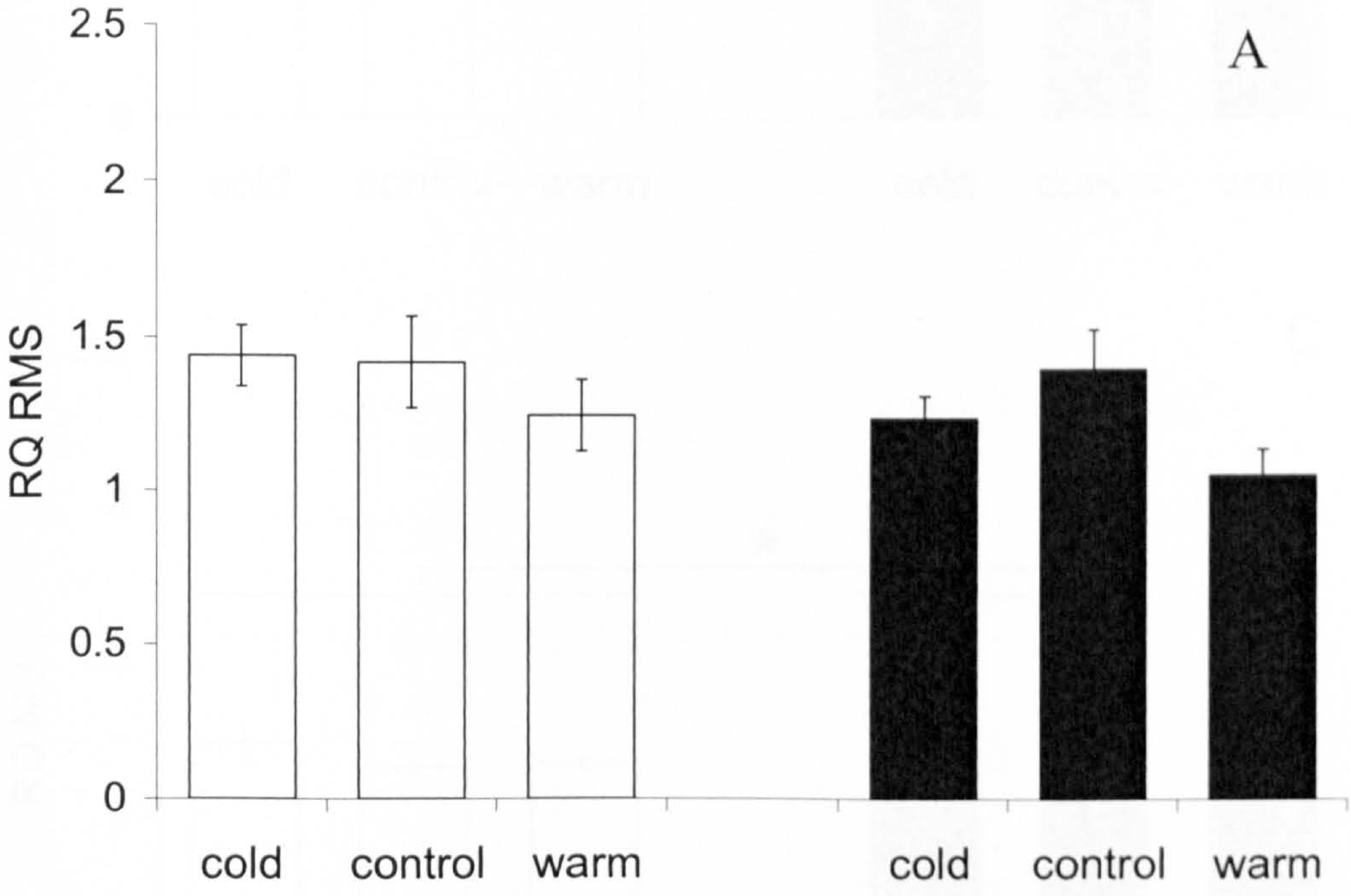
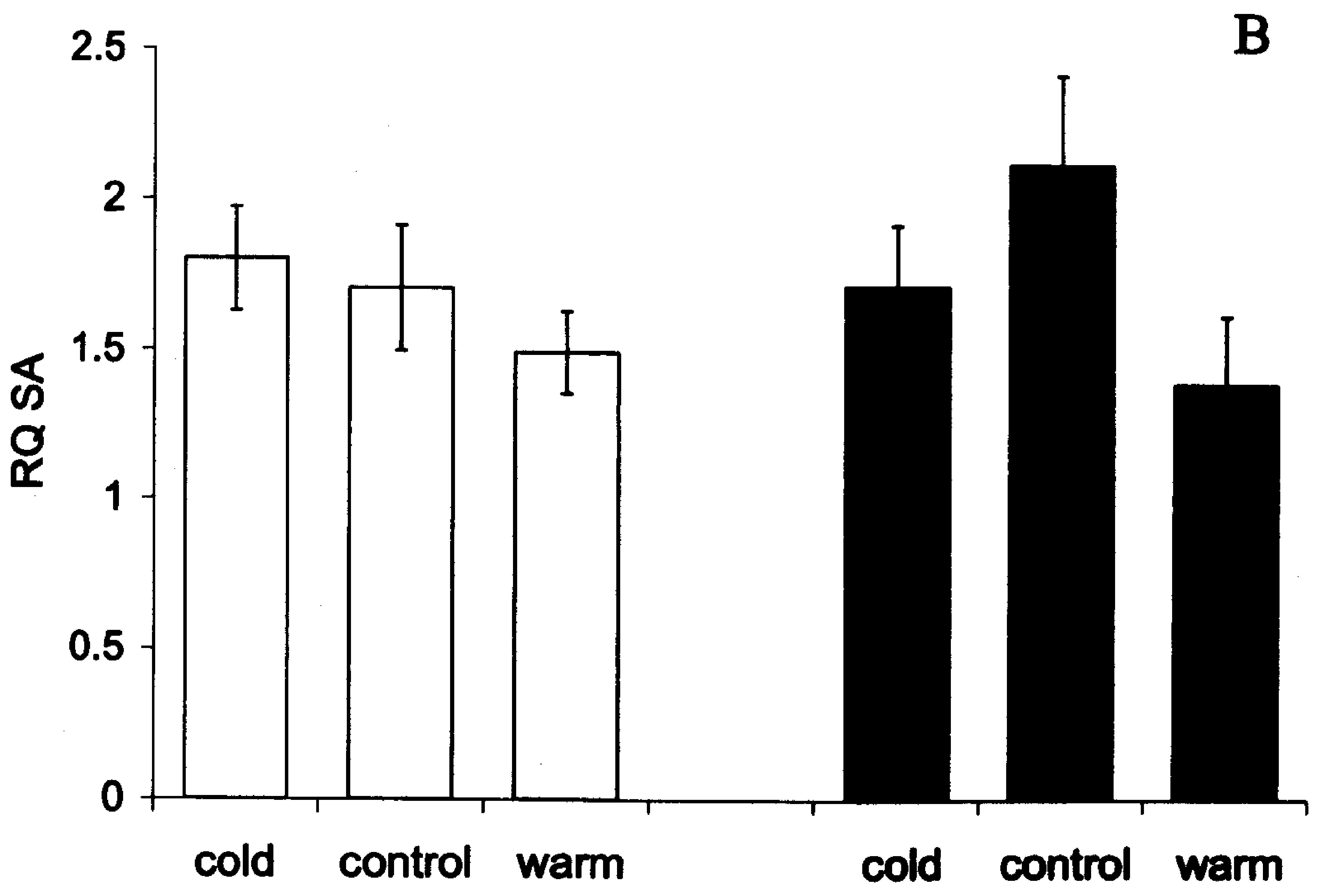


Figure 5.4. Posturography parameters during the modified Tandem assessment: RMS (A), SA (B), MV (C), MPF (D) for the cold, control and warm trials. Both young and older groups are shown for the eyes open condition and eyes closed condition. Young, eyes open □ (n=9); older, eyes closed ■ (n=9); young, eyes closed ░ (n=9); older eyes closed ▓ (n=7). * denotes significant difference between the young and older groups (P<0.05). Data are presented as mean ± SE.

The ratio between the eyes open and closing trials (Figure 5.5A, B, C, D and 5.6A, B, C, D), was not affected by temperature in either stance for any of the postural parameters. Similarly, the ratios were not different in the two age groups for both stances and the RMS, SA and MPF parameters. The only parameter which differed was the ratio for the MV, which in the Romberg stance was greater in the older group compared to the young group (ANOVA: P<0.05).




B
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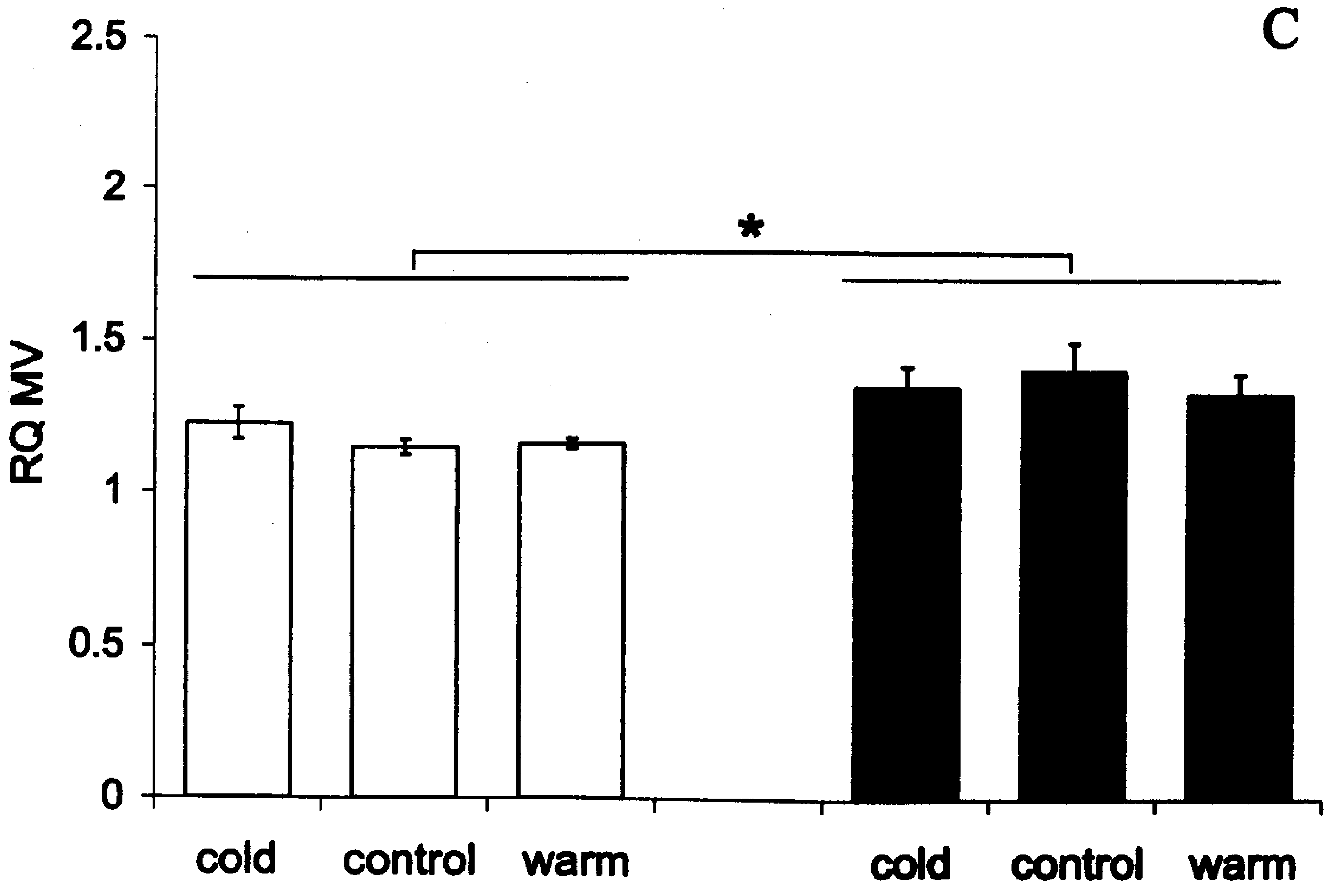
C
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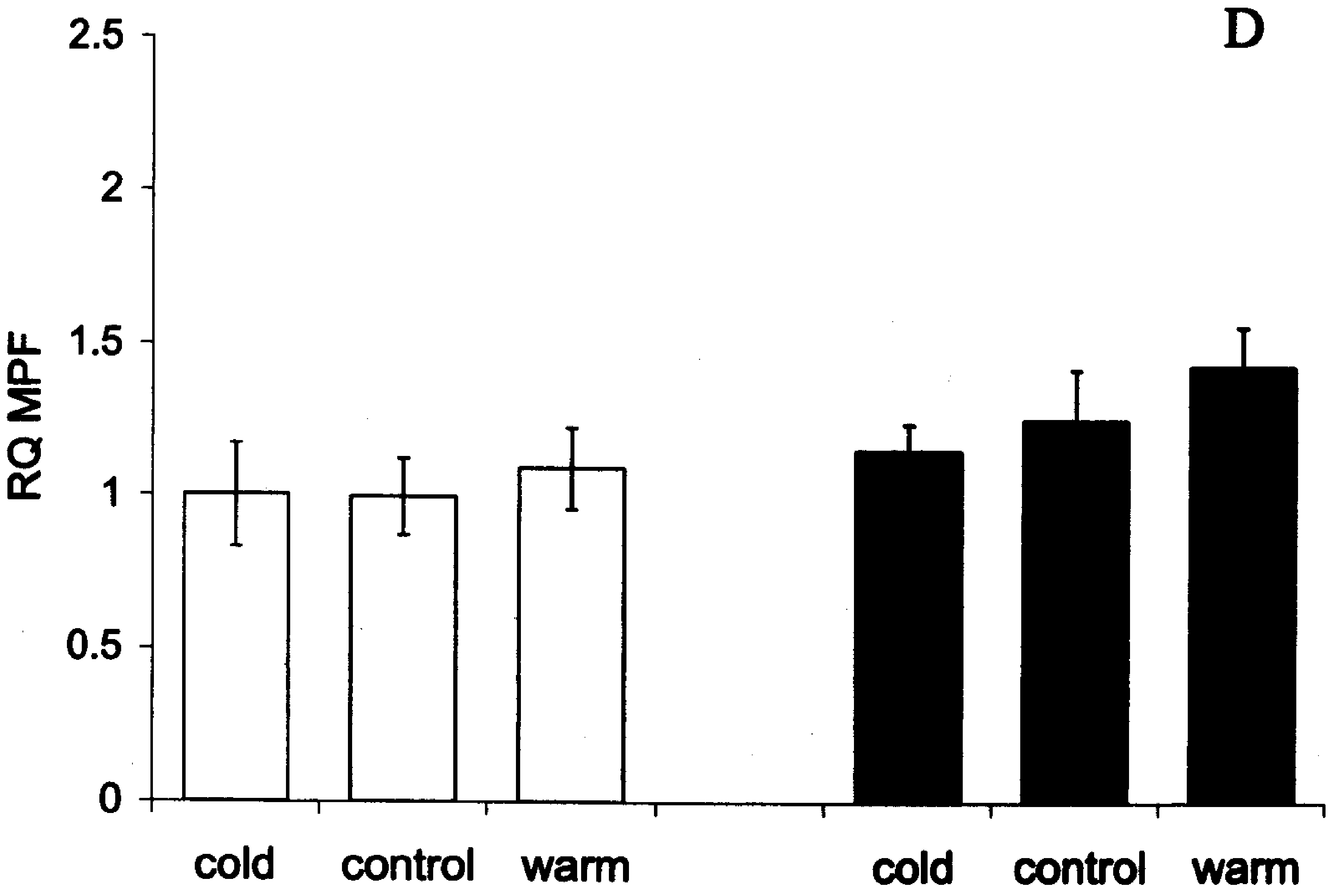
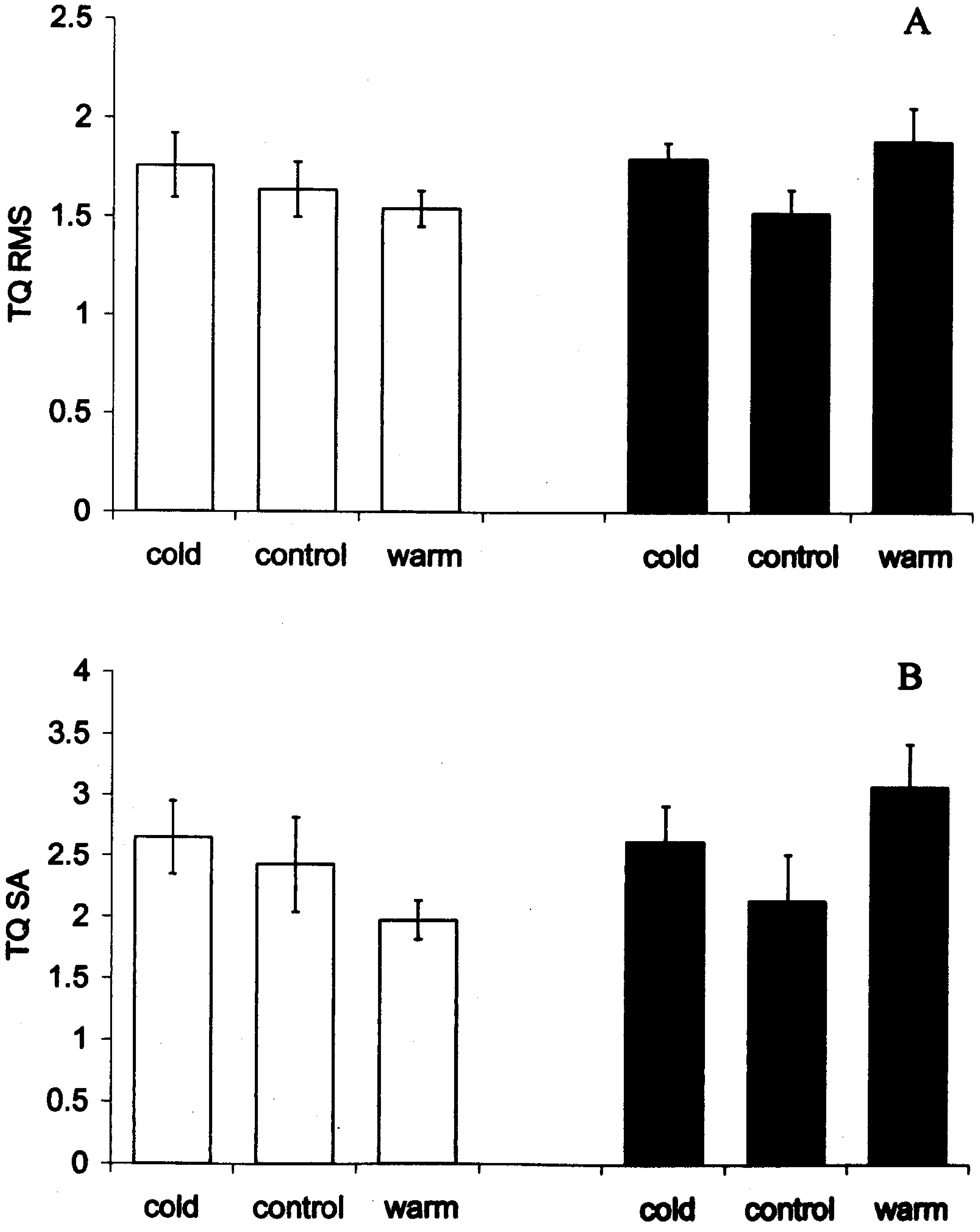


