

BILATERAL GRASP FORCE COORDINATION IN YOUNG AND OLD ADULTS

by

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ABSTRACT

The purpose of these experiments was to examine the coordination of bilateral isometric grasp force production in young and old adults during maximum and submaximum force tasks produced either simultaneously or sequentially. Thirty-six adults (12 young, 18-28y; 12 old, 65-75y and 12 old-old, 76-85y) participated in the first experiment involving maximum isometric grasp-grasp and grasp-pinch force. In the dominant hand, a force deficit was observed in bilateral compared to unilateral tasks in young adults during both maximum isometric grasp-grasp, $-12 \pm 5\%$ ($p < .05$), and grasp-pinch, $-20 \pm 4\%$ ($p < .001$), tasks. The force deficit was absent in the old group in both grasp, $+4 \pm 12\%$, and grasp-pinch, $+5 \pm 13\%$, tasks, as well as in the old-old group during both grasp, $-9 \pm 8\%$, and grasp-pinch, $-9 \pm 8\%$, tasks. Data therefore suggest that the force deficit is absent in both tasks with aging. These findings are consistent with the mechanism of transcallosal inhibition and degeneration of the corpus callosum in aging.

The second experiment examined sequential submaximum maintained grasp force tasks. Twenty-four adults (12 young, 18-28y, and 12 old, 75-85y) participated in this experiment. During sequential light or firm grasp tasks, maintained grasp force in young adults decreased during force rise, $-2 \pm 1\%$ ($p < .05$), or relaxation, $-13 \pm 2\%$ ($p < .01$), in the opposite hand. The decline in

maintained force was even greater in old adults during force rise, $-5 \pm 1\%$ ($p < .01$), and relaxation, $-15 \pm 1\%$ ($p < .01$), in the opposite hand. Overall, the decline found in maintained grasp during relaxation of the opposite hand was greater than observed during force rise, $p < .001$, for both age groups. These results were independent of the hand used to maintain force and the force level exerted in either hand. Divided attention is suggested to at least partially account for the decline in maintained force, with the anterior cingulate cortex posited as the locus for the integration of bilateral force production and attention.

CHAPTER I

INTRODUCTION

Bilateral hand use occurs at least 24 percent of each day, every day (Clark, Czaka, & Weber, 1990). With 26 muscles and 27 bones in each hand and wrist structure (Carmeli, Patish, & Coleman, 2003), bimanual grasp force production is a complex task. Adding to the complexity, hand muscles may control more than one joint, such as the long finger flexors, which exert control over two of the three phalanges of the digits. Successful performance of bilateral force tasks further requires that spatial and temporal synergies between the two hands be coordinated. However, it is still relatively unknown how the central nervous system controls grasp force in a system involving two hands, each with a large number of muscles and degrees of freedom of movement. This question, specific to isometric grasp force production, is the focus of this dissertation.

Interest in how bilateral, homologous muscles influence each other's ability to produce force has been expressed for more than half a century (Hellebrandt & Houtz, 1950; Henry & Smith, 1961; Ohtsuki, 1981a; Shinohara, Scholz, Zatsiorsky, & Latash, 2004). Research has focused primarily on maximum force production of bilateral homologous muscles in young adults (see Archontides & Fazey, 1993, and Jakobi & Chilibeck, 2001 for reviews).

During daily activities, bilateral grasp may require different hand configurations, different force levels and/or sequential force development. For example, bilateral grasp of small objects may require simultaneous grasp coupled with pinch, while simultaneous grasp may be needed to exert force on a large object. Similarly, grasp force requirements may vary. Submaximum rather than maximum grasp force is commonly, but not exclusively, required in daily tasks (McGee & Mathiowetz, 2003; Nalebuff, Torrono, & Phillips, 1995). Finally, both hands may produce grasp force sequentially, as when opening a jar.

Little is known about how old adults coordinate grasp force bilaterally, although it is known that the neuromuscular system declines with aging. Deterioration in the primary, premotor, supplementary and cingulate motor areas (Henderson, Tomlinson, & Gibson, 1980), the cerebellum (Müller & Dichgans, 1994a) and the basal ganglia (Mattay et al., 2002), as well as reduced production of the neurotransmitters acetylcholine (Freeman & Gibson, 1988) and dopamine (Goerendt et al., 2003a; Hubble, 1998; McGeer, McGeer, & Suzuki, 1977), affect the ability to produce force. Peripherally, there is a progressive loss of the number of motor units in hand muscles accompanied by processes of reinnervation leading to the emergence of larger and slower motor units (Brooks & Faulkner, 1994; Doherty, Vandervoort, Taylor, & Brown, 1993). These changes are accompanied by a decline in maximum force capabilities (Enoka, Fuglevand, & Barreto, 1992; Mathiowetz et al., 1985; Shinohara, Latash, & Zatsiorsky, 2003) and a general deterioration of the hand motor function (Ranganathan, Simionow, Sahgal, & Yue, 2001; Shiffman, 1992).

Given the limited understanding of bilateral grasp force coordination in young and especially old adults, this dissertation will examine the coordination of bilateral grasp force when produced simultaneously and sequentially. Simultaneous bilateral grasp force production will include maximum and submaximum grasp force production, as well as bilateral simultaneous grasp force production when grasp is combined with pinch force. The coordination of submaximum bilateral hand forces will be explored when submaximum grasp is produced sequentially. Together, these experiments will provide some insight into neural strategies used when young and old adults produce bilateral grasp force.

1.1. Isometric Grasp Force Production

Force is commonly regarded as a fundamental control parameter in bilateral coordination. In movement studies, force effects may be inferred from kinematic data (Spijkers & Heuer, 1995; Swinnen, Walter, Serrien, & Vandendriessche, 1992; Walter & Swinnen, 1990). However, movement amplitude depends not only on the magnitude of force but also on the temporal duration of the task. This results in potential difficulty separating force and timing effects in movement studies. In force production, by contrast, temporal control mechanisms appear to operate separately from force control mechanisms (Rinkenauer, Ulrich, & Wing, 2001), and may use different control processes (Franz, Eliassen, Ivry, & Gazzaniga, 1996; Ivry & Hazeltine, 1999). This independence of force from temporal constraints makes the use of isometric force advantageous to study bilateral coordination.

Isometric whole-hand grasp force involves combined forces produced by the four fingers and thumb. Grasp phases following contact include force rise from resting levels, maintenance and relaxation, or return to resting levels. Behaviorally, object-related force rise is characterized by an increase from near-zero force levels to the force level required for the object-related goal. Once achieved, task force may be maintained or may decline before a relatively steady maintenance phase occurs (Househam, McAuley, Charles, Lightfoot, & Swash, 2004). The greatest force in full-hand, or power, grasp is exerted by the long finger flexors (flexor digitorum sublimis and flexor digitorum profundus) (Maier & Hepp-Reymond, 1995), while intrinsic muscles, such as the lumbricals and interossei, contribute less than approximately 30 percent of their maximal force (Shinohara, Latash, & Zatsiorsky, 2003) and act to stabilize the metacarpal joints (Chao, An, Cooney, & Linscheid, 1989). Additionally, intrinsic muscles have been shown to play a greater role in the production of low compared to moderate or maximum isometric forces (Maier & Hepp-Reymond, 1995).

As multiple muscles are available for force production, variable activation patterns exist in both power grasp and pinch (Hall & Long II, 1968; Hepp-Reymond, Heusler, & Maier, 1996). The organization of the extrinsic and intrinsic flexors allows for flexibility in the development of grasp based on the area of the finger where pressure is exerted (Shinohara, Latash, & Zatsiorsky, 2003). For example, when the distal phalange presses on an object, the extrinsic flexors generate force, but when a global grasp is developed at the metacarpophalangeal joints, the intrinsic muscles are the major force generators.

In whole hand grasp, normal forces were shown to be synchronized between the index and little fingers and between the middle and ring fingers (Santello & Soechting, 2000). Force synchronization has also been shown during force production by two (Johansson, 1996), or three (Flanagan, Burstedt, & Johansson, 1999) fingers during pinch.

1.1.1. Role of Motor Unit Activation in Grasp Force Control

Grasp force development is dependent on both neural discharge rate and motor unit activation. At the peripheral level, the number of muscle fibers innervated by a single motor neuron has been found to be the most significant factor contributing to differences in motor unit force production (Enoka & Fuglevand, 2001). Recruitment of motor units follows the size principle described by Henneman (Henneman, Somjen, & Carpenter, 1965). In the hand, all motor units have been shown to be recruited by approximately 40-50 percent of maximum force in both the first dorsal interosseous (De Luca, LeFever, McCue, & Xenakis, 1982; Milner-Brown, Stein, & Yemm, 1973) and the adductor pollicis (Kukulka & Clamman, 1981). Thus, an increased rate of discharge of already recruited motor units, and not the number of muscle fibers, may be assumed to be responsible for high-magnitude force production. During sustained contractions, lasting more than several seconds, the average discharge firing rate determines the force exerted by the motor unit. Once a motor unit has achieved its peak force, the discharge rate can decline substantially without the force decreasing (Enoka & Fuglevand, 2001).

Force output can be modified, however, by factors such as the recent activation history of the muscle, muscle temperature, and muscle length (Cooper & Eccles, 1930; Thomas, Bigland-Ritchie, & Johansson, 1991). Furthermore, the number of muscle fibers innervated by a single motor neuron varies across motor unit types and muscles. This variation in innervation ratio has been shown to be the most significant factor contributing to differences in motor unit force (Kanda & Hashizume, 1992; Tötösy de Zepetnek, Zung, Erdebil, & Gordon, 1992),

It has been suggested that motor unit synchrony contributes to the temporal coordination of finger forces during grasp. Winges and Santello (1994) found that strong motor unit synchrony occurred among the compartments of the flexor digitorum profundus at the proximal interphalangeal joint of each finger, and across both the flexor digitorum profundus and the flexor pollicis longus, which produces flexion at the distal interphalangeal joint of the thumb. This synchrony allows the thumb and finger tips to flex at the same time as is seen in whole-hand grasp.

The dominant compared to nondominant hand has been shown to have both lower average firing rates, lower recruitment thresholds (Adam, deLuca, & Erim, 1998) and decreased motor unit synchronization (Semmler & Nordstrom, 1995). Adam and colleagues suggest that this is consistent with an increased percentage of slow twitch fibers in the dominant hand. An increased percentage of slow twitch fibers would allow twitch fusion and force to develop at lower firing rates. Adam et al. propose that a lifetime of preferred use of a hand may cause adaptations in the fiber composition of the dominant muscle. These factors may

help right-handed individuals initiate force earlier and maintain it longer when using the dominant compared to the nondominant hand.

Fluctuations in force during the maintenance period of a maximum voluntary isometric contraction in whole hand grasp vary with the force exerted by all the involved muscles. In contrast to single-muscle studies, force fluctuations during multiple-muscle grasp appear to be due less to motor unit properties (Fuglevand, Winter, & Patla, 1993), and more to the distribution of activity among the various muscles (Graves, Kornatz, & Enoka, 2000).