Figure 5.5. Romberg Quotient (RQ) (eyes closed/ eyes open): RMS (A), SA (B), MV (C), MPF (D) for the cold, control and warm trials. Young ☐ (n=9); older ■ (n=9). * denotes significant difference between the young and older groups (P<0.05). Data are presented as mean ± SE.


A
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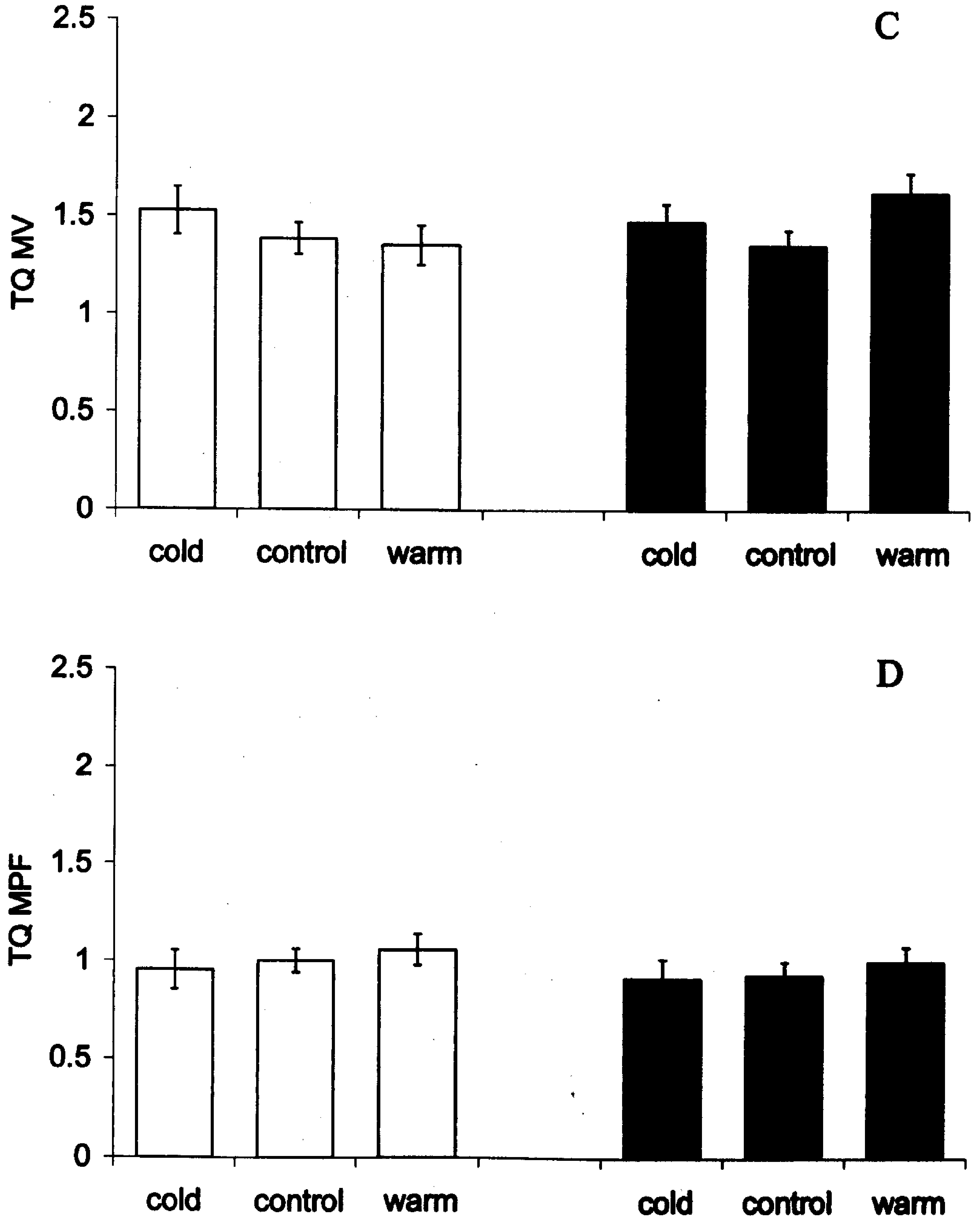


Figure 5.6. Tandem Quotient (TQ) (eyes closed/ eyes open): RMS (A), SA (B), MV (C), MPF (D) for the cold, control and warm trials. Young ☐ (n=9); older ■ (n=7). Data are presented as mean ± SE.

DISCUSSION

The main finding of the present study was that neither warming nor cooling affected postural stability, measured during quiet stance, in either the young or the older group with an increase or decrease in muscle temperature of ± 3 °C.

Under everyday circumstances upper limb muscle temperature can vary by some 10 °C (Mucke and Heuer 1989). Concerning the lower limbs, for an inactive older individual with a smaller lower limb muscle mass than a young individual a temperature variation of 6 °C, as obtained in the present study, would be expected to be within the temperature range potentially experienced by this population. This study highlights the importance of the use of muscle temperature when monitoring temperature of the lower limbs. Table 5.1 demonstrates that cooling has a much greater effect on the skin temperature when compared to the muscle temperature, whereas with warming the difference between the skin and muscle temperature was negligible, with this difference between the temperature conditions being ascribed to the methods employed.

Falling is considered one of the most serious problems facing an older individual and static postural stability is known to be a reliable predicator of falls in this age group (Maki et al. 1994). On the base of the present study results, it appears that with cold lower limbs an older person is at no greater risk of falling than compared with normal temperature. Although the Romberg assessment would be considered a relatively unchallenging assessment of postural stability, it was surprising to find that during the modified Tandem assessment, a somewhat more demanding evaluation, postural sway was not affected by the change in temperature. Indeed, this test was shown to challenge the limits of the older individuals postural control, as 2 of the 9 older subjects were unable to complete the test with their eyes closed. Not measured in the present study, however, were the effects of altered temperature on disturbed stance. Dynamic posturography has been shown, in fact, to be more sensitive than static posturography in detecting the effect of aging on postural stability (Baloh et al. 1994, Camicioli et al. 1997) hence it may also be more sensitive to detecting the effect of altered temperature on postural stability.

Since a change in temperature of ± 3 °C, as used in the present study, has been shown to have a marked effect on the short latency reflex system in both young and older adults (chapter 4) it was hypothesized that cooling could have a detrimental effect on balance especially in older subjects. Recent investigations have, however, demonstrated that neither patients with hyperexcitabily of the Ia mediated nerves or severe group Ia afferent nerve lesions have impaired postural control (Nardone et al. 1997, Nardone et al. 2000) challenging the belief that loss or damage to the Ia afferent fibres are responsible for the instability seen in individuals with peripheral neuropathies (Quintern et al. 1999, Weiss and White 1986). This suggests that Group I fibre performance, while crucial for detecting fast postural disturbances, is not as critical for quiet postural stance whereby the smaller Group II fibres may play a greater role in maintaining static stability. On the other hand, temperature is known to affect the conduction velocity of the smaller diameter Group II fibers to a greater extent than the larger Group I fibers (Paintal 1965, Matthews 1989). As a temperature dependency of the onset latency of the H reflex circuit evoked from the

Group Ia afferent has been seen with the temperature manipulation methods employed in the present study (chapter 4), it would be reasonable to assume a similar if not greater effect of temperature on the Group II afferent fibers which transfer information from the long latency pathways of the stretch reflex (Matthews 1985, 1989). In addition to effects of temperature on the onset of the reflex, temperature is known to affect the properties of the motor unit twitch, with cooling decreasing the twitch force and warming increasing the twitch force (Davies et al. 1982, Farina et al. 2005). This, however, was not measured in the present study but could potentially affect the reflex output as a smaller twitch force may not provide enough correction, whereas the larger force may cause too great a correction. One of the consequences of ageing is an increase in the twitch force (Galganski et al. 1993) this may be one of the reasons for the increased postural sway in this group. Another possible reason for the increased postural sway in the older group may be due to the decreased strength of the postural control muscles with ageing (Onambele et al. 2006). While this was not measured in the present study, a relationship has been shown between muscle strength and postural control in healthy older adults (Onambele et al. 2006, Orr et al. 2006).

Postural stability is the combination of the three sensory systems (visual, vestibular and proprioceptive) and when one of the systems is impaired, to maintain equivalent postural control, there must be compensation by an increased contribution from the remaining components (Dornan et al. 1978). This was considered in the present study with the assessment of stability under both eyes open and eyes closed visual conditions. In both age groups, however, there were no changes in the RQ in any of the postural parameters with either warming or cooling, signifying that a shift in the reliance of the visual system was not the source of the maintained postural stability. Not surprisingly, the younger group displayed better postural control than the older group, irrespective of temperature condition. It was expected that the older subjects would show a greater reliance on vision than young subjects to compensate for the well documented deleterious effects of aging on the proprioceptive system (Choy et al. 2003, Prieto et al. 1996), but this was not observed in the present study for most of the parameters with exception of the RQ for the MV which was greater in the older subjects than the young subjects. In both groups the MV was higher with vision removed, but this increase was significantly greater in the older subjects, implying that vision has a greater role in limiting the amount of postural corrections necessary for successful stability in the older group than the young group.

Conclusion

In conclusion, this study has demonstrated that during quiet standing, a moderate alteration in leg temperature does not affect postural stability in either younger or older healthy women. Further studies are necessary, however, to assess the effects temperature has on perturbed/ dynamic postural stability, which could be more functionally relevant.

CHAPTER 6

Muscle Temperature Has a Different Effect on Force Fluctuations in Young and Older Women

Data presented in this chapter are presented in the following article:

Dewhurst S, Graven-Nielsen T, De Vito G, Farina D. Muscle Temperature Has a Different Effect on Force Fluctuations in Young and Older Women. Clin Neurophysiol. 2007; 118: 762-769

Data from this chapter was presented at the following conference:

International Society of Electromyography and Kinesiology; June 2006, Turin, Italy. Effect of altered local temperature on force steadiness in young and older women.