1.1.2. Role of Sensory Input in Grasp Force Control

Sensory input plays an important role in the production and modulation of movement and force production (Marsden, Merton, & Morton, 1985; Twitchell, 1954; Westling & Johansson, 1984; Witney, Wing, Thonnard, & Smith, 2004). Skin deformation during object contact has been shown to activate cutaneous receptors that trigger the release of motor commands for force development. Cutaneous receptors also provide information about friction and slip during the maintenance of grasp force (Edin & Abbs, 1991; Johansson & Cole, 1994; Johansson & Westling, 1984, 1987; Rothwell et al., 1982; Witney, Wing, Thonnard, & Smith, 2004). However, their role while force is being maintained is still unclear. Cutaneous receptors have been shown to monitor friction and slip conditions during force maintenance. Despite this known role, Ebied et al. (Ebied, Kemp, & Frostick, 2004) found that there was a near linear fall in force from peak values needed for a safe and secure pinch during prolonged (30s) compared to shorter (10s) trials. This feature was present with or without a cutaneous nerve

block. As this finding concurred with deafferentation studies in which there was an impaired ability to maintain a constant force (Rothwell et al., 1982), Ebied and colleagues suggested that cutaneous receptors may play a limited role in maintaining force, while muscle afferents provide greater feedback.

During force maintenance in contractions of greater than ten percent of maximum force, muscle spindles provide essential sensory feedback (Edin & Vallbo, 1990; Rothwell et al., 1982). Muscle spindle feedback has been found to be more powerful than cutaneous feedback in maintenance of isometric pinch force (Henningsen, Knecht, & Ende-Henningsen, 1997).

Golgi tendon organs are sensitive to active change in muscle tension and discharge at an increasingly greater or lesser rate during a rise or decline in contractile force, respectively (Jami, 1992; Stuart, Mosher, Gerlach, & Reinking, 1972). As monitors of force change, therefore, golgi tendon organs play a crucial role in sensory feedback of force development and relaxation.

Sensory input is provided both to the spinal cord and cerebral cortex (Jami, 1992). Integration of afferent and efferent information also occurs, as convergence of descending corticospinal neurons and ascending muscle afferents (tendon organ, spindle, skin and/or joints) has been found in spinal cord interneurons (Lundberg, Norsell, & Voorhoeve, 1962). At a central level, muscle sensory input related to force control is received by both the cerebellum (Espinoza & Smith, 1990) and the cerebral cortex (McIntyre, Proske, & Rawson, 1984).

1.1.3. Central Structures Involved in Grasp Force Control

The primary motor cortex (M1) plays a fundamental role in the execution of force, with activity shown to be related to force magnitude (Evarts, 1968) and direction of force (Georgopoulos, Kalaska, Caminiti, & Massey, 1982). Lesion studies have shown that damage to M1 or its descending corticospinal neurons results in hemiparesis and loss of individuated finger movement (Hermsdörfer, Hagl, Nowak, & Marquardt, 2003; Lawrence & Kuypers, 1968; Mai, 1989).

Multiple, non-overlapping, movement representations are present within M1. Projections from these areas have been shown to converge peripherally for task-specific force production (Fetz & Tanji, 1976; Sanes, Donoghue, Thangaraj, Edelman, & Warach, 1995; Schieber, 1990). M1 activation has been shown to be stronger and more widespread during whole-hand grasp compared to pinch (Castiello, 2005; Ehrsson, Fagegren, & Forssberg, 2001; Ehrsson et al., 2000; Grafton, Fagg, & Arbib, 1998; Muir & Lemon, 1983), with contralateral primary motor cortex activation through corticospinal neurons for grasp and bilateral activation for pinch (Castiello, 2005; Ehrsson, Fagegren, & Forssberg, 2001; Ehrsson et al., 2000; Evarts, 1968; Evarts, Fromm, Kroller, & Jennings, 1983; Grafton, Fagg, & Arbib, 1998; Muir & Lemon, 1983). Specifically, fractionated finger movement and grasp is supported by the lateral, or crossed, fibers of the corticospinal tract (Chouinard & Paus, 2006).

The primary motor cortex receives input from associated secondary motor and somatosensory areas, including the premotor area, the supplementary motor area (SMA), and the cingulate motor area. Activation of the premotor area has

been shown to occur during the planning of complex sequenced tasks that are guided, triggered or paced by external sensory feedback (Passingham, Perry, & Wilkinson, 1983; Wise, 1985). In concert with the parietal lobe, the premotor area codes size, shape, and orientation of objects. In particular, the dorsal portion of the premotor area provides access to sensory and spatial information from the environment through somatosensory and parietal connections, as well as information gained through experience via prefrontal association area connections (Gardner, Ro, Babu, & Ghosh, 2007; Lu, Preston, & Strick, 1994). The dorsal premotor area is activated during programming for grasp (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). The ventral portion, in contrast, contains neurons that are activated during hand shaping or conformance on the object (Begliomini, Wall, Smith, & Castiello, 2007; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Rizzolatti & Fadiga, 1998). The role of ventral premotor neurons in coding grasp force magnitude is uncertain. While a modification in firing rate was found in ventral premotor neurons in response to changes in force during a precision grasp (pinch) task (Hepp-Raymond, Kirkpatrick-Tanner, Gabernet, & Qi, 1994), Roland and Zilles (1996) did not find ventral premotor activation in response to changes in grasp force magnitude.

There are also interconnections between the supplementary motor area and the primary motor cortex (Dum & Strick, 1991; Hyland, Chen, Maier, Palmeri, & Wiesendanger, 1989). The supplementary motor area has been shown to be involved in tasks requiring greater movement or force complexity (Gerloff, Corwell, Chen, Hallett, & Cohen, 1997; Shibasaki et al., 1993) and the

use of internal feedback such as motor imagery (Roland, Larsen, Lassen, & Skinhoj, 1980; Tanji, 1994, 1996). Supplementary motor area activation has also been associated with the initiation of movement (Hyland, Chen, Maier, Palmeri, & Wiesendanger, 1989; Stephan, Binkofski, Posse, Seitz, & Freund, 1999), motor programming (Roland, Larsen, Lassen, & Skinhoj, 1980; Roland & Zilles, 1996; Tanji, 1994), and motor learning. A role in bimanual task coordination has also been identified for the supplementary motor area (Brinkman, 1984; Gerloff & Andres, 2002; Gribova, Donchin, Bergman, Vaadia, & Cardoso de Oliveira, 2002; Stephan et al., 1999). In coordination tasks, the supplementary motor area is often associated with activity of the cingulate motor area, to which it is strongly connected.

Activation of the supplementary motor area is increased during maintained precision grip and holding (Smith, 1979), and when using low static precision grip (pinch) forces as compared to moderate or maximum force levels (Kuhtz-Buschbeck, Ehrsson, & Forssberg, 2001). Functionally, selective ablation of the supplementary motor area in nonhuman primates has led to excessive grip force in the contralateral hand and persistent difficulties in releasing objects (Smith, Bourbonnais, & Blanchette, 1981).

In grasp, the cerebellum fine tunes anticipatory and reactive responses to unexpected perturbations based on prediction from available sensory and motor information (Serrien & Wiesendanger, 1999). In the presence of cerebellar disease, pinch force magnitudes are exaggerated (Babin-Ratte, Sirigu, Gilles, & Wing, 1999; Fellows, Ernst, Schwarz, Töpper, & Noth, 2001), while the rate of

change of force development is normal (Fellows, Ernst, Schwarz, Töpper, & Noth, 2001). The cerebellum also has been shown to play a role in the ability to maintain isometric force (Mai, Bolsinger, Avarello, Diener, & Dichgans, 1988; Müller & Dichgans, 1994b).

The cerebellum may play a role in prediction of motor tasks (Nowak & Hermsdörfer, 2006; Wolpert & Flanagan, 2001). Nowak et al. suggest that, as movement occurs, an efferent copy of the movement is generated along with the predicted sensory input, referred to as corollary discharge. Comparisons are then made between the actual and predicted sensory input. Should a mismatch occur between the actual and predicted sensory input, motor corrections can be quickly triggered and the internal model updated (Flanagan & Johansson, 2002). It is thought that predictive grip force, as in grasp and lift tasks, is based on this model (Flanagan & Johansson, 2002). Finally, activation of the cerebellum is associated with timing elements of force-related tasks (Miall & Reckess, 2002).

The basal ganglia are involved in the processing of sensory information so that predictive and reactive force adjustments can be made (Nowak & Hermsdörfer, 2006). Traditionally, deficits in the basal ganglia have been associated with either diminished or excessive movement. Force studies suggest that the basal ganglia play a role in regulation of the rate of change of force (Dubrowski, Roy, Black, & Carnahan, 2005; Vaillancourt, Mayka, Thulborn, & Corcos, 2004), release of force (Kunesch, Schnitzler, Tyercha, Knecht, & Stelmach, 1995) and the processing of sensory information for use in predictive

and reactive motor programming (Kraft et al., 2007; Nowak & Hermsdörfer, 2006).

1.2. Bilateral Isometric Grasp Force Production

In young adults, when similar grasp force magnitudes are produced simultaneously, force profiles are typically coupled tightly. Absolute force values may vary, with the dominant hand typically producing greater force. Force rise, the time at which peak force is achieved, and force relaxation occur at approximately the same times in each hand, as has been shown in bilateral movement studies (Bertrand, Mercier, Shun, & Bourbonnais, 2004; Byblow, Bysouth-Young, Summers, & Carson, 1998; Heuer, Spijkers, Steglich, & Kleinsorge, 2002; Rinkenauer, Ulrich, & Wing, 2001).

Rinkenauer and colleagues (2001) studied bilateral simultaneous and sequential brief force pulses in the index finger of young adults. During bilateral simultaneous tasks, the amount of force produced in one hand was not affected by the amount of force produced in the other hand and rise times to peak force continued to be coupled. They also found that the degree of coupling decreased with increased time before a temporally predictable auditory cue. Rinkenauer et al. interpreted their findings as supportive of a coupling phenomenon when bilateral brief force pulses were produced.

However, when two different force magnitudes were produced in the two hands at the same time, each force magnitude was smaller compared to the force produced unilaterally. Increased variability was also found when different as compared to same forces were produced. Overall, Rinkenauer et al. found that

task performance worsened during bilateral tasks. These factors suggest that producing different compared to same force levels in a simultaneous bilateral task is more difficult.

1.2.1. Bilateral Force Deficit

When young adults produce maximum isometric force in homologous muscles simultaneously, a force deficit has been found reliably in the bilateral compared to the unilateral condition. This has been termed a bilateral force deficit, in that the deficit occurs in the bilateral condition. It is primarily but not universally (Henry & Smith, 1961) found in both limbs. The bilateral force deficit typically ranges from approximately five to twenty-five percent during simultaneous maximum force production in young adults (Archontides & Fazey, 1993; Jakobi & Chilibeck, 2001; Ohtsuki, 1981c). The first identification of the bilateral deficit occurred in 1961 by when Henry and Smith . Interest in the bilateral deficit has continued because its presence suggests the neuromuscular system may be limited in its ability to produce maximum force in homologous muscles of two limbs at the same time.

The presence of bilateral deficit has been found in young adults during maximum contractions of the finger flexors (Ohtsuki, 1981a, 1983, 1994), wrist flexors (Kroll, 1965b), and elbow flexors (Howard & Enoka, 1991; Ohtsuki, 1981b, 1994), as well as in the elbow extensor (Ohtsuki, 1983; Seki & Ohtsuki, 1990). In the lower limb, it has been found in the knee extensors (Howard & Enoka, 1991; Koh, Grabiner, & Clough, 1993; Owings & Grabiner, 1998) and ankle plantarflexors (Kawakami, Sale, & MacDougall, 1995). A bilateral deficit

occurs more often in upper compared to lower extremities, as shown in 12 of 17 studies of untrained subjects (Henry & Smith, 1961; Kroll, 1965a; Oda & Moritani, 1994, 1995a, 1995b; Ohtsuki, 1981a, 1981c, 1983; Seki & Ohtsuki, 1990). It has also been found in reaction time (Ohtsuki, 1994), ramp and step isometric contractions (Koh, Grabiner, & Clough, 1993), dynamic contractions (Taniguchi, 1998) and reflexively evoked contractions (Khodiguian, Cornwell, Lares, DeCaprio, & Hawkins, 2002).

Despite the large body of literature on the bilateral deficit, it has not been consistently demonstrated. It is restricted to simultaneous activation of homologous muscles. No bilateral deficit has been found when nonhomologous muscles contract simultaneously, for example in concurrent right elbow flexion and left elbow extension (Ohtsuki, 1983). Furthermore, a number of factors have been shown to modify the bilateral deficit effect. Habitual use of bilateral homologous muscles, such as in cycling or weightlifting, may result in inhibition of a bilateral deficit or lead to an observed increase in force production in the bilateral compared to unilateral task (bilateral facilitation) (Howard & Enoka, 1991).

To assess the effect of fiber type on the deficit, Koh and colleagues (Koh, Grabiner, & Clough, 1993) had young participants generate maximum isometric knee extension torque either quickly, in a step paradigm, or slowly, in a ramp paradigm. A greater bilateral deficit was found when muscle torque was developed quickly, suggesting that the deficit may be due to a decreased ability to activate fast motor units. The results of Kawakami and colleagues (Kawakami,

Sale, & MacDougall, 1995) also supported this hypothesis. They assessed the bilateral deficit during ankle plantarflexion, which involves both the soleus, primarily composed of slow twitch muscle fibers, and the gastrocnemius, which has a mixed fiber composition (Chilibeck, Patterson, Cunningham, Taylor, & Noble, 1997). Results indicated a larger bilateral deficit when the gastrocnemius was activated, supporting the hypothesis that the bilateral deficit is due to decreased ability to recruit fast twitch motor units.

The presence of a bilateral deficit in isometric knee extension has been frequently but not universally found (Häkkinen, Kraemeer, & Newton, 1997; Howard & Enoka, 1991; Schantz, Moritani, Karlson, & Johansson, 1989; Vandervort, Sale, & Moroz, 1984; Vandevort, Sale, & Moroz, 1984). In a series of three experiments investigating isometric knee extension in young and old adults, Häkkinen et al. failed to find a bilateral deficit in isometric knee extension (Häkkinen et al., 1996; Häkkinen, Kraemeer, & Newton, 1997; Häkkinen, Pastinen, Karsikas, & Linnamo, 1995). Thus, it is still uncertain whether the bilateral deficit is present in aging.

Finally, instruction also appears to have an effect on the degree of deficit observed. Sahaly and colleagues (Sahaly, Vandewalle, Driss, & Monod, 2001) found that instructions emphasizing both maximum force and maximum rate of force development compared to just maximum rate of force development resulted in a greater bilateral force deficit.

Mechanisms underlying the bilateral deficit are still largely unknown. Suggested mechanisms have included cross-talk at the cortical level (Ohtsuki,

1981c; Steglich, Heuer, Spijkers, & Kleinsorge, 1999), and neural inhibition at a supraspinal level, such as the corpus callosum (Oda & Moritani, 1995a, 1995b; Taniguchi, 1998). Early investigations focused on the role of motor unit recruitment, on the premise that the nervous system was unable to fully recruit all motor units in a bilateral compared to a unilateral contraction. An inability to activate all motor units during voluntary force production has been shown to result in a relative decrease in the number of available large motor units (Belanger & McComas, 1981), as expected by the size principle (Henneman, Somjen, & Carpenter, 1965).

To examine further the ability to activate all motor units during voluntary force production, maximum voluntary force production was compared to the absolute force produced when a supramaximal tetanic stimulus was added. It was assumed that there would be no limitation in force production capability if the two magnitudes were the same. Such similar force magnitudes have been found in upper and lower limb muscles, including the small muscles of the hand (Bigland & Lippold, 1954a), supporting the concept of an unconstrained neural drive. Oda and Moritani (1995b) measured motor-related cortical potentials during maximum unilateral and bilateral elbow flexion. In addition to lower force and electromyographic activity in the bilateral condition, they also found that cortical activity declined during bilateral activity, suggesting that neural inhibition is at least partly responsible for the deficit. Taniguchi et al. (Taniguchi, 1998; Taniguchi, Burle, Vidal, and Bonnet, 2001) found that bilateral training resulted in a reduction of the bilateral deficit whereas unilateral training increased the deficit.

They interpreted these findings as evidence that the bilateral deficit is, in part at least, mediated at the supraspinal level.

1.2.2. Central Structures Involved in Bilateral Grasp Force Control

The supplementary motor area is especially important in bilateral force production. The role of the supplementary motor area in coordination of bimanual and rapid alternating tasks has been well established in lesion studies of primates (Brinkman, 1981) and humans (Dick, Benecke, Rothwell, Day, & Marsden, 1986; Freund & Hummelsheim, 1985; LaPlane, Talairach, Meininger, Bancaud, & Orgogozo, 1977). Supplementary motor area hand representations in the two hemispheres are strongly interconnected through the corpus callosum (Rouiller et al., 1994; Stephan et al., 1999). The supplementary motor area is activated during movement initiation (Smith, 1979), motor planning and bilateral coordination (Brinkman, 1981; LaPlane, Talairach, Meininger, Bancaud, & Orgogozo, 1977). In the hand, supplementary motor area activation has been shown to occur with both bilateral finger movement (Sadato, Yonekura, Waki, Yamada, & Ishii, 1997) and pinch force production (Smith, 1979).

The corpus callosum connects homologous cortical areas for purposes of interhemispheric transfer and integration (Preilowski, 1972; Schieppati, Musazzi, Nardone, & Seveso, 1984; Seymour, Reuter-Lorenz, & Gazzaniga, 1994). Identified roles of the callosum include the unifying of sensory information such as stimulus identity and shape (Gazzaniga, Bogen, & Sperry, 1962) and the organization of bilateral motor output (Elliasen, Baynes, & Gazzaniga, 2000).

The contribution of the corpus callosum to fast, coordinated bilateral performance is well established (Geschwind & Kaplan, 1962; Mark & Sperry, 1968), especially but not exclusively through the anterior fibers (Preilowski, 1972). Bimanual hand deficits during movement by acallosal participants have been well documented in studies involving reach (Jakobson, Servos, Goodale, & Lassonde, 1994; Preilowski, 1972), drawing (Franz, Elliassen, Ivry, & Gazzaniga, 1996) and tapping tasks (Helmuth & Ivry, 1996). The callosum appears to have a greater role in spatial rather than temporal coordination of movement (Elliassen, Baynes, & Gazzaniga, 2000), and also appears to have a role in the spatial coordination of bimanual forces. Spatial coupling during bimanual force pulsing tasks has been observed, with dissimilar force pulse magnitudes approximating each other (Steglich, Heuer, Spijkers, & Kleinsorge, 1999). In this experiment, different bimanual target forces could be produced only when there was sufficient time for participants to prepare their responses (Rinkenauer, Ulrich, & Wing, 2001; Steglich, Heuer, Spijkers, & Kleinsorge, 1999). This spatial coupling was not found in acallosal participants, and temporal desynchronization was also present (Diedrichsen, Hazeltine, Nurss, & Ivry, 2003). Hemispheric asymmetries affecting intracortical inhibition and facilitation have been shown in right-handed but not left-handed individuals (Civardi, Cavalli, Naldi, Varrasi, & Cantello, 2000; Kawashima, Inoue, Sato, & Fukuda, 1997; Kawashima et al., 1993; Kim et al., 1993).

1.3. Age-related Changes Affecting Grasp Force Production

It is well known that hand function declines with aging. Finger mobility is generally reduced (Shiffman, 1992) and muscle fibers atrophy (Brooks & Faulkner, 1994; Faulkner, Brooks, & Zerba, 1990). There is up to a 50 percent decline in strength and a 40 percent loss of muscle mass between 50 and 80 years of age (Tseng, Marsh, Hamilton, & Booth, 1995). In the hand, atrophy occurs in the thumb muscles (Carmeli, Patish, & Coleman, 2003) as well as the first dorsal interosseus, where a decrement of as much as 77% may be present (Doherty, Vandervoort, & Brown, 1993). Thinning of the epidermal layer of skin occurs, (Bolognia, 1989), resulting in an inability to fully comply with an object's surface, thus increasing the frictional force needed to prevent slippage (Cole & Beck, 1994; MacKenzie & Iberall, 1994). The number of eccrine (sweat) glands also declines with age, leading to decreased lubrication of the hand and further increasing friction requirements (Cole & Beck, 1994; MacKenzie & Iberall, 1994). As a result of this decreased friction, old adults may produce object-related grasp forces that are two to three times larger than those produced by young adults.

Decreased sensory capabilities also affect grasp force in aging. Loss of joint and tendon afferents occurs, which leads to an overall decrease in proprioception (Proteau, Charest, & Chaput, 1994; Skinner, Barrack, & Cook, 1984) and decreased stretch reflex activity (Corden & Lippold, 1996). A reduced number of fast-adapting type I, Meissner, afferents near the surface of the skin results in impaired tactile function with aging (Bolton, Winkelmann, & Dyck, 1966). This decreased tactile sensibility results in decreased information about

object shape, edges and surface texture, thus affecting friction, and grasp force magnitude (Bolton, Winkelmann, & Dyck, 1966; Cole, 1991; Cole & Beck, 1994; Johansson & Westling, 1984)

Old compared to young adults show a decline in grasp force capability in both voluntary isometric and dynamic contractions (Enoka, Fuglevand, & Barreto, 1992; Häkkinen, Kraemeer, & Newton, 1997; Häkkinen, Pastinen, Karsikas, & Linnamo, 1995). Not only is less force produced, but it takes longer to produce force in old compared to young adults (Bohannon, 1990). During a dynamic grasp force task, old compared to young adults have been shown to have greater difficulty tracking a moving force signal and maintaining force at lower force levels (Mai, Averello, & Bolsinger, 1985; Mai, Bolsinger, Avarello, Diener, & Dichgans, 1988; Voelcker-Rehage & Albers, 2005; Voelcker-Rehage, Stronge, & Albers, 2006). Not only is force tracking more difficult, but slow and accurate force release from the tracking task is also more variable for old compared to young adults (Voelcker-Rehage & Albers, 2005).

Bilateral force production in aging has not been extensively studied. In movement, it has been shown that old adults have a slower reaction time, with greater time differences between the two limbs at movement onset and termination compared to differences in young adults. Greater movement variability during bilateral tasks has also been shown (Stelmach, Amrhein, & Goggin, 1988; Wishart, Lee, Cunningham, & Murdoch, 2002). Furthermore, old compared to young adults show increased movement time, which increases in concert with increasing task complexity (Stelmach, Amrhein, & Goggin, 1988).