ABSTRACT

This study investigated the effect of muscle temperature on force fluctuations during isometric contractions in young and older females. Fifteen young (23.6 ± 3 years; mean ±SD) and 11 older (68.6 ± 5.7 years) subjects performed 3 × 30-s long submaximal isometric ankle dorsi-flexions (5, 10, 15% of the maximal force). Tibialis anterior muscle temperature was monitored with an intramuscular probe and manipulated to obtain a cold, control, and warm condition. The coefficient of variation (CofV) and the relative power in the frequency bands 0-3 Hz (low), 4-6 Hz (middle), and 8-12 Hz (high) of the force signal were computed to characterise steadiness. Intramuscular EMG signals were recorded from the tibialis anterior muscle to assess motor unit discharge pattern. CofV was higher in the older than in the young subjects ($P < 0.001$) in all conditions. In the older group only, CofV increased with cooling with respect to control temperature ($P < 0.001$), whereas in the young group only, relative power of force fluctuations at high frequency decreased with cooling. Motor unit discharge rate and inter-pulse interval variability were not different between groups and across temperatures. The findings indicate a different effect of temperature in the ability to maintain constant force in young and older subjects. These results highlight the risk of further impairment to the motor control of older individuals with varying temperature.

INTRODUCTION

During a steady muscle contraction, the force output fluctuates around the target value. The amount of fluctuations is affected by factors such as age, temperature and force (Christou et al. 2002, Lakie et al. 1994, Tracy and Enoka 2002). Motor unit properties and the stretch reflex loop contribute to the fluctuations in force output in low-force isometric contractions. The contractile and control properties of the active motor units determine the degree of fusion of the force twitches (Christakos 1982; Moritz et al. 2005). Additionally, during isometric contraction, the muscle spindle has been reported to respond to small force fluctuations, consequently facilitating the activation of motor units (Lippold 1970).

Different neural mechanisms cause force fluctuations at distinct frequency bands. Allum et al. (1978) have associated the low frequency component of the fluctuations (≤ 3 Hz) with the net activity of the motor neuronal pool, including changes in the discharge rate and number of active motor units. The long and short latency stretch reflex contribute to oscillations at frequencies ~7 Hz and ~10 Hz, respectively (Marsden 1978).

In older individuals the force fluctuations are larger than in young subjects (Bazzucchi et al. 2004, Tracy and Enoka 2002, Vaillancourt and Newell, 2003) due to mechanisms not yet fully clarified. Variability in motor unit discharge rate has been identified as a critical factor in isometric force fluctuations (Moritz et al. 2005). With respect to aging, variability in motor unit discharge rate has been shown to increase in some studies (Laidlaw et al. 2000), although this observation was not confirmed in all reports (Galganski et al. 1993, Vaillancourt et al. 2003). The amplitude of twitch force of motor units recruited at submaximal force increases with ageing (Galganski et al. 1993) but simulation studies revealed that this has negligible effects on force fluctuations (Taylor et al. 2002). The stretch reflex response is also altered with ageing. This includes a slowing of the reflex onset latency, caused by a decrease in the transmission efficiency of the signal, as well a reduction in sensitivity and number of spindles (Adinolfi et al. 1991, Henderson et al. 1980, Swash and Fox 1972). The contribution of a slower stretch reflex loop to the increase in force fluctuations in the older individual is, however, not known.

Temperature is an external factor that has been shown to affect the amount of force fluctuations in both healthy and diseased subjects. Everyday variations in limb muscle temperature have been reported to be ~10 °C (Mucke and Heuer 1989). However, studies on the effect of temperature on force fluctuations reported conflicting findings. Improvement in fine manual dexterity tasks and reduction in force fluctuation follow arm cooling in healthy young adults, multiple sclerosis patients and essential tremor patients (Feys et al. 2005, Lakie et al. 1994), however opposite results have been also reported (Havenith et al. 1995, Cheung et al. 2003). Temperature alters the muscle fiber membrane and contractile properties. Motor unit twitch duration increases and peak tension decreases with decreasing temperature, affecting the fusion of the tetanic output (Davies et al. 1982, Ranatunga et al. 1987). Temperature also alters the reflex response latency measured from electrical stimulation of the reflex loop as reported in chapter 4 and alters spindle sensitivity in cats (Fischer and Schäfer 1999).

There are no studies that investigated the contribution of temperature to the impaired motor control mechanisms of the older individual during fine motor tasks. The purpose of the study was, therefore, to investigate the effects of altered muscle temperature on force steadiness in low-force isometric contraction of the dorsi-flexors in young and older women.

METHODS

Subjects

Fifteen young (mean ± SD; age 23.6 ± 3.4 years, stature 1.64 ± 0.08 m, mass 58.0 ± 8.6 kg) and 11 older (age 68.6 ± 5.7 years, stature 1.63 ± 0.04 m, mass 70.2 ± 18.2 kg) women volunteered to participate in the study. All subjects were healthy with no known neuromuscular disorders. Older subjects were medically stable according to Greig et al. (1994). All subjects were moderately active, participating in recreational physical activity no more than twice a week. All experimental tests were performed in the morning. The procedures were approved by the local ethics committee. Written informed consent was obtained from all subjects.

EMG recordings

Intramuscular EMG was recorded from the tibialis anterior muscle of the dominant leg. Electrodes were inserted 5 mm above the motor point of the muscle. The motor point was located using the methods described in chapter 2 using a 16 channel surface EMG array. After cleaning the skin with an alcohol wipe, 2 sterile Teflon coated stainless steel wire electrodes (A-M Systems, Carlsberg, WA, USA) were inserted at the muscle belly, ~5 mm into the muscle using a 25-G needle. Approximately 1 mm of the wire insulation was removed at the tip to detect the intramuscular signals. The needle was removed leaving the wires in the muscle. Signals were recorded in monopolar mode, with respect to reference self-adhesive surface electrodes placed on the skin over the tibia, with one recording from each wire. Signals were amplified (counterpoint electromyography, Dantec medical, Skovlunde, Denmark), band-pass filtered (500 Hz- 5 kHz), sampled at 10000 Hz, and stored after 12 bit A/D conversion.

Temperature recordings

Muscle temperature was recorded from the muscle belly of the tibialis anterior muscle of the dominant leg, lateral to the EMG wire insertion point with a flexible intramuscular temperature probe (Ellab Ltd, Copenhagen, Denmark). The probe was inserted ~10 mm into the muscle at a 45° angle in the direction of the muscle fibres. Moreover, skin temperature was recorded next to the muscle temperature probe using a skin thermistor (Ellab Ltd, Copenhagen, Denmark). The temperature from both thermistors was continuously recorded with a Medical Prevision Thermometer (DM 852, Ellab Ltd, Copenhagen, Denmark). Covered ice packs were used to cool the muscle by ~4 °C degrees from the control temperature and a heat lamp was used to warm the muscle by ~4 °C degrees from the control temperature. Both the ice pack and the heat lamp covered the entire length of the tibialis anterior muscle. Muscle temperature was continuously monitored ensuring consistent temperatures during each contraction.

Experimental procedures

Subjects were in a seated position with the foot of the dominant leg attached to a footplate with ankle angle set at 90° and knee angle at 120°. The foot was secured into the footplate using a metal brace and a foot mould. This allowed for isometric dorsi-flexion of the foot. The signal from a load cell was amplified in the bandwidth

0-100 Hz (force amplifier, Aalborg University, Aalborg, Denmark) and sampled at 10000 Hz.

Following placement of the sensors and electrodes, subjects performed 3 × 5 s maximal isometric contractions (MVC) of the dorsi-flexors with 3 min rest in between under control temperature condition only. MVC was not measured at the other temperatures in order to prevent movement of the intramuscular EMG electrodes between conditions. Previous studies, including results from chapter 3, have reported no change in MVC with increased (Stewart et al. 2003, Thornley et al. 2003) or decreased (Thornley et al. 2003) muscle temperature. Verbal encouragement to exert maximal force was given to all subjects. The maximum torque obtained from the 3 trials was used to define relative submaximal forces. Force fluctuations were assessed during submaximal contractions at the three muscle temperatures. The control temperature was followed by cooling and warming in randomized order. Three 30 s long contractions at 5, 10, and 15 % MVC, separated by 3 min rest, were performed at each temperature. The target force output was displayed on a PC monitor located 1 m in front of the subject with the gain adjusted to view ±10% of the target force value on a 20 cm high display. Subjects were requested to match the actual force output as closely as possible to the target force for the full duration of the trial. Increasing or decreasing temperature took approximately 30 min allowing a full recovery between test conditions.

Data analysis

Data were analysed off line with Matlab (The MathWorks, Natick, MA). Each extracted variable was computed over 1 s signal epochs and averaged over 5 s in order to obtain six values during the 30 s contractions. After checking for the absence of any trend in time (see Results), the six values were also averaged. The coefficient of variation (CofV) of the force fluctuations was calculated as the ratio between standard deviation and mean force in each 1 s epoch and expressed in percentage. Since the energy of the force fluctuations signal is distributed in a frequency bandwidth smaller than 12 Hz for isometric contraction at forces <20% MVC (Vaillancourt and Newell 2003), frequency analysis of the force signal was performed using Fast Fourier Transform ($P(f)=|x(f)|^2$) and split into three sub- bands: 0-3 Hz (low frequency band), 4-6 Hz (middle frequency band), and 8-12 Hz (high frequency band) (Kouzaki et al. 2004). After removal of the mean value, the power spectrum was estimated from the force signal with the periodogram estimator (an example of the power spectrum is given in figure 6.1 below) and the relative power in the three bands was computed as the percent ratio between the integral of the power spectrum in each band and the integral of the power spectrum between 0-12 Hz. The periodogram was computed from the same epochs used for CofV, with rectangular window and no window overlapping.

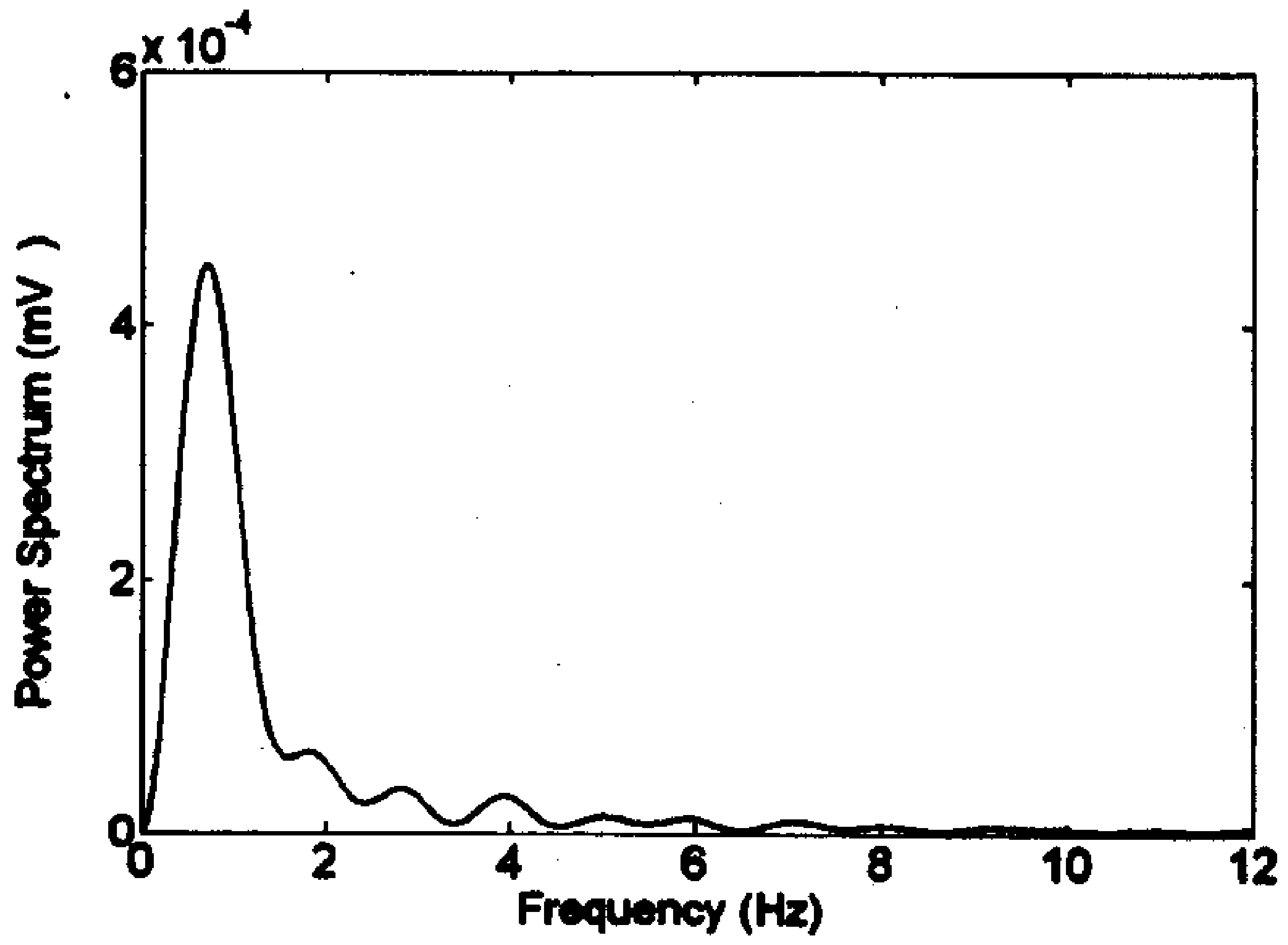


Figure 6.1. Power spectrum of the force signal for a young subject performing a 10%MVC contraction during the control temperature condition.

The intramuscular EMG signals were decomposed using a technique based on a segmentation phase by an amplitude threshold and a classification based on temporal template matching. An example of this matching is given below in figure 6.2 whereby similar motor units are shown to be superimposed. This algorithm has been previously described by Farina et al. (2002a). For each subject and each force level, one motor unit which could be clearly identified for the three temperatures, at the same force level, was selected for statistical analysis. This led to three motor units analysed per subject. Discharge rate and inter-pulse interval variability were computed from the estimated times of occurrence of the action potentials. Inter-pulse interval variability was computed as the ratio between standard deviation of the inter-pulse interval and mean inter-pulse interval and expressed in percentage.