1.3.1. Neurophysiological Changes with Aging

Motor units decrease in numbers especially during and following the seventh decade of life (Doherty, Vandervoort, Taylor, & Brown, 1993). Motor unit remodeling appears to occur with aging through denervation of type II or fast-twitch muscle fibers and reinnervation of some of these fibers from type I or slow-twitch neurons (Brooks & Faulkner, 1994; Faulkner, Brooks, & Zerba, 1990; Roos, Rice, & Vandervoort, 1997). While fast-twitch fibers selectively decline, the proportion of slow-twitch muscle fibers increases, from 39% of total muscle fibers between the ages of 20 and 29 years to 66% in the first half of the seventh decade (Roos, Rice, & Vandervoort, 1997). As a result, slow-twitch fibers are responsible for a greater relative proportion of maximum isometric force development. Slow-twitch fibers are responsible for less than 25 percent of maximum voluntary isometric contraction in young adults, with the remaining force increase produced by fast-twitch fibers. In old adults, however, slow-twitch fibers are activated during approximately 50 percent of isometric force development (Akataki, Mita, Watakabe, & Ito, 2002). Additionally, there is a slowing of muscle contractile properties (Roos, Rice, & Vandervoort, 1997), changes in muscle metabolism (Proctor, Sinning, Walro, Sieck, & Lemon, 1995), and a reduction in the conduction velocity of motor neuron fibers (Campbell, McComas, & Petito, 1973; Doherty, Vandervoort, Taylor, & Brown, 1993).

Force variability increases in old compared to young adults (Galganski, Fuglevand, & Enoka, 1993; Laidlaw, Bilodeau, & Enoka, 2000). As motor units tend to be recruited in order of ascending size, and as initial discharge rates are

low, fluctuations in force during an isometric contraction may be due to unfused tetani of the most recently recruited motor units (Christakos, 1982). Therefore, as fewer motor units are available in aging, there is an enlargement of motor unit territories, with increased magnitudes of force fluctuations (Laidlaw, Bilodeau, & Enoka, 2000). However, this variation is greatest during weak isometric contractions of less than 10-20 percent maximum voluntary contraction (Galganski, Fuglevand, & Enoka, 1993; Laidlaw, Bilodeau, & Enoka, 2000; Tracy, Maluf, Stephenson, Hunter, & Enoka, 2005; Yakovlev & Rakic, 1966). Such variation has been found consistently in studies of small but not larger muscles. Enoka et al. (2002) found that motor unit twitch force, the number of motor units innervating a muscle, and nonuniform activation of the agonist muscle did not affect force fluctuations, while variability in the motor unit discharge rate in both the agonist and antagonist muscles was found to best reflect differences in force fluctuation in young and old adults.

A decline in central motor areas also affects the ability to produce force. Up to 49% of large and 38% of small neurons are lost in the primary, premotor, supplementary and cingulate motor areas, between 20 and 90 years of age (Henderson, Tomlinson, & Gibson, 1980). In the primary motor cortex, a significant decrease in the number of large Betz cells occurs (Allen et al., 1983; Scheibel, 1979; Scheibel, Tomiyasu, & Scheibel, 1977), resulting in a decline in fast transmission of motor commands. Isometric, dynamic and visually paced whole hand grasp tasks were associated with decreased activity in the ipsilateral but not the contralateral primary motor cortex in old compared to young adults

(Ward & Frackowiak, 2003). In the spinal cord, there is a loss of dendritic connections to the alpha neurons (Scheibel, Tomiyasu, & Scheibel, 1977).

In the cerebellum, important for coordinated movement, purkinje fibers decrease in number and exhibit thinning of arboreal branches (Hall, Miller, & Corsellis, 1975; Müller & Dichgans, 1994a; Rogers, Silver, Shoemaker, & Bloom, 1980). The anterior portion of the corpus callosum, important for the interhemispheric transfer of motor-related information, also has been shown to degenerate, especially in women (McGeer, McGeer, & Suzuki, 1977; Salat, Ward, Kaye, & Janowsky, 1997). There is a reduction in the number of neurons of the substantia nigra of the basal ganglia (Mattay et al., 2002), and a decline is also seen in production of the neurotransmitters acetylcholine (Freeman & Gibson, 1988) and dopamine (Goerendt et al., 2003b; Hubble, 1998; McGeer, McGeer, & Suzuki, 1977).

1.4. Other Factors affecting Bilateral Grasp

Bilateral grasp force may be affected through modulation of attention. Johansen-Berg and Matthews (2002) used functional magnetic resonance imaging to show that attention to movement can modulate motor responses. When a distractor task was completed in concert with button presses, changes in the sensorimotor cortex and cingulate motor area were observed. When similar imaging studies were examined during cyclic hand and foot movements (Heuninckx, Wenderoth, Debaere, Peeters, & Swinnen, 2005a), older adults showed stronger and more extended brain activity than young adults across all

motor tasks. The increase in areas activated suggested that old adults relied less on automatized, internal movement generation than young adults, and more on higher-level integration of auditory and somatosensory information. Therefore, attention may play a role in the production of bilateral grasp force in both young and old adults.

1.5 Rationale and Significance of the Study

A review of the literature has shown that a force deficit is typically observed in young adults during bilateral compared to unilateral maximum force tasks. If a force deficit is present during bilateral tasks, it suggests that the central nervous system may be limited in its ability to simultaneously produce force in homologous muscles. If bilateral activation presents a problem for the neuromuscular system in young adults, one might expect to see similar differences in their production of submaximum forces. Alternatively, it may be that this limitation to the neuromuscular system occurs only with maximum neural activation, as during bilateral production of maximum forces. In this case, a force deficit would not be expected in bilateral submaximum force production. Given the limited research concerning bilateral submaximum force production, it is not clear whether a force deficit exists.

Evidence for the bilateral deficit has primarily been found in young adults. With conflicting results from the small number of prior studies, it is unclear whether a force deficit exists in old adults. Given known neural degenerative changes with aging, the study of bilateral force production in aging could assist in

identifying underlying mechanisms of the force deficit. For example, degeneration of the corpus callosum results in a decline in inhibition between the two hemispheres. If the callosum is involved in the force deficit in aging, a decline in the force deficit could be expected.

As function, musculoskeletal components and neurophysiological mechanisms decline incrementally with aging, stratification of adults by age allows examination of bilateral coordination under conditions of increasing degeneration. As motor unit changes typically begin in the seventh decade, resulting in motor slowing and force decline, this appears to be a likely initial age range for old adults. Ten-year increments are commonly used in aging studies, so comparisons with other studies are possible.

The presence of a force deficit has only been studied using bilateral homologous muscles, such as the dominant and nondominant biceps brachii or knee extensors. The hand offers a unique opportunity to examine bilateral force production in a more complex task than the bilateral grasp task. In a maximum grasp-pinch task, the same effectors are activated, i.e., the finger flexors through tendons to each finger. However, in the hand producing pinch, fewer fingers are activated and the joint at which the greatest force is produced may vary. This results in different hand configurations and absolute force capabilities. If neural activation is comparable for the two bilateral tasks, then one would expect to see a comparable force deficit.

When bilateral grasp is performed during object manipulation, it typically occurs with one hand maintaining force while the other hand produces a transient

force during manipulation of an object. Only following this transient force production is maintained force released. Despite the frequency of grasp and manipulation tasks, it is not known whether maintained force is affected by the transient force production and release in either young or old adults. Nor is it known whether the use of same or different force magnitudes in the two hands affect the ability to maintain force. Examination of this paradigm can determine whether and how maintained grasp force is affected by transient force production, and whether the effect is similar or different in young and old adults. This is a first step in understanding how the neuromuscular system coordinates bilateral force when it is produced sequentially rather than bilaterally.

1.5.1. Purpose and Hypotheses of Experiment 1

The purpose of the first experiment was to compare, in young, old, and old-old adults, the ability to produce maximum grasp bilaterally in simultaneous grasp combined with grasp and grasp with pinch. The primary hypothesis was that young but not old or old-old adults would demonstrate a bilateral deficit in grasp-grasp and grasp-pinch force tasks, on the basis of known degeneration of callosal fibers.

1.5.2. Purpose and Hypotheses of Experiment 2

The purpose of the second experiment was to examine, in young and old adults, the effect of a sequenced transient force on the stability of force production in the contralateral hand maintaining force before, during and after transient force production. The hypothesis was that old compared to young

adults would demonstrate greater changes in maintained force during transient hand force production, given known changes in force development with aging. It was further hypothesized that this change would be greater when different compared to same forces were produced in each hand during a bilateral sequential task.

Experiment 2 also examined bilateral submaximum force production in young and old adults. The primary hypothesis was that no bilateral deficit would be present in young or old adults as a result of the production of less than maximal forces.

CHAPTER II

METHODS

Two experiments were conducted which involved bilateral isometric force production in young and old adults. The methods used in these experiments are described in this chapter.

2.1. Experiment One

2.1.1. Participants

Participants were healthy, right-handed young, old and old-old females who were independent community dwellers. The terminology for the elderly age groups denotes age ranges and is in common epidemiological use (Spirduso, 1995). In the first experiment, the term old is used for adults aged 65-75 and old-old for adults aged 76-90 years. Exclusion criteria for all adults included left hand dominance, the presence of neurologic, orthopedic or musculoskeletal conditions affecting hand function, such as a history of cerebrovascular accident, hand/finger fracture, rheumatoid arthritis, decreased cognition so that the ability to follow directions was impaired, or observed or self-perceived loss of hand function due to any condition. Osteoarthritis was not considered an *a priori* exclusion factor, as osteoarthritis is present in approximately 90 percent of those older than 65 years (Hughes, Edelman, Chang, Singer, & Schuette, 1991;

Kelsey, 1984). If osteoarthritis was present, participants were excluded if they identified skill loss or decreased comfort during hand and finger activities. All old participants were recruited from the Ann Arbor area. Young adults were students at the University of Michigan. Only right dominant women were included to avoid potential gender-related differences in force production (Christ, 1992), brain morphology (Hellige, Taylor, Lesmes, & Peterson, 1998) and neuroanatomical decline with aging (Hatazawa, Masatoshi, Harutsuzu, & Matsuzawa, 1982; Hubbard & Anderson, 1983). Participants gave informed consent and the protocol was approved by the University of Michigan Behavioral Sciences Institutional Review Board (B03-00002640).

2.1.2. Clinical Assessments

Participants were classified as right-handed on the basis of the laterality quotient derived from the Edinburgh Handedness Inventory (Oldfield, 1971). (Oldfield, 1971). Inclusion criterion for right hand dominance was set at greater than .50 on a scale from zero to one, where greater numbers indicate greater laterality.

Perceived health status, dominance and the ability to understand basic questions and follow directions were assessed through a brief interview prior to acceptance into the study. Three clinical assessments were performed: a clinical neurological examination, self-completion of the Arthritis Impact Measurement Scales 2 (AIMS2), (Meenan, Mason, Anderson, Guccione, & Kazis, 1992) and the Mini-Mental State Examination (MMSE) (Folstein, Folstein, & McHugh, 1975). Finger-to-nose, alternating supination-pronation, rapid alternating movements of

the fingers and tests for muscle tone were used to assess cerebellar function (Haerer, 1992). Clinical tests for radial, medial and ulnar nerve integrity were also administered (Dellon, 1983).

Cognitive status was assessed using the 30-point Mini-Mental State Examination (MMSE) (Folstein, Folstein, & McHugh, 1975), which has been shown to have good validity and reliability with aging (Folstein, Folstein, & McHugh, 1975). Inclusion in the study required a score of 24 or greater, as below 24 is considered indicative of cognitive impairment (Trenkwalder, 2006). The Arthritis Impact Measurement Scales 2 (AIMS2) was used to measure function and perceived health status. The AIMS2 is a self-report tool that has been shown to have good reliability and validity in aging populations (Hughes, Edelman, Chang, Singer, & Schuette, 1991; Meenan, Mason, Anderson, Guccione, & Kazis, 1992). General health status and four independent functional scales were used, Arm Function, Hand and Finger Function, Self-Care Tasks, and Household Tasks. Normalized scores range from zero to five, where higher scores indicate greater impairment.

Hand coordination was evaluated using subtests from the Jebsen Hand Function Test (Jebsen, Taylor, Trieschmann, Trotter, & Howard, 1969) and the Purdue Pegboard Test. The JHFT (Jebsen, Taylor, Trieschmann, Trotter, & Howard, 1969) is comprised of seven subtests that represent a variety of daily hand tasks, including writing, turning over cards, picking up and placing small objects, stacking light discs, and moving light and heavy aluminum cans. It has been shown to have good reliability (Jebsen, Taylor, Trieschmann, Trotter, &

Howard, 1969). JHFT results for an elderly population were derived from a study by Hackel and colleagues (Hackel, Wolfe, Bang, & Canfield, 1992) of 121 males and females over the age of 60 years and grouped by ten-year increments. Normative data for young adults was taken from the original study (Jebsen et al., 1969). In the current study, one subtest was omitted as not germane to the purposes of this experiment. This did not impact test interpretation.

The Purdue Pegboard (PP) (Lafayette Instruments) (Tiffin & Asher, 1948) is a test of fine manual dexterity. Test-retest reliability for testing with elderly adults is good to excellent, varying from 0.66 to 0.90 (Desrosiers, Hébert, Bravo, & Dutil, 1995). In this test small metal pins are removed individually from a well at the top of the test board and placed sequentially into a row comprised of 25 holes. Testing was done both unilaterally and bilaterally, following the test procedure identified by Tiffin (Tiffin & Asher, 1948). Normative data was derived from two sources. Elderly data were derived from a study of 180 males and females over the age of 60 years and categorized by age group (Desrosiers et al., 1995). Normative data for young adults was derived from a study of 373 female hourly production workers at a manufacturing plant (Tiffin & Asher, 1948).

2.1.3. Task

Prior to testing, all participants washed their hands to normalize surface friction. Participants were seated at a table with the arm slightly abducted, the elbow supported and flexed to approximately 90°, the forearm in neutral or semi-pronated position, and the wrist in 20-30° extension (see Figure 2.1). Once the limb was appropriately placed, the position was outlined on the table, so that all

trials were completed using the same position. The head was maintained in an upright position with forward and centered gaze throughout testing. Using an instrumented grasp force device stabilized on the table, participants produced maximum voluntary grasp forces during unilateral grasp, bilateral grasp and bilateral grasp-pinch tasks. Instructions were to increase force, following an auditory cue, “as quickly and smoothly as possible” to the maximum force level and maintain it for the remainder of the 5s trial. Subjects were not provided with visual feedback. Grasp forces were recorded in blocked and counterbalanced order for both the dominant (D) and nondominant (N) hands, with 3 trials recorded for each task. A 2-min rest period was provided after each trial (Chaffin, 1975). After every 6 trials, participants rested for an additional 10-15 minutes.



Figure 2.1. Upper limb and hand position for grasp force production.

2.1.4. Recording Apparatus

Whole hand grasp force was measured in both experiments using a custom-designed grasp device composed of a split polyetherimide cylinder 3.5 cm in diameter and 14 cm in length, in which a strain gauge force transducer was centrally embedded. Polyetherimide (Ultem, McMaster-Carr) was selected for these properties: perceived subject comfort during grasp, ease of machine cutting, ability to be easily cleaned between subjects, and high mechanical strength and dimensional stability, so that product wear would not occur with repeated use. The strain gauge used was a bonded foil compression strain gauge load cell (Omega, Stamford, CT). Each load cell was capable of measuring force output from zero to 1112 N. The zero balance of each cell was $\pm 5\%$, with a repeatability rating of ± 0.1 of full scale, and hysteresis of 0.2%, as identified by the manufacturer. The button mount model allowed force to be received from multiple directions, thus capturing force output from all fingers during a whole-hand grasp and also allowed for a design appropriate for hand grasp.

Lateral pinch force was measured using a similar strain gauge force transducer, measuring zero to 222 N, that was placed between two flat stainless steel bars 11 by 2 cm in length. Linearity of all strain gauge force signals was established by linear regression prior to data collection.

2.1.5. Data Acquisition and Analysis

A frequency analysis determined that the best cutoff frequencies for grasp force data were between 3 and 15 Hz. Data were digitized at 250 Hz, filtered using a fourth-order Butterworth filter with a cutoff frequency of 4 Hz, and analyzed off-line using LabVIEW © (National Instruments) software for data point selection. No outliers were removed from this study; 11 trials, or less than three percent of all trials, were omitted due to technical problems. Onset time and force values were defined as the time when the force profile exceeded two standard deviations above the mean of the first 300 ms of data collection.

Peak time and force values were selected from the first derivative of the filtered force record. Task peak time was defined as the first negative-going zero crossing of the first derivative of the force record in the time interval between onset and the absolute force peak, with the additional condition that that the corresponding force peak was within 90% of the absolute peak force value. For example, in figure 2.2., d.1, the task peak is the negative-going zero-crossing in the derivative record, which corresponds to a local maximum in the force record (Figure 2.2, D).

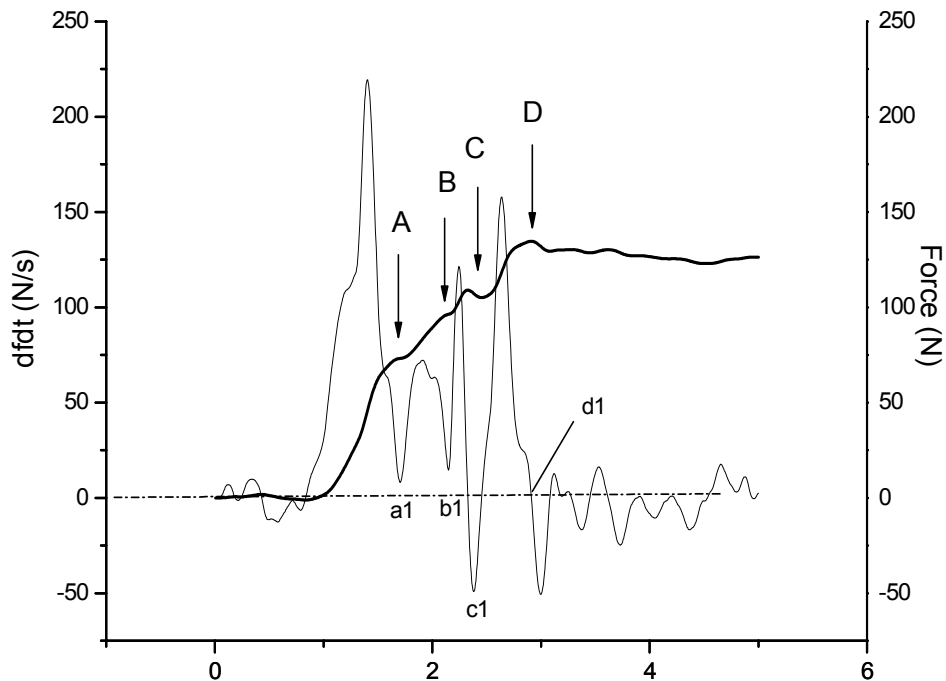


Figure 2.2. Grasp force profile (heavy line) and first derivative (light line). Force inflections during force rise are shown at A, B and C. Note that the local peak before C is not within 90 percent of the maximum force magnitude; therefore D was selected as the task peak force value. a1, b1, c1 and d1 indicate corresponding values in the first derivative record.

Inflections between onset and task peak times were identified as a local minimum following a local maximum in the first derivative of the force record (Figure 2.2., a1, b1, c1). Inflections appeared in the force record either as a local maximum (Figure 2.2., C) or as a changing slope characterized by a shallow positive slope between two steep positive slopes (Figure 2.2., A and B). To exclude trivial inflections, a change of greater than 15 N/s was required between the minimum and maximum values in the first derivative record. All onset and task peak data points were further verified through visual inspection. The percent

bilateral change was calculated for all trials as follows: $C = \left(\frac{B}{U} - 1 \right) * 100$ where

C is the percent bilateral change, B is bilateral force, and U is unilateral force.

2.1.6. Statistical Analysis

A normal distribution of all variables was identified and descriptive statistics were obtained. A 3 (Group: Young, Old, Old-Old) X 2 (Hand: dominant, nondominant) X 3 (Task: unilateral grasp, bilateral grasp, grasp with pinch) analysis of variance was used to determine age, task and hand differences for the grasp force values generated. The hand and task factors were repeated measures. No significant difference was found among the three trials for each participant; therefore, averaged means were used for data analysis. A probability level of .05 was established. Post-hoc analysis was obtained, with significance levels adjusted using the Bonferroni correction.

2.2. Experiment Two

2.2.1. Participants

Participants were recruited from the same university and community areas. All were healthy, right-handed young and old females who were independent community dwellers. Exclusion criteria were the same as those used in the previous experiment. Participants gave informed consent and the protocol was approved by the University of Michigan Behavioral Sciences Institutional Review Board (H05-0000-7860-1).

2.2.2. Task

The same upper limb and hand position was used for grasp force production as described in the previous experiment. Subjects produced isometric submaximal grasp forces of the same and different force levels during unilateral, bilateral simultaneous and bilateral sequential tasks.

Grasp force was initiated “as quickly as possible” in response to auditory tones. A single tone was used to initiate unilateral and bilateral simultaneous trials while sequential trials used tones that occurred at approximately 4s intervals. The hand that maintained grasp force throughout bilateral sequential trials (approximately 12s) was termed the static hand, and was the hand of interest in this experiment. The opposite hand was identified as the transient hand, and developed and held a force level for a 4s interval during the period of static hand force maintenance. Each hand was tested in both the static and transient condition.

Grasp force production and relaxation during bilateral sequential trials occurred in response to auditory tones occurring at 4s intervals, with the following sequence: static hand grasp force development, transient hand grasp force development, transient hand grasp force relaxation, static hand grasp force relaxation. Three trials were recorded for each task, with a two-minute rest between trials (Chaffin, 1975). Fatigue was operationally defined as the presence of self-perceived discomfort on questioning.

Force levels included a self-selected firm and light force. The phrase “like squeezing but not breaking an uncooked fresh egg” was used to explain the

desired light force level to participants, and the phrase, “like a firm handshake” was used for the firm force level. Operationally, light and firm forces were defined as less than 15% and between 40-70% of a maximum voluntary contraction force, respectively. Three or more practice trials were provided to ensure relatively consistent force level production at the preferred force value. Bilateral sequential tasks included similar and different force levels: static light / transient light (LL), static firm / transient firm (FF), static firm / transient light (FL), and static light / transient firm (LF). Unilateral and bilateral simultaneous tasks were completed in randomized blocks of trials prior to bilateral sequential tasks, and blocks of the same force were randomized and completed before blocks using different force levels.

2.2.3. Recording Apparatus

The same grasp force device was used as described in the previous experiment.