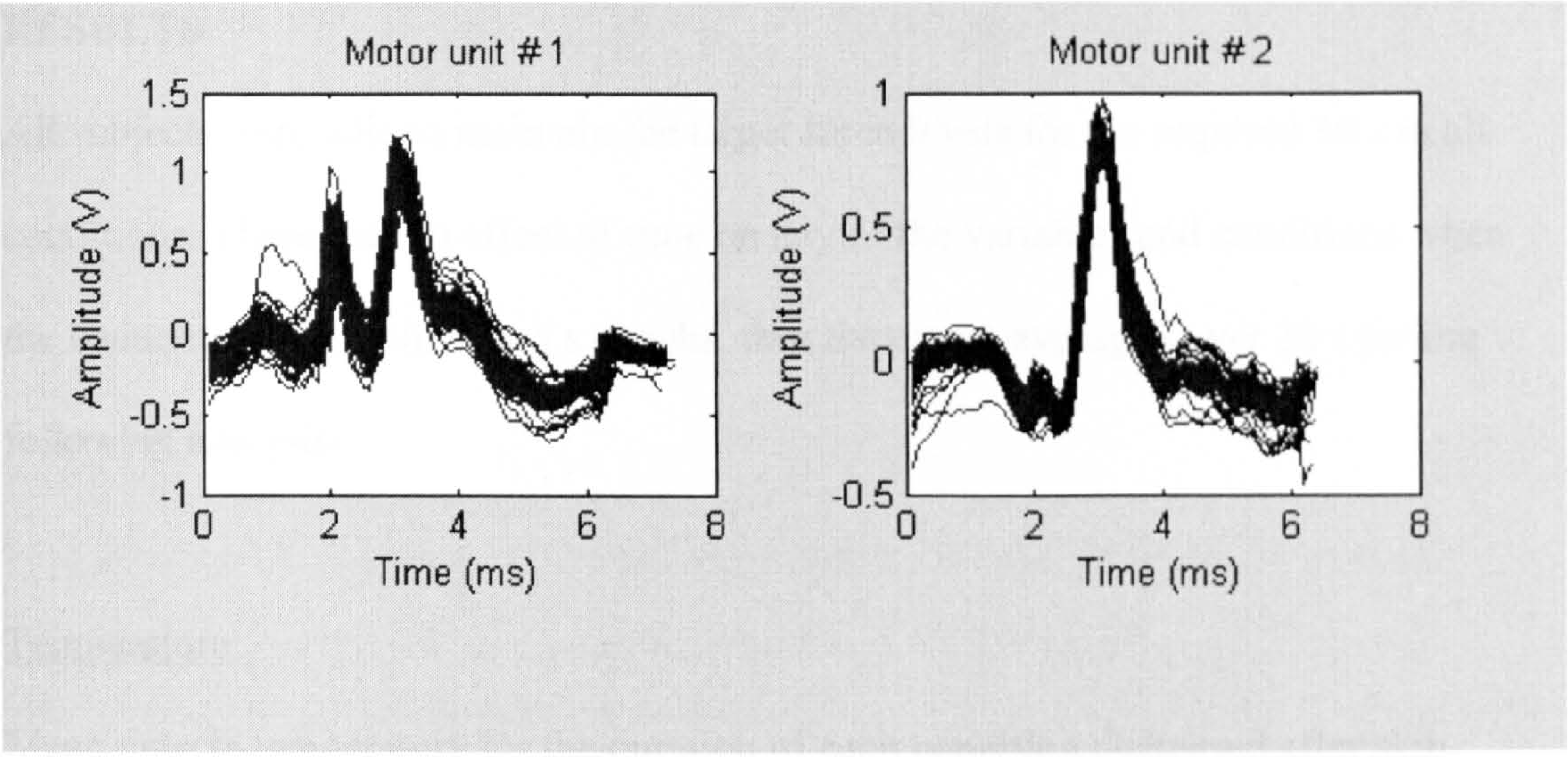


Figure 6.2. An example of the identification of single motorunits, decomposed using a classification based on temporal template matching.

Statistical analysis

Data were analysed with three-way mixed model ANOVA (age × temperature × force level). In addition, two-way (age × time) ANOVA was performed to exclude the presence of changes over time in the analysed variables. An alpha level of 0.05 was used for all statistical comparisons and post-hoc comparisons (Student-Newman-Keuls (SNK)) were performed when the ANOVA was significant. This analysis was repeated for CofV and each of the frequency bands as well as for muscle and skin temperature. For the discharge rate and inter-pulse interval variability of the selected motor units, a two-way mixed model ANOVA (age × temperature) was performed for each force level due to different motor units being analysed at each force level. Differences in the MVC between the groups were analysed using a Student's *t*-test. Data are given as mean ± standard error (SE) unless otherwise indicated.

RESULTS

All subjects were able to maintain the target force levels for the required 30 s in all conditions. There was no effect of time on any of the variables and conditions when the contraction was split into 5 s epochs, thus data were averaged over 30 s for the following analysis.

Temperature

Mean muscle temperature for the duration of each condition decreased after skin cooling by 4.3 ± 0.3 °C and 3.8 ± 0.7 °C (different with respect to control temperature, SNK: $P < 0.001$) and increased with skin warming by 3.9 ± 0.3 °C and 4.0 ± 0.4 °C (different with respect to control temperature, SNK: $P < 0.001$) for the young and older subjects, respectively. Skin temperature decreased by 6.1 ± 0.6 °C and 7.8 ± 0.8 °C (SNK: $P < 0.001$) with cooling and increased by 7.5 ± 0.8 °C and 6.9 ± 0.9 °C (SNK: $P < 0.001$) with warming for the younger and older subjects, respectively. There was no difference in either muscle or skin temperature between the young and older groups and no interaction between age and temperature (Table 6.1).

		Cold	Control	Warm
T_m (°C)	Young	29.5 ± 0.4*	33.2 ± 0.2	37.4 ± 0.2*
	Older	30.4 ± 0.7*	34.3 ± 0.4	38.2 ± 0.1*
T_{sk} (°C)	Young	22.9 ± 0.9*	28.6 ± 0.6	36.1 ± 1.0*
	Older	20.7 ± 2.1*	29.2 ± 0.6	36.8 ± 1.3*

Data are means ± SE; n= 15 young, 11 older. T_m= muscle temperature, T_{sk}= skin temperature.

*Condition significantly different from control condition (Student- Newman-Keuls; $P < 0.001$).

Table 6.1. Mean muscle and skin temperature for the young and older subjects during the cold, control and warm conditions (mean temperature for the duration of each condition).

MVC

MVC for the young subjects (182.7 ± 8.6 N) was greater compared to the older subjects (63.5 ± 3.6 N) (*t*-test: $P < 0.0001$).

Coefficient of variation of force fluctuations

A representative example of the force fluctuation at 15% MVC for both the young and older subjects at under cold, control and warm temperature conditions is given in figure 6.3. It should be noted that the recording started after the subject reached the target force level (approx 3 seconds). The figures display the target force line with ± 20% of this value to allow comparison between the recordings due to the differing absolute target forces.

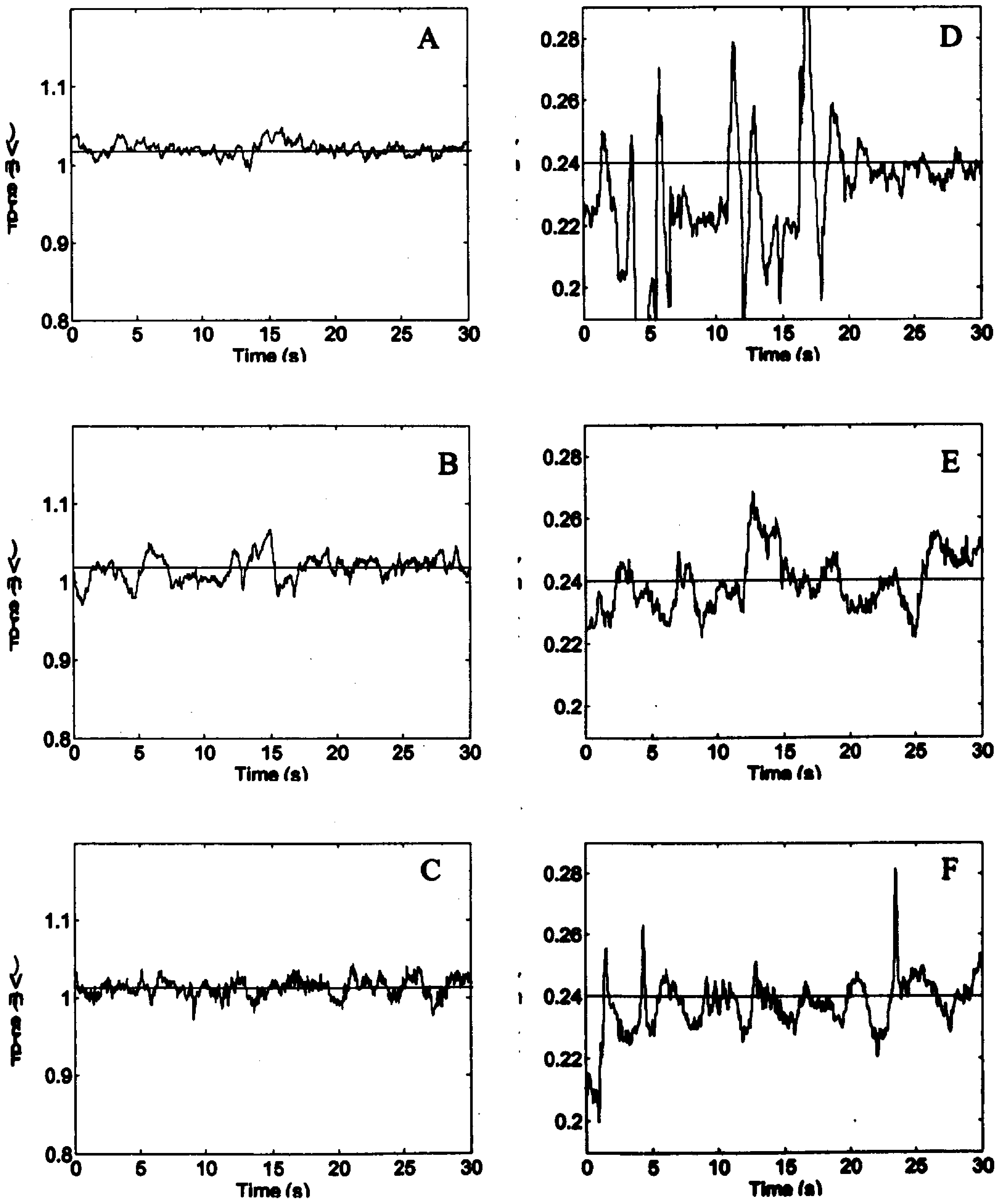
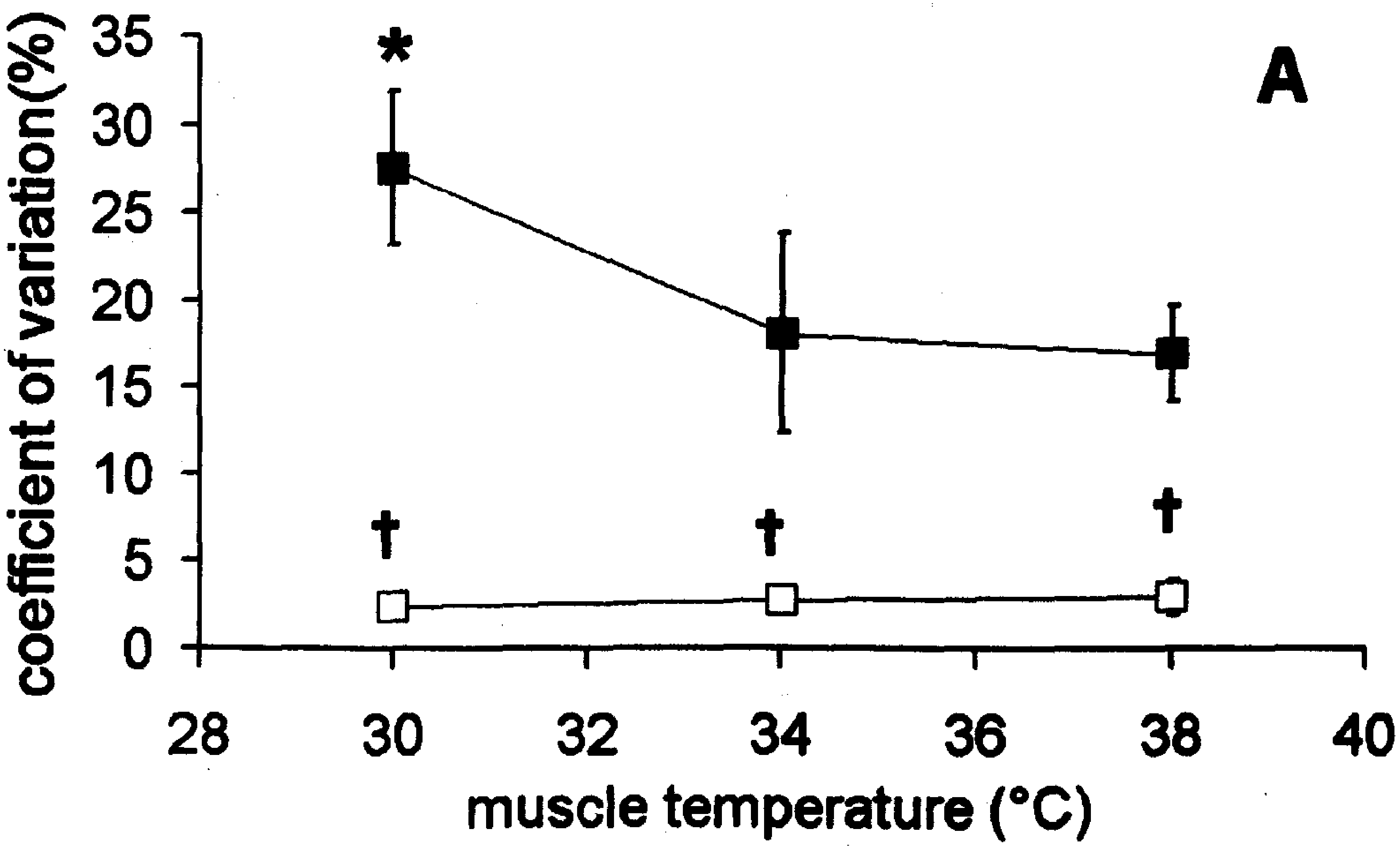


Fig 6.3. Example of force fluctuation recorded during the 15% maximal voluntary contraction (MVC) trial. The subject was provided with visual feedback and attempted to maintain the actual force output as close as possible to the target force for the 30s duration. Figures are normalised to show ± 20% of target force. Data are from one young and one older subject whose data best represent the group data; A: young, cold condition, B: young, control condition, C: young, warm condition, D: older, cold condition, E: older, control condition, F: older, warm condition.

CofV of force depended on the group (ANOVA: P<0.001), with the older group showing higher CofV than the younger subjects (Figures 6.4). In addition, there was a significant interaction between age and temperature (ANOVA: P< 0.001). For the younger subjects, CofV did not vary with temperature, whereas for the older subjects CofV was higher in the cooling condition compared to control and warm (SNK: P < 0.001).