2.2.4. Data Acquisition and Analysis

Data were digitized at 100 Hz, filtered using a fourth-order Butterworth filter and cutoff frequency of 8 Hz and analyzed offline using LabVIEW© (National Instruments) software for data point selection. Force and temporal values at onset, peak and termination were determined through differentiation of the force record and verified by visual inspection. Onset force and time were defined as the first time that force increased to two standard deviations greater than the force mean of the first 300ms. The offset force and time, used only in

sequential force tasks, was similarly defined as the last time that force was two standard deviations greater than the mean of the final 300ms. The peak force value was identified as the force value occurring at the first negative-going zero-crossing of the differentiated record after force onset. The relaxation value was defined as the last negative-going zero-crossing of the differentiated record before force offset. A graphic presentation of sequential force values is shown in Figure 2.3.

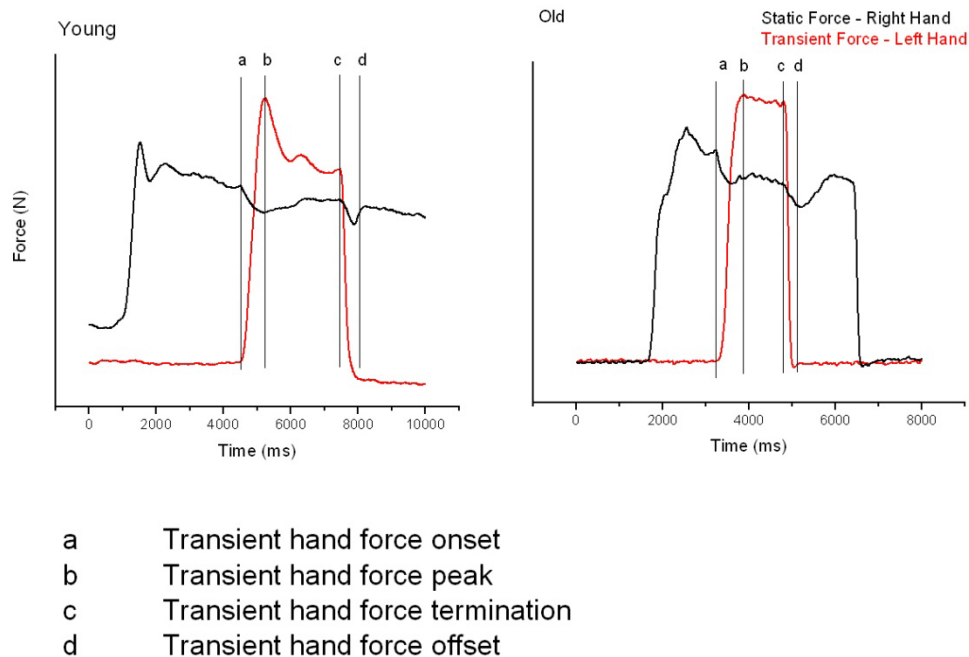


Figure 2.3. Force record with identified onset, peak, relaxation and offset data points for a young and old adult during bilateral sequential grasp force production. Firm force was produced in both hands. In the example shown, a = transient hand force onset, b = transient hand force peak, c = transient hand force relaxation, and d = transient hand force offset.

Static force values were examined between the times of transient hand onset and peak. The percent difference between the maximum (f_M) and minimum (f_m) static forces was defined as $\pm 100(f_M - f_m) / f_M$. The sign was

assigned as positive (negative) if the minimum (maximum) occurred first. Static force values were similarly examined between the times of transient hand relaxation and offset + 50 ms.

Force maintenance data was gathered for 2s during the period between onset and decline. During the 10s unilateral and bilateral trials, this period was operationally defined as the time period occurring between 4.5 and 6.5s after the initial tone. Force maintenance data for the longer sequential trials was gathered before (1s), during (2s) and following (2s) transient hand force production, as shown in Figure 2.4. Static hand force maintenance was assessed for 2s between 5.8s and 7.8s after the initial tone (at 4.1s in figure 2.4). To measure static hand force magnitude before transient hand onset, data was collected for 1s between 3s and 4s after the first tone onset. This period was shorter than other periods to allow for the force level to stabilize prior to transient force onset. To measure static hand force magnitude after transient hand release, data was collected for 2s from 9s to 11s after the initial tone.

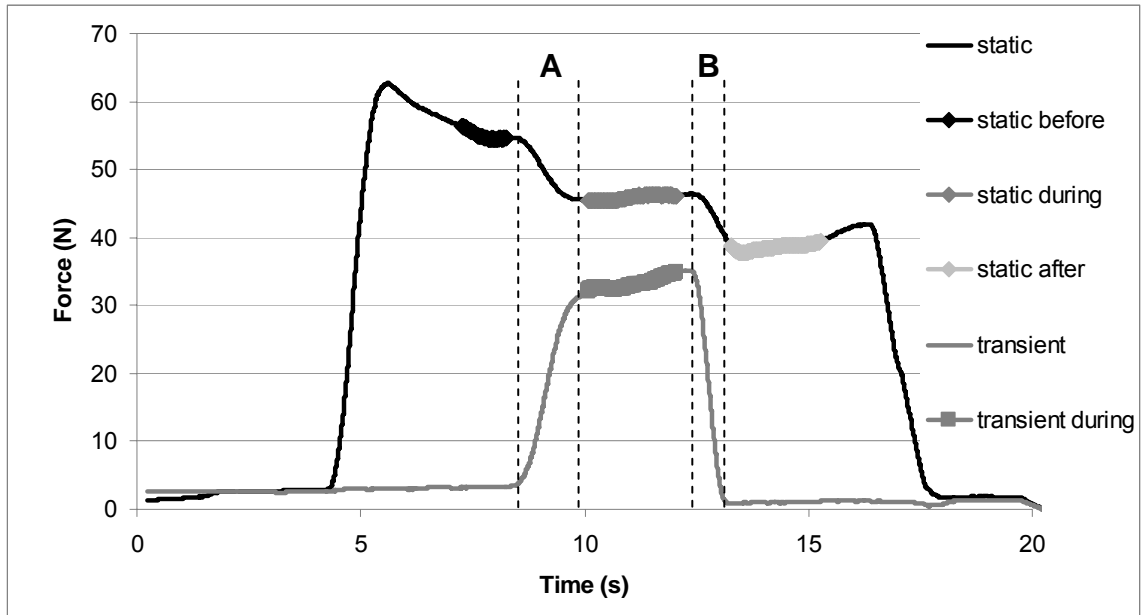


Figure 2.4. Identification of time periods used for data analysis of static hand force before, during and after transient hand force production. Maintenance of transient hand force is also identified.

The rate of change of force was defined as the change in force values divided by the change in time. Variability of maintained force was measured by the coefficient of variation (standard deviation/mean) value for the maintained force time period. Response time was defined as the time period between initial tone and force onset. Responses less than 100ms or more than 800ms were rejected as anticipation errors and delayed responses, respectively, comparable to those identified by Plat and colleagues (Plat, Praamstra, & Horstink, 2000) in their study of reaction time and force production in Parkinson's disease.

2.2.5. Statistical Analysis

A normal distribution of all variables was identified and descriptive statistics were obtained. Statistical significance was primarily examined using a 2

(age: young, old) x 2 (hand: dominant, nondominant) x 2 (force: firm, light) x3 (condition: unilateral, bilateral simultaneous, bilateral sequential) repeated measures ANOVA, with hand, force and task as repeating factors. Student's *t* test was used to assess differences between two sets of data. The level of significance was established at .05.

CHAPTER III

RESULTS

This chapter presents the results from two experiments that explore the coordination of bilateral grasp force in young and old adults. The first experiment examined the production and coordination of bilateral maximum forces using the same (grasp-grasp) or different (grasp-pinch) tasks. Results from the second experiment are then presented, which examined the coordination of same and different submaximal bilateral grasp forces when produced simultaneously or sequentially.

3.1. **Experiment One: Bilateral Simultaneous Maximum Grasp Force Production**

3.1.1. Participant Characteristics

Twelve young (Y) (18-28y), 12 old (O) (65-75y) and 12 old-old (OO) (76-85y) healthy community-dwelling females participated in the study. All were right-handed, with no difference across laterality (handedness) indices for the three age groups, $F(2,33) = .33$, $p = 0.72$. Table 3.1 summarizes mean age and laterality indices for experiment one participants.

Table 3.1. Age and Laterality of Participants in Experiment One.

Characteristics	Young(n=12)	Old(n=12)	Old-Old(n=12)
Age (y) mean (SD)	21.2 (2.8)	69.6 (2.9)	80.4 (2.9)
Range	18-28	65-75	76-85
Laterality Mean (SD)	0.85 (1.2)	0.92 (0.1)	0.89 (0.2)
Range	0.63-1.0	0.64-1.0	0.52-1.0

During the initial interview, old and old-old adults identified an average of 1.6 and 3.0 medical conditions, respectively, with the most commonly reported conditions in old adults being self-reported but non-diagnosed osteoarthritis not affecting the hand, and high blood pressure. In old-old adults, these conditions were also present, as well as slight decreases in vision and/or hearing. Despite these self-reported medical conditions, no old or old-old adult identified any difficulty performing hand grasp tasks. Clinical assessment of muscle tone revealed a slight increase in one old adult, and functional testing of motor coordination revealed mild incoordination in four old adults. No abnormalities in upper limb and hand function or muscle tone were identified upon clinical examination in any young adult.

The Mini Mental State Examination was given to all participants to screen cognitive skills, with scores below 24 considered indicative of cognitive impairment. Scores by age group are provided in Table 3.2. The young compared to old group showed significantly greater cognitive skills, $F(2,33) = 6.70$, $p < 0.01$. No statistically significant differences were found between the young and old-old or old and old-old groups.

The Arthritis Impact Measurement Scales 2 (AIMS) measured self-reported daily function. Group means and standard deviation for each scale are provided in Table 3.2, with lower values indicating greater function. All group means for the four subscales were within normal age-based limits. On inspection, however, the subscale for hand and finger function was the most sensitive to change with aging. Young adults reported significantly fewer problems in hand and finger function than either the old or old-old groups, $F(2,33) = 6.78, p < 0.01$.

The Jebsen Hand Function Test assessed speed of hand function during the performance of simulated tasks. While means for all adults were within age-related norms, young adults performed the task more quickly compared to both old and old-old adults as shown in Table 3.2. In the right hand, young adults were significantly faster than both old and old-old adults, $F(2,33) = 7.26, p < 0.01$, while, in the left hand, young adults were significantly faster compared to old-old but not old adults, $F(2,33) = 4.15, p < 0.02$.

Table 3.2. Cognition, Daily Tasks, and Hand Dexterity of Participants in Experiment One

Clinical Assessments	Young (n=12)	Old (n=12)	Old-Old (n=12)
MMSE			
Mean (SD)	30 (0)	29 (.85)	29.4 (.74)
Range	30	27-30	28-30
AIMS Subscale Mean (SD)			
Hand and Finger	0.0 (.1)	0.3 (.4)	0.5 (.6)
Upper Extremity	0 (0)	0.1 (0.3)	0.2 (0.6)
Self Care	0 (0)	0 (0)	0 (0.1)
Household Care	0 (0)	0 (0)	0.1 (0.2)
R Jebsen (s) Mean (SD)			
Writing	11.1 (4.9)	12.3 (1.6)	13.2 (2.7)
Card turn	3.9 (0.7)	5.3 (1.9)	5.8 (1.9)
Small Objects	5.8 (0.5)	6.6 (1.0)	6.9 (1.1)
Spoon	7.1 (1.3)	7.4 (1.2)	7.5 (1.2)
Checkers	3.2 (1.2)	4.5 (1.7)	5.0 (1.9)
L Jebsen (s) Mean (SD)			
Writing	25.8 (9.9)	29.9 (7.4)	32.8 (9.9)
Card turn	4.0 (0.8)	5.3 (1.6)	5.3 (1.4)
Small Objects	6.0 (0.8)	6.7 (0.8)	7.1 (1.0)
Spoon	8.2 (2.9)	9.1 (2.0)	9.5 (1.4)
Checkers	3.5 (1.6)	4.9 (1.6)	5.4 (2.3)
Purdue Pegboard:Pins Mean (SD)			
Right	16.4 (2.3)	13.3 (1.6)	12.8 (1.5)
Left	14.3 (2.5)	12.9 (0.8)	11.3 (1.5)
Bilateral	13.1 (1.7)	10.7 (1.6)	9.6 (1.4)

The Purdue Pegboard was administered to measure fine manual dexterity. Scores for the dominant, nondominant and bilateral placing subtests, shown in Table 3.2, were within accepted age-based ranges. In right hand tasks, young compared to old and old-old adults were significantly more dextrous in both unilateral, $F(2,33) = 13.97, p < 0.001$, and bilateral, $F(2,33) = 14.96, p < 0.001$, tasks. When comparing left hand performance, young were significantly more dextrous than old-old $F(2,33) = 9.00, p < 0.001$, but differences between young and old adults were not statistically significant.

3.1.2. Grasp Force Profiles

Representative force records associated with the maximum bilateral grasp/grasp task are shown for a young (A), old (B) and old-old (C) adult in Figure 3.1. In general, grasp force production was characterized by a relatively uninterrupted increase to maximum force levels, regardless of hand or bilateral task (i.e., grasp-grasp or grasp-pinch task). This was followed by maintenance of grasp force at approximately the same force magnitude.

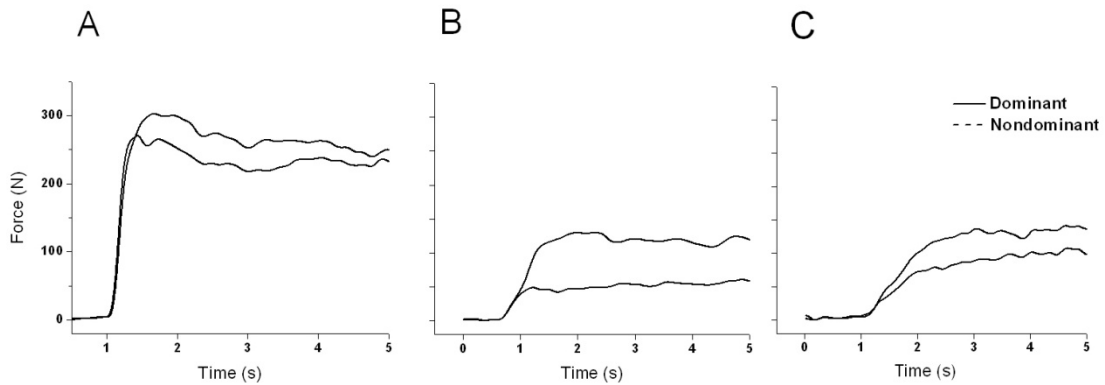


Figure 3.1. Typical bilateral grasp-grasp force profiles for a young (A), old (B), and old-old (C) adult.

Across all age groups, force was occasionally produced in two relatively distinct stages with each stage maintained for at least 1s. This occurred in approximately 12 percent of all trials, with 23, 16, and 22 trials respectively for unilateral, bilateral grasp-grasp and bilateral grasp-pinch trials. The maximum force produced in these trials occurred in the second stage, and represented an additional gain of at least 50N compared to the first stage of force development.

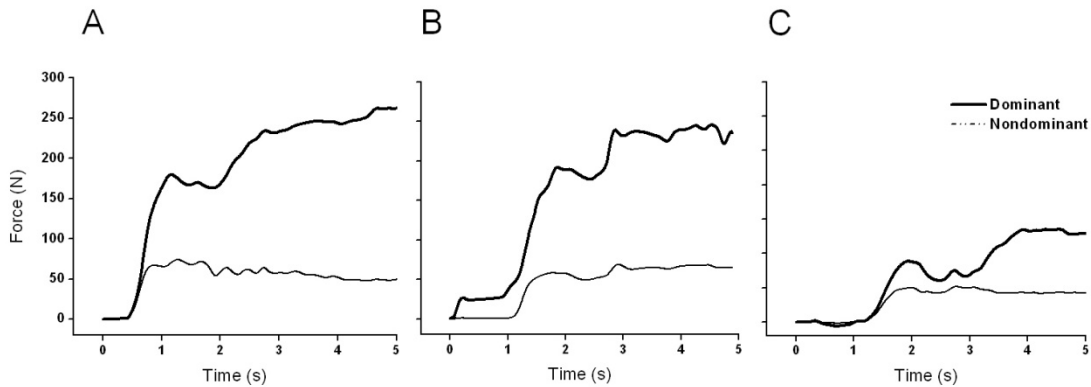


Figure 3.2. Typical records of force produced in two stages for each age group. Profiles are for a young (A), old (B) and old-old (C) adult.

3.1.3. Force Inflections

Force inflections during force rise were present in all age groups during force rise to maximum force, but a main effect for age, $F(2, 33) = 4.58, p < .02$, was found, as shown in Figure 3.3. Inflections seen in grasp force development increased with age in both the percentage of trials in which they were found and in the mean number of inflections observed in each trial. Inflections during force rise were observed in 14, 44 and 87 percent of trials in young, old, and old-old adults, respectively. The mean number of inflections increased from about 1.5 in young adults to 2.5 in old and 3.5 inflections in the old-old group. Post hoc analysis revealed a greater number of inflections in old-old compared to young adults ($p < .02$).

When all age groups were combined, a main effect for hand, $F(1, 33) = 8.02, p < .01$, was found when unilateral, grasp-grasp and grasp-pinch trials were combined. Post hoc analysis showed that the greater number of inflections were observed in the dominant compared to the nondominant hand, $p < .01$, in old-old

adults. The greatest number of inflections was found during unilateral force development in the dominant hand and in nondominant grasp in the grasp-pinch task in old-old adults. The number of inflections was relatively constant across tasks and in each hand for young adults, while the old and old-old groups varied in the number of inflections across both task and hand.

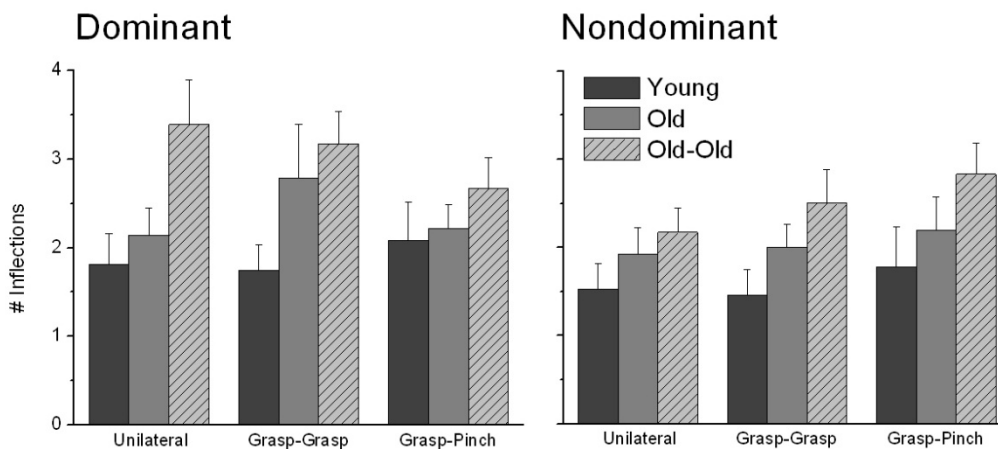


Figure 3.3. Mean (+1SE) number of inflections during force rise by age, task, and hand.

3.1.4. Peak Force Magnitude

Across all tasks, maximum grasp force magnitude was significantly greater in young compared to either old or old-old adults, $F(2, 33) = 39.69$, $p < .0001$, as shown in Figure 3.4. There was a significant interaction of age and hand, $F(1,21) = 10.53$, $p < .01$, with the dominant compared to the nondominant hand producing greater grasp force in each age group. Old compared to young adults showed a decrease of 48 and 52 percent in the dominant and nondominant hands, respectively. A further force decrease occurred in old-old compared to old adults, with additional decreases of 17 and 19 percent in the

dominant and nondominant hands, respectively. However, the difference in maximum force capabilities of old and old-old adults was nonsignificant.

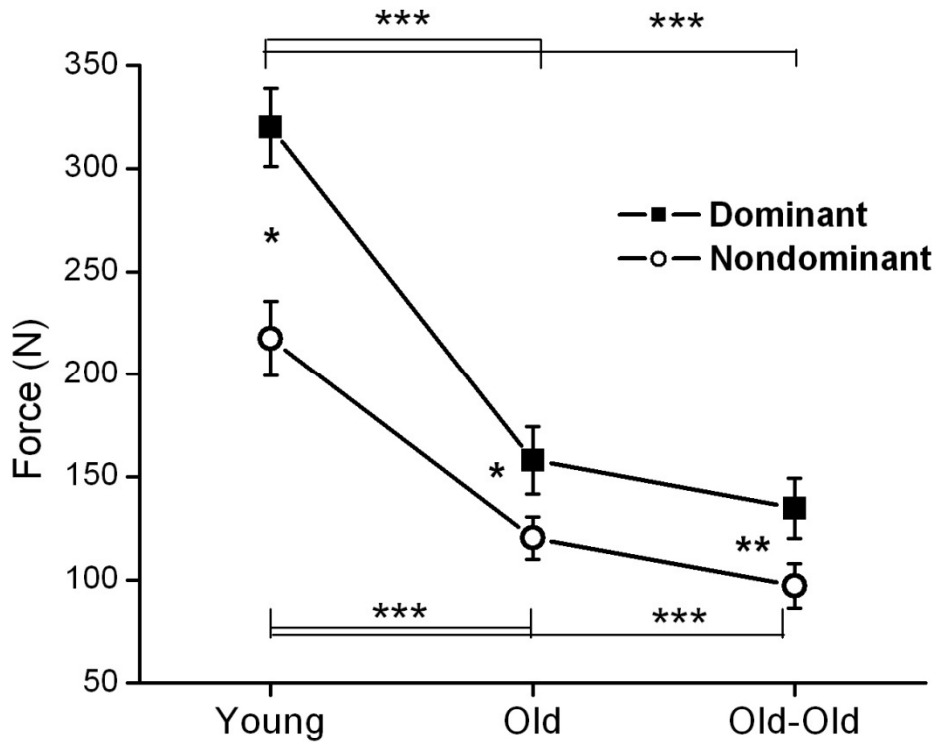


Figure 3.4. Mean ($\pm 1SE$) unilateral maximum force magnitude by age and hand. * $p < .05$, ** $p < .01$, *** $p < .001$.

3.1.5. Change in Force during Bilateral Tasks

In the young group, a significant force deficit was found in the dominant hand in both bilateral grasp-grasp, $t(11) = -2.29$, $p < 0.05$, and grasp-pinch, $t(11) = -4.97$, $p < 0.001$, tasks, as shown in Table 3.3 and Figure 3.5. In the nondominant hand, however, no significant change was found although a trend toward a bilateral facilitation was observed.

In the old group, no significant force change was found for the dominant or nondominant hand in either grasp-grasp or grasp-pinch tasks. There was also no significant force change in the old-old group.