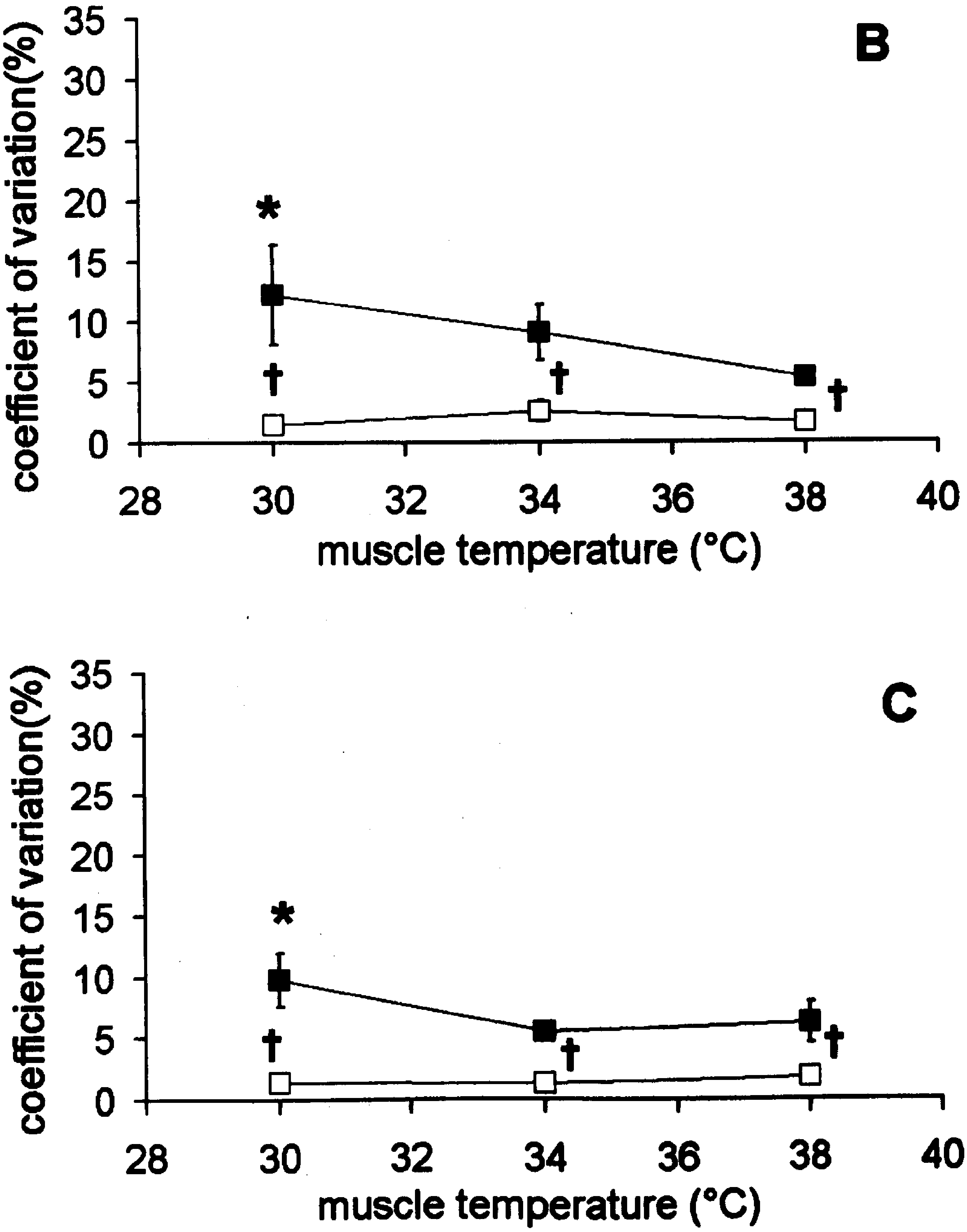
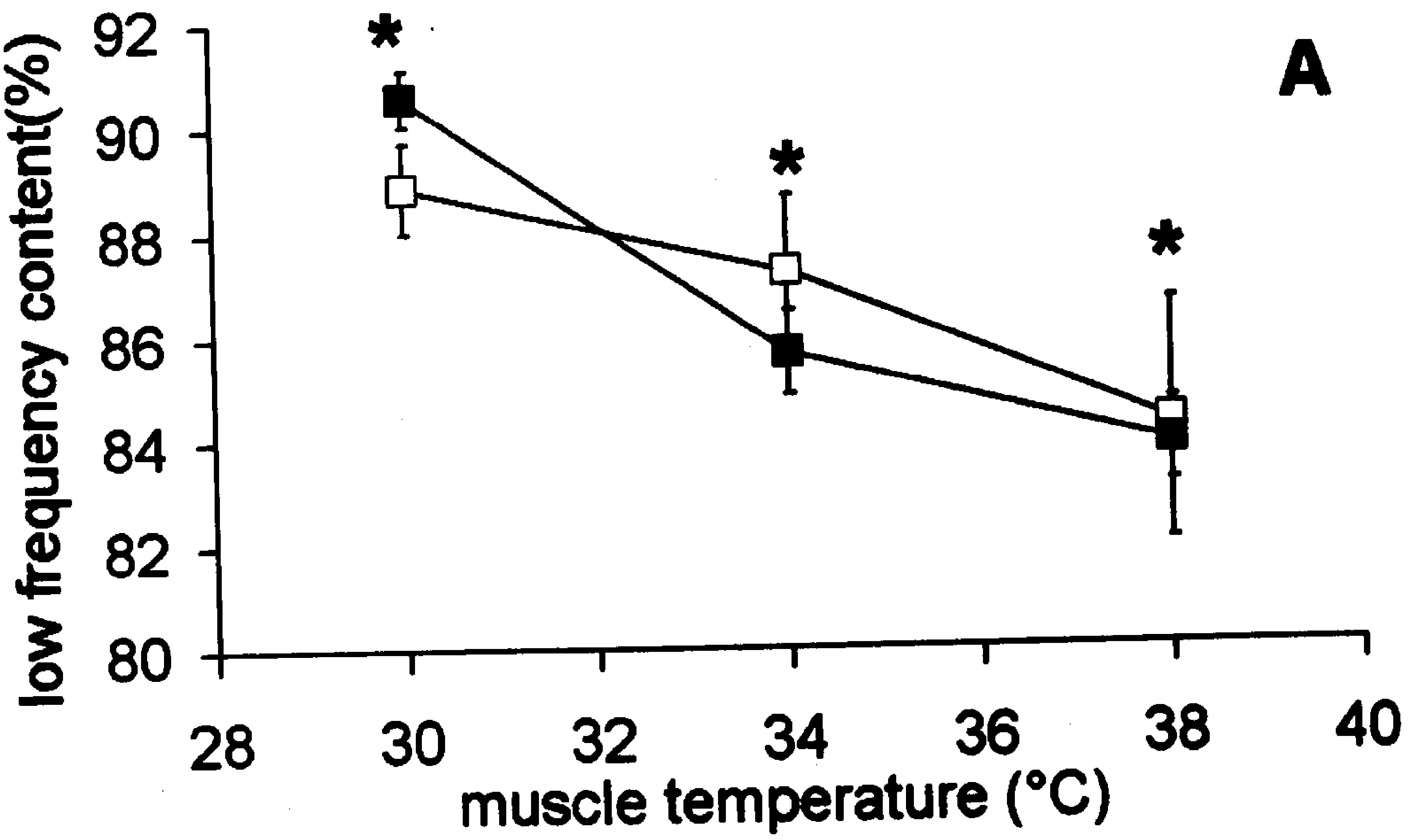


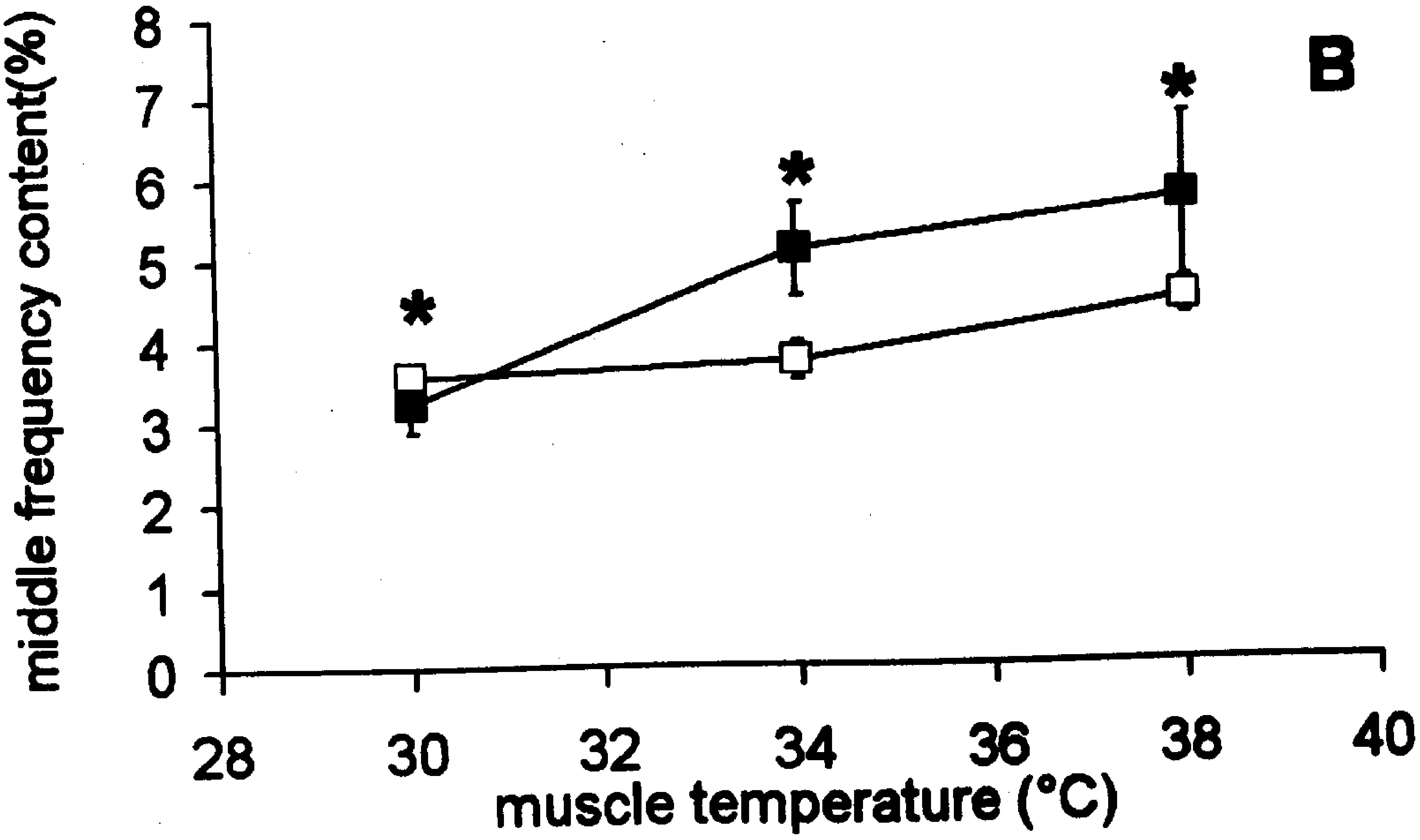
Figure 6.4. Coefficient of variation (CofV) (mean ± SE) of force fluctuations as a function of temperature (cold, control, and warm) for the young (-□-) and the older group (-■-) (A: 5% MVC, B: 10% MVC, C: 15% MVC). * denotes significantly different from control and warm ($P < 0.01$). † denotes significantly different with respect to older group ($P < 0.01$).

There was a significant interaction between contraction force level and age (ANOVA: $P < 0.001$). Force did not affect CofV in the younger subjects whereas CofV decreased with increasing force in the older group (SNK: $P < 0.05$).

Frequency analysis of force fluctuations

The percent of power in the low frequency band depended only on temperature (ANOVA: $P < 0.001$; Figure 6.5A). Cooling increased and warming decreased the power at low frequencies compared to the control condition (SNK: $P < 0.01$) (Figure 6.5A). The relative power in the middle frequency band depended on temperature (ANOVA: $P < 0.001$), decreasing with cooling (SNK: $P < 0.05$) and increasing with warming compared to control (SNK: $P < 0.05$) (Figure 6.5B). The power in the high frequency band was larger in the young compared to the older subjects (ANOVA: $P < 0.01$). The high-frequency band was affected by temperature only in the younger group, where cooling decreased the relative power from 2.8 ± 0.4 % to 1.9 ± 0.1 % compared to control (SNK: $P < 0.05$), while warming increased relative power to 3.9 ± 0.4 % (SNK: $P < 0.001$). In contrast, the older subjects showed no effect of temperature on the high frequency band (Figure 6.5C).


A
low frequency content(%)
92
90
88
86
84
82
80
28
30
32
34
36
38
40
muscle temperature (°C)
*
*
*


B
middle frequency content(%)
8
7
6
5
4
3
2
1
0
28
30
32
34
36
38
40
muscle temperature (°C)
*
*
*

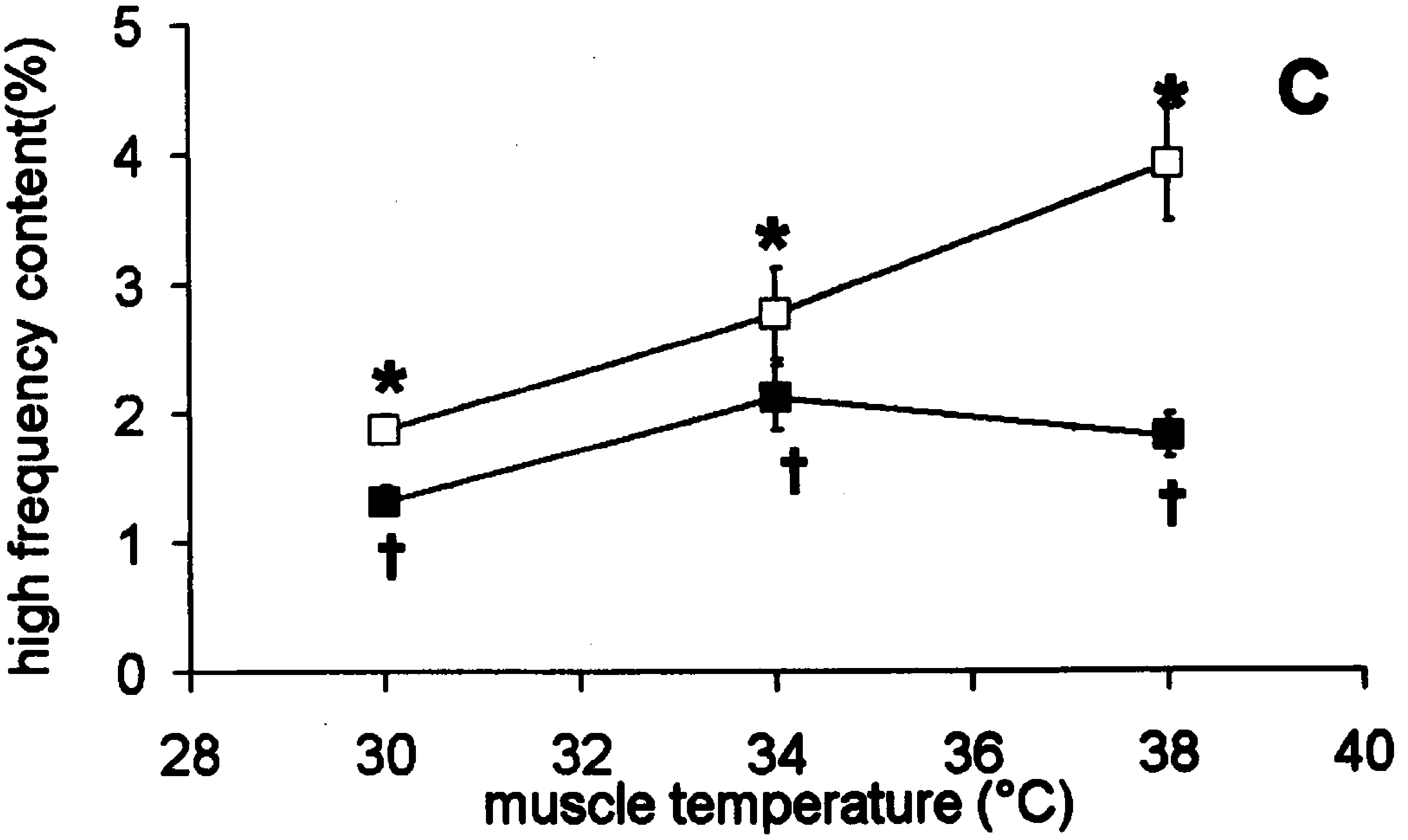


Figure 6.5. Frequency analysis of force fluctuations. Relative power (mean ± SE) in the low frequency (A), middle frequency (B), and high frequency (C) band as a function of temperature (cold, control, and warm) for the young (-□-) and the older group (-■-). Data presented are the mean of all contraction intensities * denotes significantly different from all other temperature conditions ($P < 0.05$) (A and B both young and older group; C young group only). † denotes significantly different with respect to older group ($P < 0.05$).

Motor unit discharge characteristics

Discharge rate of the selected motor units (mean over the three temperatures and the two groups: 5% MVC: 9.7 ± 0.3 pps; 10% MVC: 10.3 ± 0.3 pps; 15% MVC: 10.6 ± 0.2 pulses per second) and inter-pulse interval variability (5% MVC: 22.7 ± 1.3 %; 10% MVC: 23.5 ± 1.3; 15% MVC: 26.2 ± 1.0 %) were not affected by either age or temperature.

DISCUSSION

Young and older women performed a low-force isometric contraction under cooled, control, and warmed muscle temperature conditions. The two groups responded differently to cooling, with the older individuals increasing the force fluctuations and the younger subjects showing no change. Frequency analysis of the force fluctuations also revealed different responses of the two groups, with no sensitivity of the high-frequency band to temperature in the older, as opposed to the young subjects.

Coefficient of variation of force and age

CofV of force output was higher in the older group in comparison to young subjects, in agreement with previous studies which analysed different muscles. A two-fold increase in the variation of force fluctuations in the older group was previously observed when the finger abductors were considered (Galganski et al. 1993, Laidlaw et al. 2000, Vaillancourt et al. 2003). In the present study the increase was almost 4-fold at 5% MVC and was reduced to approximately 3-fold at 10 and 15% MVC under control conditions. The larger difference between groups compared to previous studies may be attributed to the different muscles analysed as the effects of ageing on neuromuscular control are more apparent in the lower limbs (Frontera et al. 1991, Lynch et al. 1999). The tibialis anterior is an important postural muscle, thus the greater variability in force in the older compared to young subjects may partly explain the reduced postural stability of older individuals (Maki and McIlroy 1996, Prieto et al. 1996). The difference between the groups varied with the force level. The difference was greatest at 5% MVC and lowest at 15% MVC, in agreement with previous results (Galganski et al. 1993, Tracy and Enoka 2002, Vaillancourt et al. 2003).

Coefficient of variation of force and temperature

Temperature affected the degree of force fluctuations differently in the two groups. Differential response to cooling has been previously observed between patient groups. Cooper et al. (2000) reported that patients with essential tremor benefited from cooling, whereas Parkinson disease patients benefited from warming when completing manual dexterity tests. In the present study, the variability of force fluctuations of the young subjects was not affected by either warming or cooling. This finding adds to the lack of consensus regarding the effects of cooling on fine motor control in healthy young subjects, as previous findings are conflicting (Lakie et al. 1994, Havenith et al. 1995, Cheung et al. 2003, Feys et al. 2005). These studies present, however, methodological differences that make comparison of findings difficult. All of them considered only the cooling of forearm and hand reporting only skin and not muscle temperature. In addition, both males and females were included in previous studies with no comparisons between the genders. The present study, for the first time, studied the effects of temperature on force fluctuations of the lower limb, monitoring both muscle and skin temperature in females. In these conditions, warming had no effect on the degree of force fluctuations in either group. The increase in force fluctuations with cooling in the older subjects reflects a diminished ability with ageing to maintain successful fine control of the lower limbs following a change in the external environment. Moreover, from a functional and clinical perspective the result suggest that for successful performance of tasks requiring fine motor control, it is important that older individuals live in a warm environment preventing a below normal muscle temperature.

Motor unit discharge pattern and force fluctuations

The low frequency band of the force fluctuations signal reflects the contribution from motor unit discharge properties (Allum et al. 1978, Marsden 1978). Young and older individuals had similar low frequency content, suggesting that the statistical properties of motor unit discharge patterns were similar in the two groups. Direct analysis of single motor unit activities confirmed this conclusion. Both the discharge rate and inter-pulse interval variability were the same for the two groups, in agreement with previous results (Galganski et al. 1993, Roos et al. 1997, Vaillancourt et al. 2003). This indicates that the mechanisms determining the discharge characteristics of the motor units were preserved in the older individuals performing low-force isometric contractions. It had however to be noted that only one motor unit per contraction force was analysed in this study. This was due to difficulties in detecting more than one motor unit at all temperatures. The sample of analysed motor unit was thus rather small and this may have masked differences between groups and temperatures.

Remodelling of the motor unit pool is a known consequence of ageing. This phenomenon includes a decrease in the total number of motor units, a shift in the fibre type ratio, with older individuals showing a higher type I to type II ratio and an augmented innervation ratio of the slow twitch fibres (Brown 1972, Larsson et al., 1978, Kanda and Hashizume 1989). Although not measured in this study, it is unlikely that changes in muscle fibre contractile properties were responsible for differential responses between groups and with cooling in the older group. Although both age (Galganski et al. 1993) and temperature (Davies et al. 1982, Farina et al. 2005) have been shown to affect the amplitude of motor unit twitch force, computer simulations revealed that motor unit twitch tension has negligible effect on force fluctuations (Taylor et al. 2002). This is supported by the observation that a strength training program may decrease force fluctuations in older individuals while having no effect on low-threshold motor unit twitch torque amplitude (Keen et al. 1994). In addition, cooling decreases twitch torque and increases its duration (Davies et al. 1982) which should reduce rather than increase force fluctuations, contrary to the observations in the older group.

Stretch reflex loop and force fluctuations

Force fluctuations are influenced by the peripheral feedback loop. The long and short latency stretch reflex are thought to be responsible for the middle (4-6 Hz) and high (8-12 Hz) frequency bands of force fluctuations (Marsden 1978). Both age and temperature are known to affect the delay of the stretch reflex loop. In the present study, the relative power in the middle frequency band increased with increasing temperature in both groups. The relative power in the high frequency band, however, was larger in the young compared to the older subjects with decreased (increased) power with cooling (warming).

Older individuals have a slower reflex response than their younger counterparts, as measured from the H reflex (Chapter 4, Kido et al. 2004). This factor, in addition to a decreased number of muscle spindles (Swash and Fox 1972) and decreased sensitivity of the spindles (Corden and Lippold 1996), could explain the lower power in the high frequency band in older subjects compared to the young. The reflex loop is also temperature sensitive, with a quickening of the reflex onset with increasing temperature described in chapter 4. This is in agreement with the increase in the high frequency power with increasing temperature in the young group. However, temperature did not affect the power in the high frequency band in the older subjects, suggesting that the reflex loop in the older group is not as sensitive to temperature as that of the young group. The lack of sensitivity of the reflex loop to temperature may alter the timing of the feedback. It has been speculated that younger individuals have the ability to desynchronise the central reflex mechanism preventing synchronisation of reflex and cortical oscillations (Baker et al. 2003). It is possible that ageing reduces this mechanism with a reduced adaptation of the reflex loop to changed muscle condition, e.g., induced by temperature. This explanation can not be fully proven from the results of the present study. However, these results suggest a different response of the stretch reflex loop to temperature in the two groups which may underline partial lack of adaptation of the system to changed muscle conditions with ageing. This finding is supported by the results of chapter 4, whereby younger subjects modulated the excitability of the stretch reflex loop following cooling, as seen through an increase in the spinal reflex excitability, measured by the H_{max}/M_{max} ratio of the H reflex, while older individuals were seen to be to have a less adaptable spinal reflex excitability with a consistent level of excitability irrespective of muscle temperature. Finally, the role of the Golgi tendon organs (GTOs) should also be considered for interpreting the present results. The GTOs appear to be sensitive to all degrees of change in muscle tension including changes generated by just 1 or 2 single muscle fibres (Reinking et al. 1975). Therefore, autogenic inhibition and possibly excitation would be expected in response to force fluctuations during isometric contraction.

Conclusion

Young and older individuals responded differently to changes in muscle temperature when performing a low-force isometric contraction. Cooling increased force fluctuations in the older but not in the young subjects. Temperature has thus a different impact in fine motor control in young and older subjects.

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CHAPTER 7

GENERAL DISCUSSON

The aim of this thesis was to investigate the effects of temperature, both localised cooling and warming, on neuromuscular control in young and older individuals. To this end, the main findings concerned the differing response to cooling, but not warming, between young and older participants during maximal isokinetic contractions, fine motor control and spinal reflex excitability response.

The first study (chapter 3) investigated the effects of cooling and warming on maximal isometric and isokinetic muscle contractions. As expected, neither cooling nor warming affected the torque output during the isometric task. However, torque produced during an isokinetic task was reduced following cooling in the young subjects only. Warming had no effect on the isokinetic torque output in either group. Muscle fibre conduction velocity (MFCV) was higher in the warm condition compared to the cold condition in both groups, suggesting that the muscle fibre membrane responds similarly in the conduction of the action potential following temperature change irrespective of age.

The second study (chapter 4) looked at the effect of cooling and warming on the spinal reflex excitability, measured as the H_{max}/M_{max} ratio. Cooling increased this ratio in the young subjects only, with older subjects showing no such modulation. Warming had no effect on the ratio in either group. The reflex onset latency was increased with cooling and decreased with warming in both groups, supporting the finding from study 1 (Chapter 3) which suggested that the conduction of the action potential along the muscle fibres is affected similarly by temperature in both groups.

In this study, in fact, it appears that the conduction of the action potential along the nerve is affected similarly by temperature in both groups.

The third study (chapter 5) followed on from the findings of the second study (chapter 4). It was hypothesised that the slowing of a reflex response with cooling and a quickening following warming would affect the precision of response of the proprioceptive system when performing a balance task, as detection and response to sway during standing are vital to the maintenance of successful postural control. The results of the study, however, found that postural sway was not affected by either cooling or warming of the legs in either the young or the older group.

The final study (chapter 6) looked at the effects of warming and cooling on fine motor control. Subjects were asked to perform low level contractions (5/ 10/ 15 % maximal voluntary contraction (MVC)) as precisely as possibly. The force fluctuation during the contraction was unaffected by temperature, either cooling or warming, in the young subjects. In the older subjects, however, following cooling the force fluctuation was increased. When the power spectrum of the fluctuation was analysed it was found that the young subjects, but not the older subjects, decreased the amount of power in the high frequency band (8-12 Hz) following cooling, which was thought to represent an increase in the short latency stretch reflex (Marsden 1978). In the discussion of study 4 (chapter 6), it was speculated that young subjects were able to maintain a consistent level of force fluctuation following cooling by reducing the amount of stretch reflex activity. This fits with the findings of study 2 (chapter 4), as the results of study 2 showed that young subjects had the ability to modulate spinal reflex excitation levels following cooling, whereas older subjects did not show such adaptability. However, this conflicts with the speculation in the discussion of study 2, which made the case that the increase in the spinal reflex excitability was due to an increase in muscle spindle discharge in the secondary afferent of the muscle spindle as proposed by Chapman et al. (1979), and Michalski and Séguin (1975).

The increase in the force fluctuation during fine motor control following cooling of the tibialis anterior muscle in older subjects would be expected to influence the postural control of the older group, since balance is about fine responses to small fluctuations; however, as seen in study 3 (chapter 5), this did not transpire.

Localised cooling and warming, as opposed to whole body cooling and warming, was used in the present studies. It is acknowledged that a change in environmental conditions, such as the temperature of a room, may affect the whole body as opposed to just the limbs, however, it was felt that as the present study was looking at the neuromuscular response of temperature, by specifically changing the temperature of the limb or muscle group only, this would eliminate the concurrent responses that a change in body temperature would bring, such as a change in whole body blood flow and patient discomfort. It was also important to maintain a consistent core temperature during the cooling experiments in order to prevent a shivering response. An infrared tympanic thermometer was used to monitor changes in core temperature. This temperature is only an estimate of core temperature; however, this was chosen for the present studies since the more accurate methods of measuring either rectal or oesophageal temperature are invasive and uncomfortable, especially taking into consideration the duration of the experiments and the comfort of the older participants. One of the biggest criticisms of infrared tympanic thermometer is that it is affected by environmental temperature (Hansen et al. 1996). With respect to the present studies, however, this was not an issue as room temperature was kept constant. Additionally, previous data from our laboratory have shown a linear relationship between the temperature measured with an infrared tympanic thermometer and the rectal temperature (Stewart et al. 2003).

Future studies using whole body warming and cooling would provide interesting practical information on the performance parameters studied in the present thesis, such as fine and gross motor control. On the other end, these would not enable the identification of the mechanisms responsible for any potential outcome changes.

In the first study presented in the thesis (chapter 3), maximal strength was measured during voluntary contractions. This may be criticised by some investigators who have shown, by twitch interpolation techniques, that older adults were not able to maximally activate a muscle or muscle group, thus underestimating the measure of maximal muscle strength (Harridge et al. 1999b, Yue et al. 1999, Bilodeau et al. 2001a). In contrast, other investigators have demonstrated that a superimposed stimulus added little or nothing to the voluntary force produced by older individuals (Connelly et al. 1999, De Serres and Enoka 1998, Jakobi and Rice 2002, Kent-Braun and Ng 1999, Phillips et al. 1992, Roos et al. 1999, Scaglioni et al. 2002). Jakobi and Rice (2002) suggest that the possibility of underestimating the "real" maximum should be discounted if at least one session of familiarisation is practised (Jakobi and Rice 2002). This was strictly adhered to with all subjects being fully familiarised with all tasks 5-7 days prior to the experimental session.

In the first study (chapter 3), MVC was, as expected, unaltered by cooling and warming even in the older subjects. There is no indication, therefore, from these finding of a change in the ability to maximally activate the muscle group under different muscle temperature conditions.

It has been suggested that temperature affects the velocity component of voluntary muscle contractions to a greater extent than the force component, as the amount of tension per cross bridge remains the same at different temperatures, and that it is the population shift in the number of cross bridges that gives rise to the temperature effect on force output (Coupland et al. 2001, Wang and Kawai 2001, Zhao and Kawai 1994). The second study showed that torque was reduced following cooling during the dynamic contractions suggesting a leftward shift in the force- velocity curve described by Hill (1938). This is in agreement to the results of Sargeant (1987), who reported a leftward shift in the curve during higher velocity contractions following cooling. Relatively low velocity isokinetic contractions were used in study 1 (chapter 3) as opposed to high velocity contractions, which have been described as being more temperature sensitive (Sargeant et al. 1987). Although movements of day to day living occur at low velocity, however, they are not isokinetic. Isotonic contractions are more realistic representations of the day to day tasks where individuals have to work against resistance and overcome speed (Harridge et al.

1999a). Isokinetic contractions were chosen as opposed to isotonic contractions, despite the Biodex dynamometer having an isotonic option, since the movement is not truly isotonic as the force is not constant throughout the entire range of motion, thus making comparisons difficult. However, should this problem be solved, it would be of interest to replicate the first study using isotonic movements, where each individual would be asked to carry out their movements at the optimal combination of load and speed. A mechanical cycle ergometer where a constant load is set would be an example of how this could be done with very high velocity contractions, such as the methods previously described by Gray et al. (2006). As high velocity contractions have been shown to be more temperature sensitive (Sargeant 1987), this protocol may be more sensitive to the effects of temperature on maximal muscle performance of the older individuals, although this would be of little relevance to motor control during day to day tasks.

The surface EMG, utilised in the first study (chapter 3), is used as a method of estimating changes in the recruitment pattern (Basmajian and De Luca 1985) and has been suggested as a method of estimating muscle fibre type proportions (Gerdle et al. 1991, Kupa et al. 1995, Moritani et al. 1985, Wretling et al. 1987, Farina et al. 2004, 2006). However, the findings from the first study displaying the effects of temperature on EMG show that MFCV increases with warming and decreases with cooling, MNF decreases with cooling and RMS is decreased with warming. These findings highlight to the investigators the importance of taking into consideration the ambient temperature and, more specifically, muscle temperature of the subjects. This is especially relevant for studies in which repeated measures span over different seasons.

In study 2 (chapter 4), the H reflex was used as a method of assessing spinal reflex excitability (Schieppati 1987). This is described as the electrically induced equivalent of the mechanically evoked stretch reflex. The benefits of using the H reflex are that changes at the spinal level can be assessed without the influence of changes at receptor level, i.e. the muscle spindle. On the other hand, the stretch reflex assessment is an indicator of what happens in the full circuit, which has more practical relevance as it is the muscle spindle that detects a change in the length of the muscle. The original methods of the second study (chapter 4) included the assessment of the stretch reflex using an identical set up to the H reflex assessment; however, the stretch reflex was evoked by rotating the footplate of the dynamometer by 10° at a velocity of 150°/s in a dorsiflexion direction. This speed was the highest speed obtainable without jerking of the equipment causing antagonist activation. The stretch reflex data were not presented in the thesis, as the identification of the three parts of the reflex (short, medium, and long latency) was not accurate even under control conditions in the young subjects. Identification of the onset of each response (slow, medium and long latency), was attempted using the latencies indicated by previous works (Toft et al. 1989); however when the slowing of the reflex with ageing was compounded with the effects of cooling and warming on the reflex latency, it was found to be impossible to accurately identify the different responses.

Throughout this thesis only females participants were included. Although the relative rates of decline in muscular strength and muscle mass are similar between males and females, females start at a lower absolute strength than males and are therefore likely to reach the critical level for functional ability before males (Skelton et al. 1994). The majority of research investigating the muscle contractile characteristics throughout the menstrual cycle suggest that fluctuations in female reproductive hormones do not affect muscle contractile characteristics including strength (for review see: Janse de Jonge 2003). Nevertheless, where possible, young subjects were requested to attend the laboratory in the follicular phase of the menstrual cycle in attempt to control for potential hormonal influences. However, in some instances (study 4, chapter 6) this was less strictly adhered to due to time constraints and subjects' availability. As all testing sessions were completed in the same day, the effects of the menstrual cycle phase on the between temperature condition comparisons would not be affected.

A decline in the level of many hormones in the older subjects contributes to the factors affecting sarcopenia and neuromuscular control. These hormones include growth hormone (Rudman et al. 1990, Welle et al. 1996a), insulin like growth factor 1 (Butterfield et al. 1997), testosterone (Tenover 1992, Urban et al. 1995) and oestrogen (Phillips et al. 1993, Skelton et al. 1999), but how these changes are related to strength and power is still largely unclear (Short and Nair 1999) making any speculation to their potential role in results of the present studies difficult. However, they cannot be discounted until further understanding of there role in sarcopenia is achieved.

Many studies have reported regional differences in the way muscle strength declines with ageing with the lower body being more affected that the upper body (Candow and Chilibeck 2005, Janssen et al. 2000, Lynch et al. 1999). It would be of value to replicate the protocol of study 4 (chapter 6) on the effects of cooling on fine motor control of the muscles of the upper limbs, for example muscles of the hand, whereby fine control, such as writing, picking up and holding an object, is frequently performed.

CLINICAL AND PRACTICAL IMPLICATIONS

From a clinical perspective, the results of the present study have equivocal messages. While a lack of adaptation at the spinal level was reported in study 2 (chapter 4), it appears that older subjects are less affected than their young counterparts when there is change in muscle temperature during the performance of tasks involving maximal contractions. As mentioned in study 1 (chapter 3), this outcome has both positive and negative practical implications. The original concern was that, should older individuals respond similarly to young individuals with cooling by decreasing the maximal torque production during a dynamic task, then this could put them in danger through lowering the torque output to a level whereby they would be unable to generate enough force to successful complete a functional task, such as rising from a chair or lifting shopping bags. However, as the force generated by the older individuals was found not to be affected by cooling, then they should not be further impaired by a reduction in muscle temperature when in a cold environment. Similarly, despite a slowing of the H reflex response latency and an increase in force fluctuation in the older group, postural stability was not compromised following cooling. On the other hand, young subjects have previously been shown to increase force output during dynamic contractions following warming (Berg and Ekblom 1979, Sargeant 1987), which was not found in the present thesis (first study, chapter 3). Therefore, it was originally hypothesized that muscle warming may have been used as a method to increase the torque output and, therefore, the functional ability of the older subjects. However, the results of the present study denied this hypothesis. In contrast, when looking at fine motor control, which is important for performing low intensity tasks such as writing or holding a cup with liquid, cooling the muscles was found to worsen the performance by increasing the amount of force fluctuation (study 4, chapter 6). Therefore, for the performance outcome of fine motor tasks in older people, it is advised to prevent limb cooling.

Older the subjects used in the present study were healthy individuals with no known neuromuscular disorders, since it was decided not to include the very old or frail individuals, however, even in the healthy older subjects in the present study, differences in the response to cooling were seen when compared to the young subjects in all experiments except the posturography assessment (chapter 5). It would be expected that the lack of response to temperature seen, for example, in force output and H reflex response would also be seen in a much older population, on the other hand, the most significant finding in terms of the effects on day to day living in old individuals was the finding that cooling worsens fine motor control as seen in chapter 6. Should the results be extended to even older individuals it would be expected that a further worsening of fine motor control following cooling would be experienced, possibly to a level whereby many tasks become impossible.

With respect to the young individuals, the findings from the investigations can be extended to an athletic environment, for example, the finding from chapter 3, where torque was seen to be reduced following cooling, reemphasises the importance of not having cold muscles prior to performing short duration, maximal explosive tasks such as weightlifting. In chapters 5 and 6, however, it appears that during postural static tasks, necessary for gymnastic performances, and during fine motor control tasks, such as target shooting, the effects of either cooling or warming on the task is not an issue.

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APPENDIX 1.1: SUBJECTS INFORMATION FOR CHAPTER 2

Subject Information

Effects of altered local temperature on neuromuscular performance

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STUDY OUTLINE

Background: Recent investigations into the effects of ageing on different parameters of the body have revealed that older people demonstrate a reduced ability to respond to changes in the environment such as extreme changes in external temperature. Cooling of the limbs is known to have a detrimental effect on reflex responses which are slowed down. In younger individuals muscle warming is known to have advantageous effects on both muscle strength and power, whereas cooling has detrimental effects on performance. The extent to which altered temperature affects the mobility and therefore the functional ability has of yet not been investigated in older individuals. Do they tend to be more affected than their younger counterparts as with reflex responses?

Aims: From the above rationale it is our aim to assess the effect of both elevated and reduced muscle temperature on the strength and power of both young and older females. In addition, the underlying mechanisms responsible for any changes will be investigated.

Relevance of research: The information gained from this study will be of paramount importance since the proportion of older adults is continuously growing in our society. An increased knowledge of the ageing processes could allow a better development of preventative strategies to reduce the incidence of functional incapacities and help maintain independence.

<u>What you get out of this:</u> You are likely to find the experience of being a subject for scientific research very interesting and your knowledge of the ageing process of your body will be greatly increased. Testing will be carried out within an informal-atmosphere. To enhance your enjoyment of the experience drinks and snacks will be provided after the testing is complete. Where necessary, taxis will be provided to and from the University campus. Most of all you will have the satisfaction of knowing you have done your bit for research into ageing.

<u>Possible risks and discomfort:</u> As we will be measuring muscle temperature a thin, flexible needle will be inserted into your leg which may cause slight discomfort. To minimise the risk of discomfort only persons trained and qualified in this technique will insert the needle. Testing will be stopped and the needle removed at any point should you request. After a short time (usually a couple of minutes) you will be unaware that the needle is in place.

<u>Subject selection:</u> You will be one of 30 female subjects who will be assessed in this study (15 young subjects, 15 older subjects). Young subjects will be between the ages of 18-28 years and older subjects will be between the ages of 65-75 years. Heart activity will be recorded using an electrocardiogram and analysed by a physician for those young subjects who are not training regularly. Young subjects should be healthy with no known neuromuscular disorders and should not be exercising more than twice a week. Older subjects should be in good health, this will be confirmed prior to testing with a medical questionnaire and a recording of the heart activity will be performed using an electrocardiogram to ensure normality. Before testing commences you will be again advised of all procedures and will be asked to give signed consent. **You will be free to withdraw at any stage without giving reason.**

Methods: You will attend the laboratory situated at the Jordanhill campus of the University of Strathclyde on 2 separate occasions- one familiarisation session and one testing session.

VISIT 1- Familiarisation:

- This will last about 1.5 hours. Shorts, T- shirt and trainers/ soft shoes are required.
- The familiarisation session will commence at least 7 days before the testing session.
- Electrocardiogram will be recorded and analysed by a physician and medical details will be discussed and a questionnaire completed to ensure suitability to the tests. Consent forms will be completed.
- All subjects will receive a verbal explanation of all procedures including a demonstration and familiarisation of all procedures.

VISIT 2: Testing Session

- This will take around 4.5 hours. Shorts, T shirt and trainers/ soft shoes are again requested.
- To control for hormonal influences of the menstrual cycle young subjects will be requested to complete the testing session within the first two weeks of the menstrual cycle after the onset of menses.
- Tests will commence in the morning. Activity levels should be kept to a minimum before testing. You are requested to refrain from caffeine and alcohol ingestion 24 hours before the test.
- Height and weight will be measured. Skinfold measurement (thickness of the skin) will be taken from the thigh. This is a pain free procedure using specialised calipers.
- The testing session will consist of trials with resting muscle temperature, increased muscle temperature and reduced muscle temperature.
- Prior to the testing session a flexible needle (used to measure muscle temperature)

is inserted 1cm below the layer of skin in the thigh. Skin thermistors (used to measure skin temperature) are attached (on top of the skin) to the front and back of the thigh. Body temperature will be measured using an infrared beam into the ear (similar to the one use to monitor the presence of fever).

- Surface electrodes will be placed front and back of the thigh. These are self adhesive strips which are attached to the skin. These record the electrical activity of the muscle and are totally painless.
- The testing session consists of a series of maximum leg extension exercises. This is to test of the strength of your thigh muscles, whereby you will be asked to push against resistances of different weights. The machine used is similar to the machines seen in modern gyms but adapted to each individual physical capability. The testing session will be repeated for 3 different muscle temperatures (normal, cold, warm). Rests will be provided between temperature conditions and whenever requested.
- The muscles at the front of the thigh will be warmed using hot water bottles and cooled using a bag of compressed ice.
- All techniques have been approved by the University of Strathclyde ethics committee.

Confidentiality:

All data will be dealt with under the strictest of guidelines and according to the Data Protection Act. You will be numerically coded and your data will be discussed amongst the lead investigators only.

Further Information:

If you think you might be interested in participating in this study or if you would like any further information please do not hesitate to contact me.

Susan Dewhurst Work no. 0141 950 3109

Email. s.dewhurst@strath.ac.uk

APPENDIX 1.2: SUBJECT INFORMATION FOR CHAPTERS 3 AND 4

Subject Information

Influence of age and muscle temperature on balance control and spinal reflex excitability

Applied Physiology Group, Strathclyde Institute for Biomedical Sciences, University of Strathclyde, Jordanhill Campus, 76 Southbrae Drive, Glasgow, G13 1PP

Investigators

Susan Dewhurst, PhD student; Dr. Giuseppe De Vito, Medical Doctor, Reader of exercise physiology

STUDY OUTLINE

Background: The control of balance is of primary concern within the older population. Poor balance has been identified as a contributor to the greater incidence of falls within this population and injury as a consequence of falling is a primary health concern. One important neuromuscular mechanism identified as being important in balance control is the spinal reflex systems, which partially determines your ability in maintaining or regaining balance. Ageing has been shown to be associated to a worsening of the integrity of this reflex system.-In young subjects this reflex system has been shown to deteriorate when the muscles are cooled, suggesting reduced balance control and therefore an increased likelihood of falls. It is therefore of interest to assess whether this also occurs in the older adult when muscles are cooled and to what extent this further decreased reflex control would have on balance. On the other hand it is also of interest to investigate if an increased muscle temperature could have the potential to improve the reflex response when responding to situations of instability, therefore, allowing for more efficient balance control.

Aims: From the above rationale it is our aims to assess the effects of both elevated and reduced muscle temperature on balance control and spinal reflex responses in young and older females.

Relevance of research: The information gained from this study will be of paramount importance since the proportion of older adults is continuously growing in our society and an augmented knowledge in this sensitive area could allow a better development of preventative strategies to reduce the incidence of falls and consequent injuries in this population.

What you get out of this: You are likely to find the experience of being a subject for scientific research very interesting and your knowledge of the ageing process of your body will be greatly increased. Testing will be carried out within an informal-atmosphere. To enhance your enjoyment of the experience drinks and snacks will be provided after the testing is complete. Older subjects will be supplied with a T- shirt and a skirt for the duration of the test and taxis will be provided to and from the University campus. Most of all you will have the satisfaction of knowing you have done your bit for research into ageing.

Possible risks and discomfort: As we will be measuring muscle temperature a thin, flexible needle will be inserted into the leg which may cause slight discomfort. To minimise the risk of discomfort only persons trained and qualified in this technique will insert the needle. Testing will be stopped and the needle removed at any point should you request. During the balance assessment if balance is particularly poor then there is slight risk of losing balance and possibly falling. This risk will be minimised by having an investigator at the side of the subject at all times during the balance test to provide support if necessary.

Subject selection: You will be one of 20 female subjects who will be assessed in this study (10 young subjects, 10 older subjects). Young subjects will be between the ages of 18-28 years and older subjects will be between the ages of 65-75 years.

Young subjects should be healthy with no known neuromuscular disorders and should not be exercising more than twice a week. Older subjects should be in good health (this will be confirmed with verbal questioning). Before testing commences you will be again advised of all procedures and will be asked to give signed consent. **You will be free to withdraw at any stage without giving reason.**

Methods: You will attend the laboratory situated in the Scottish School of Sport Studies building on the Jordanhill campus of the University of Strathclyde on 2 separate occasions- one familiarisation session and one testing session.

VISIT 1- Familiarisation (see Diagram p6):

- This will last about 30 minutes. Shorts, T- shirt and trainers required (young subjects), trainers required (older subjects- T-shirt and skirt will be supplied if necessary).
- The familiarisation session will commence at least 7 days before the testing session.
- Medical details will be discussed to ensure suitability to the tests and consent forms will be completed.
- All subjects will receive a verbal explanation of all procedures including a demonstration and familiarisation of all procedures.

VISIT 2: Testing Session (Diagram p6)

- This will take around 5 hours, wearing the clothing detailed in the familiarisation.
- To control for hormonal influences of the menstrual cycle young subjects will be requested to complete the testing session within the first two weeks of the menstrual cycle after the onset of menses.
- Tests will commence in the morning. Activity levels should be kept to a minimum before testing. You are requested to refrain from caffeine and alcohol ingestion 24 hours before the test.

- Height and weight will be measured. Skinfold measures (thickness of the skin) will be taken from 2 sites on the leg. This is a pain free procedure using specialised calipers.
- The testing session will consist of three sets of trials, one with resting muscle temperature (control trial), one with increased muscle temperature and one with reduced muscle temperature
- In the control trial you will sit relaxed for 30minutes while a flexible needle (used to measure muscle temperature) is inserted 1cm below the layer of skin. Skin thermistors (used to measure skin temperature) are attached (on top of the skin) to the upper and lower leg. Body temperature will be measured using an infrared beam into the ear (similar to the one use to monitor the presence of fever).
- Reflex measurements will be taken. The first measurement involves sitting relaxed on customised chair while a short low amplitude current is passed into the nerve at the back of the knee. The second measurement involves resting the foot on a footplate that rotates the ankle so the foot moves up and down.
- Postural assessments will then be completed. Spectacles can be worn if required to help focus on a visual target.
- You will then have a break before the trial is repeated with heated and cooled muscles which will be administered at random.
- Muscle heating and cooling will be done using an electric heated blanket and a cool blanket respectively until the required muscle temperature is achieved.
- All techniques will be approved by the University of Strathclyde ethics committee.

Confidentiality:

All data will be dealt with under the strictest of guidelines and according to the Data Protection Act. You will be numerically coded and your data will be discussed amongst the lead investigators only.

Further Information:

If you think you might be interested in participating in this study or if you would like any further information please do not hesitate to contact me.

Susan Dewhurst	Work no.	0141 950 3753
	Mobile no.	07813991624
	Email.	s.dewhurst@strath.ac.uk

APPENDIX 1.3: SUBJECT INFORMATION FOR CHAPTER 5

Subject Information (English translation)

Effects of temperature on force fluctuations and muscle fibre properties during sustained contractions

Center for Sensory- Motor Interaction (SMI), Department of Health, Science and Technology, Aalborg University, Fr.Bajers Vej 7D3, Aalborg.

Investigators

Susan Dewhurst, PhD student; Associate Professor Dario Farina, PhD; Associate Professor Thomas Graven-Nielsen, PhD

STUDY OUTLINE

Background: Recent investigations into the effects of ageing on different parameters of the body have revealed that older people demonstrate a reduced ability to respond to changes in the environment such as extreme changes in external temperature. In younger individuals muscle warming is known to have advantageous effects on both muscle strength and power, whereas cooling has detrimental effects on the performance of varying tasks. The extent to which altered muscle temperature affects the performance of tasks in older individuals is less clear, however previous studies by the investigators have suggested that performance is less affected by temperature in this group. The reasons for this difference have not yet been investigated.

Aims: From the above rationale it is our aim to investigate the underlying mechanisms responsible for differences in the response to altered temperature between younger and older individuals by looking at what happens to a very small area of the muscle when it produces a very small force for a period of 3 minutes at different muscle temperatures.

Relevance of research: The information gained from this study will be of paramount importance since the proportion of older adults is continuously growing in our society. An increased knowledge of the ageing processes could allow a better development of preventative strategies to reduce the incidence of functional incapacities and help maintain independence.

What you get out of this: You are likely to find the experience of being a subject for scientific research very interesting and your knowledge of the ageing process of your body will be greatly increased. Testing will be carried out within an informal-atmosphere and you will be paid 300 DKK. Most of all you will have the satisfaction of knowing you have done your bit for research into ageing.

Possible risks and discomfort: As we will be measuring muscle temperature a thin, flexible wire will be inserted beneath the skin through a needle. The needle will be removed immediately after the wire is in position. To measure the activity of the muscle very thin wires will be inserted beneath the skin again through a fine needle (again this will be removed immediately after insertion). This process may cause slight discomfort during the incision however once the needles are removed you should be unaware of the wires. To minimise the risk of discomfort only persons trained and qualified in this technique will insert the needle. Testing will be stopped and the wires removed at any point should you request.

At all stages of the experiment a qualified medical doctor will be present.

Subject selection: You will be one of 30 female subjects who will be assessed in this study (15 young subjects, 15 older subjects). Young subjects will be between the ages of 18-28 years and older subjects will be between the ages of 65-75 years. Young subjects should be healthy with no known neuromuscular disorders and should not be exercising more than twice a week. Older subjects should be in good health; this will be confirmed prior to testing with a medical questionnaire which will be checked by a qualified medical doctor. Before testing commences you will be again advised of all procedures and will be asked to give signed consent. **You will be free to withdraw at any stage without giving reason.**

Methods: Prior to visiting the university older subjects will be phoned by a native Danish speaker and will be provided with further details about the visit. You will then be sent out a detailed medical questionnaire in which you will be asked to complete to confirm your health status. If the medical questionnaire is satisfactory (confirmed by a qualified medical doctor in the department), you will attend the laboratory situated in Aalborg University. The details of this visit are detailed below.

  - As it is the muscles of the bottom half of the leg we will be studying, volunteers are requested to wear trouser (or a skirt) that can be comfortably rolled up above the knee. Tights should be avoided or removed.
  - At the time of your appointment you will be met by one of the investigators who will show you to the room in which the testing will take place.
  - All subjects will receive a verbal explanation of all procedures including a demonstration and familiarisation of all procedures.
  - Consent forms will be completed.
- Activity levels should be kept to a minimum before testing. You are requested to refrain from caffeine on the day of test and alcohol ingestion 24 hours before the test.
- Height and weight will be measured.
- The session will consist of trials with resting muscle temperature, increased muscle temperature and reduced muscle temperature.
- Prior to the testing session a flexible wire (used to measure muscle temperature) is inserted below the skin at the muscle of the front of the leg. Skin thermistors (used to measure skin temperature) are attached on top of the skin. This is totally painless. Body temperature will be measured using an infrared beam into the ear (routinely used to monitor the presence of fever).
- Surface electrodes will be placed at the front of the leg. These are self adhesive strips which are attached to the skin. These record the electrical activity of the muscle and are totally painless.

- The testing session consists of you being asked to point your foot upwards pushing against a pad. This will allow us to record the muscle at the front of the leg which is causing this movement. You will be asked to push as hard as possible against the pad for 5 seconds only. For the 3 different muscle temperatures (normal, cold, warm) you will be asked to push against the pad at very low force levels. Rests will be provided between temperature conditions and whenever requested.
- The muscles at the front of the thigh will be warmed using a warm heat lamp and cooled using a bag of compressed ice.
- All techniques have been approved by both Aalborg University and University of Strathclyde ethics committees.
- **At all times there will be a qualified medical doctor and native Danish speaker present.**

Confidentiality:

All data will be dealt with under the strictest of guidelines and according to the Data Protection Act in accordance to both Aalborg University and University of Strathclyde. You will be numerically coded and your data will be discussed amongst the lead investigators only.

Further Information:

If you think you might be interested in participating in this study or if you would like any further information please do not hesitate to contact me.

Susan Dewhurst Office no. 9635 8820
Email. s.dewhurst@strath.ac.uk

Or

Thomas Graven- Nielsen (native Danish speaker)
Office no. 96359832
Email. tgn@smi.aau.dk

PAGE
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APPENDIX 2.2: CONSENT FORM FOR CHAPTER 6

Consent Form (English Translation)

Muscle fibre conduction velocity during sustained contractions with localised warming and cooling.

You are invited to participate in the present study on the effects of temperature on muscle properties in which you will be requested to complete a series of contractions using the muscles at the front of the lower leg. The contractions will be repeated after the muscles have been both cooled and warmed.

To monitor muscle activation, 2 very fine wires will be inserted into the muscle through a fine needle. The needle will be removed immediately after insertion. This will be repeated a maximum of 3 times. Additionally, to measure muscle temperature a slightly thicker wire will be inserted using the same procedure (once only).

You will be asked to attend the laboratory on one occasion only for a duration of about 3 hours. For participation in the entire experiment you will receive payment of 300 kr. Participation is on a completely volunteer basis and you can withdraw at anytime without giving reason.

Best regards,

Susan Dewhurst, BSc

Dario Farina, Assoc. Prof., PhD

Center for Sanse-Motorisk Interaktion
Aalborg University
Tlf: 96358820

Center for Sanse-Motorisk Interaktion
Aalborg University
Tlf.: 96358799

Consent form:

“I hereby declare that I have received the above information both orally and in text and agree to participate in the experiment: *Muscle fibre conduction velocity during sustained contractions with localised warming and cooling.*

I understand that participation is based on a completely voluntary basis and participation can be can withdraw at any time without consequences.”

Date:

Name:

Signature:

APPENDIX 3: MEDICAL QUESTIONNAIRE FOR OLDER SUBJECTS (Greig et al. 1994)

MEDICAL QUESTIONAIRE

NAME: **DATE:**

Have you or are you suffering from:

1. Myocardial infraction within the previous 2 years	Y	N
2. Cardiac illness: symptoms of aortic stenosis, acute pericarditis, Acute myocarditis, aneurysm, severe angina, clinically significant valvular disease, uncontrolled dysrrhythmia, claudication, within the previous 10 years	Y	N
3 Thrombophlebitis or pulmonary embolus within the previous 2 years	Y	N
4. History of cerebrovascular disease	Y	N
5. Acute febrile illness within the previous three months	Y	N
6. Severe airflow obstruction	Y	N
7. Uncontrolled metabolic disease (e.g. diabetes, thyroid disease)	Y	N
8. Major systemic disease active within the previous 2 years (e.g. Cancer, rheumatoid arthritis)	Y	N
9. Significant emotional distress, psychotic illness or depression within the previous 2 years	Y	N
10. Lower limb arthritis, classified by inability to perform maximal contraction of the lower limbs without pain	Y	N

11. Lower limb fracture sustained within the previous 2 years Y N

12. Upper limb fracture sustained within the previous 6 months Y N

13. Non arthroscopic lower limb joint surgery within the previous 2 years Y N

14. Any reason for a loss of mobility for greater than 1 week in the previous 2 months or greater than 2 weeks in the previous 6 months Y N

15. Resting systolic blood pressure >200mmHg or resting diastolic blood pressure > 100mmHg Y N

16. Taking beta- blockers or digoxin, or not in sinus rhythm (excluded from ergometry because of difficulty interpreting heart rate) Y N

17. On daily analgesia Y N

18. Please list all drugs, prescribed and non prescribed you are presently taking

MEMORANDUM

To : Dr G De Vito, Strathclyde Institute for Biomedical Sciences

copy : Members of Ethics Committee
Ms A Stevenson, Finance Office

From : Mrs Gwen McArthur, Senior Assistant Registrar (Court) [Secretary to the Group]

Date : 27 March 2003

PROTOCOL APPROVAL

Project No: EC21 : 02/03

Project Title: Influence of age and muscle temperature on postural control and spinal reflex excitability

Investigators: Dr G De Vito, Professor M A Nimmo, Ms S Dewhurst, Postgraduate Student, Applied Physiology Group, Strathclyde Institute for Biomedical Sciences

Location: Applied Physiology Laboratory, Scottish School of Sport Studies

Insurance: University Policies

I can confirm that the University Ethics Committee has now approved the above protocol. As you are aware, Ms S Dewhurst is not approved to conduct the intramuscular temperature measurements until she has completed her training in this procedure. Once she has completed her training and the Ethics Committee is satisfied, then she may be added to the list of those recognised to perform this procedure.

I would remind you that if there are any changes made to the protocol the Committee must be informed of these and given the opportunity to consider them.

I would draw to your attention that the Committee would expect you to report back on the outcome of the project with an account of anything which may have occurred within the project that may prompt ethical questions for any similar future project and with anything else you feel the Committee should know.

Should you have any queries or require further information please to not hesitate to contact me. On behalf of the Committee I wish you every success with your project.

GMcA

PUBLICATIONS AND PRESENTATIONS

Publications

Dewhurst S, Riches PE, Nimmo MA, De Vito G. Temperature dependence of soleus H-reflex and M wave in young and older women. Eur J Appl Physiol. 2005; 94: 491-499.

Dewhurst S, Riches PE, De Vito G. Moderate alterations in lower limb muscle temperature do not affect balance control during quiet standing in both young and older women. J Electromyogr Kinesiol. 2007; 94: 491-499.

Dewhurst S, Graven-Nielsen T, De Vito G, Farina D. Muscle temperature has a different effect on force fluctuations in young and older women. Clin Neurophysiol. 2007; 118: 762-769.

Oral Presentations (published abstract):

International Society for Ageing and Physical Activity; August 2004, Ontario, Canada. The effects of altered localised temperature on spinal reflex excitability and postural sway in young and older women (J Aging Phys Activ. 2004; 12: 309-310)

The Physiological Society; March 2004, Glasgow, UK. Effects of altered localised temperature on spinal reflex excitability in young and older women (Refereed abstract: J Physiol; 557P, C66).

XVI Congress of the International Society of Electromyography and Kinesiology; June 2006, Turin, Italy. Effect of altered local temperature on force steadiness in young and older women (congress proceedings; p 198)

FELLOWSHIPS AND AWARDS

University of Strathclyde postgraduate scholarship, 1/10/2002- 31/1/2006

The Physiological Society, affiliate members grant, 14/6/2004

Marie-Curie fellowship (EC), (project: Danish Marie-Curie training site in biomedical science and engineering, Aalborg University, Denmark), 1/2/2005 – 14/8/2005.