Table 3.3. Percent Bilateral Change in Maximum Force

Age group		Dominant grasp-grasp	Dominant grasp-pinch	Nondominant grasp-grasp	Nondominant grasp-pinch
Young	Mean (SE)	-11.6 (5.1)	-19.9 (4.0)	6.5 (5.4)	24.2 (13.8)
Old	Mean (SE)	4.2 (12.2)	4.5 (12.6)	-2.4 (9.3)	4.1 (13.0)
Old-Old	Mean (SE)	-8.8 (7.8)	-8.9 (8.0)	-1.9 (8.9)	6.0 (16.2)

A force deficit is indicated by a minus sign.

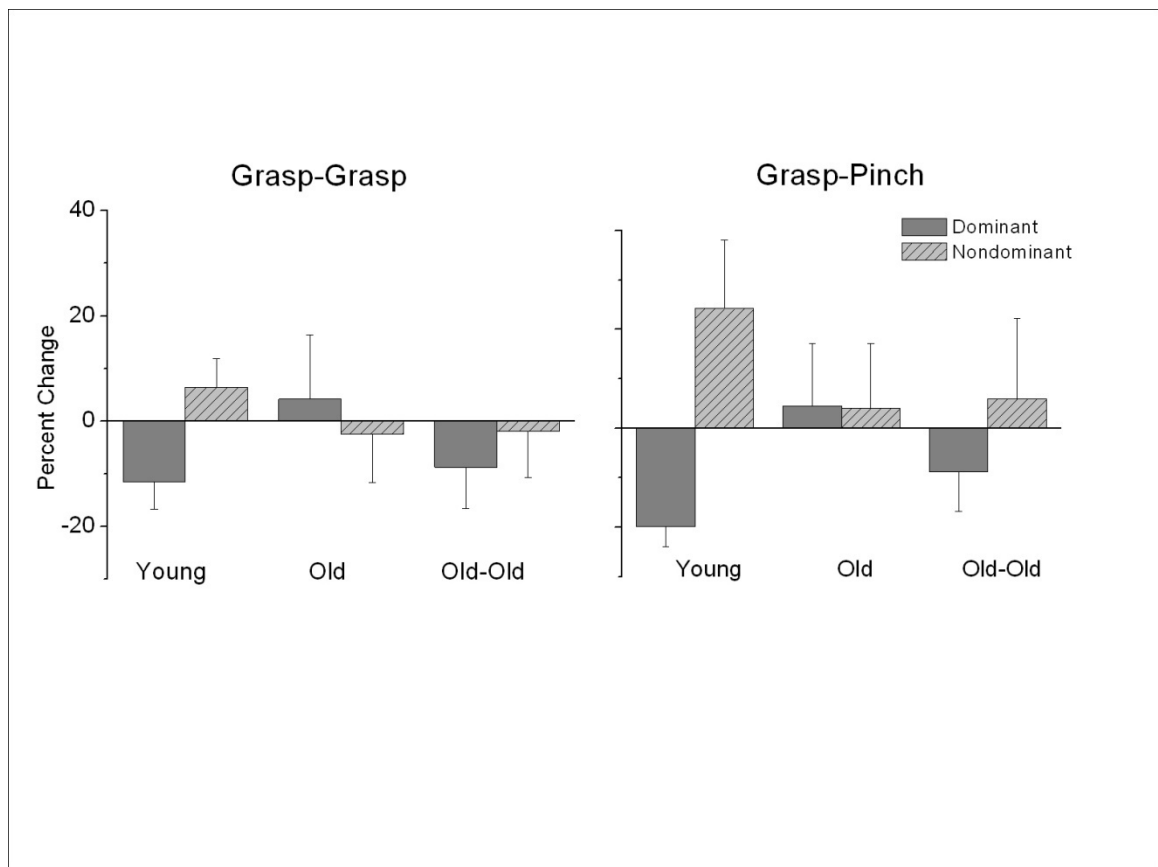


Figure 3.5. Mean (+1SE) percent bilateral change in maximum force by age and hand.

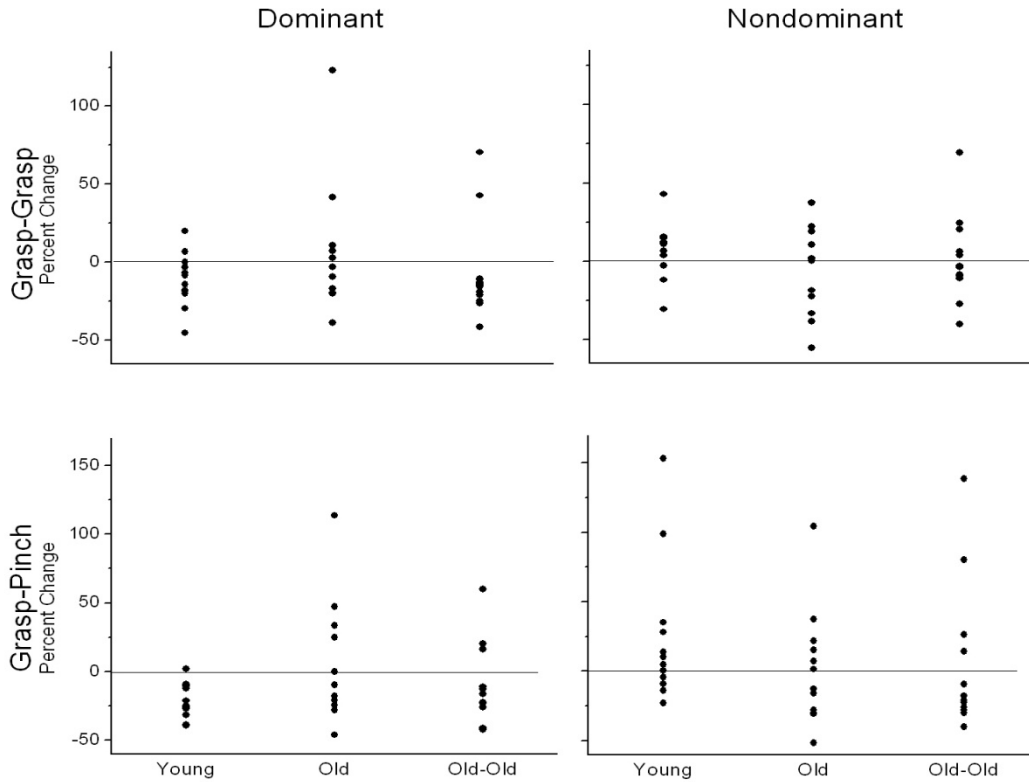


Figure 3.6. Individual means for grasp-grasp and grasp-pinch tasks by age and hand

As reflected in Table 3.4, and Figure 3.5, considerable inter-participant variability in the amount and direction of the force change occurred, for all age groups, with the exception of the dominant hand in young adults. This is further shown in Figure 3.6, where individual participant means are presented. In the nondominant hand of young adults, and in both hands of old and old-old adults, considerable individual variation occurred. In each age group, there were one or two participants who showed a large force facilitation, i.e., whose force was greater during the bilateral compared to unilateral task.

Individual bilateral versus unilateral force values are cross-plotted in Figure 3.7. In the old group, no consistent change in force production was observed, as reflected by the distribution of data points above and below the line of unity in all tasks. A similar pattern of distribution was also observed in the old-old group.

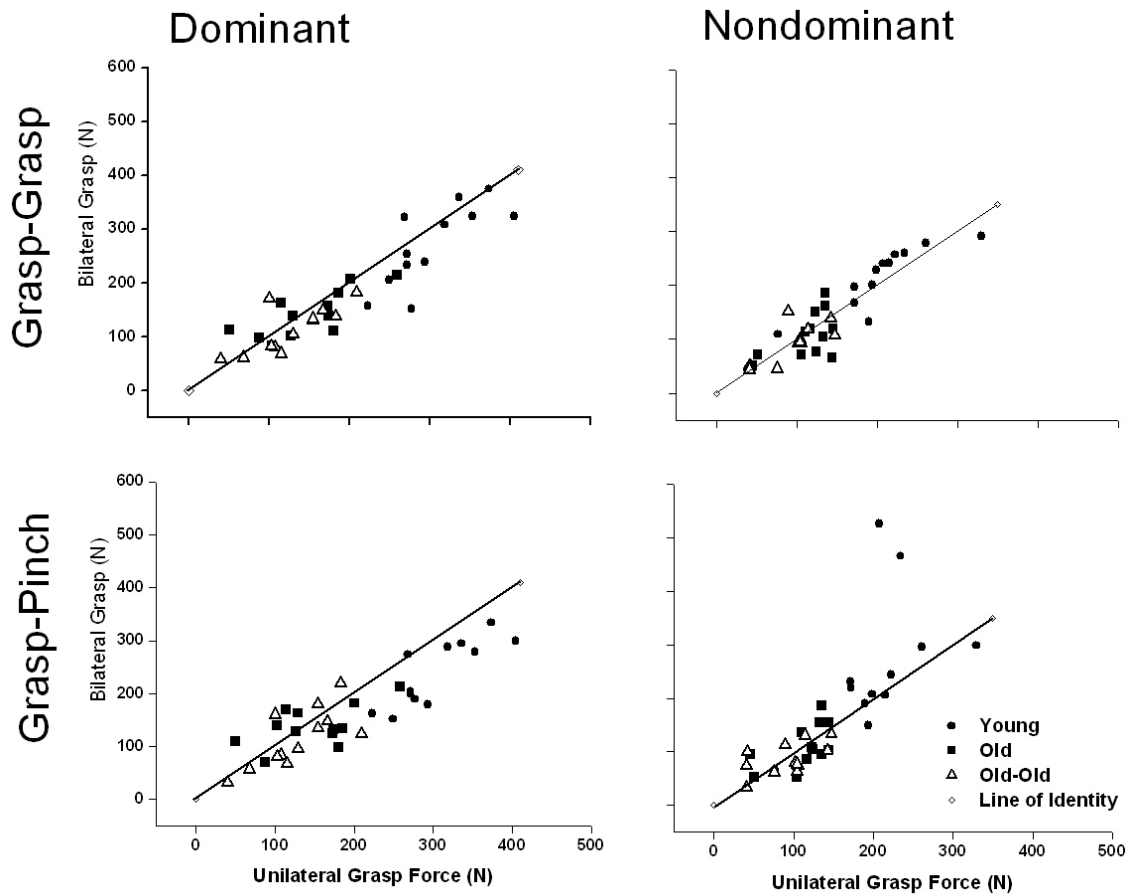


Figure 3.7. Cross-correlation plots between unilateral and bilateral grasp force for (A) grasp-grasp and (B) grasp-pinch tasks. Data below the line of unity indicate a bilateral deficit, data above the line indicate a bilateral facilitation. Each data point represents the average of three trials for an individual participant.

3.1.6. Temporal Coordination of Force Onset During Bilateral Tasks

Temporal coordination of force onset during bilateral force production showed a main effect for age when all age groups were examined, $F(2,33) = 11.251, p < .001$. As shown in Table 3.4, a significant difference in dominant and nondominant grasp onset time was found between young and both old groups, and between the old and old-old group. The mean difference between dominant and nondominant hand onset times increased for each age group from grasp-grasp to grasp-pinch tasks. Post-hoc analysis revealed a difference in dominant-nondominant onset times between young and old, $p = .019$, as well as between old and old-old adults, $p < .0001$. On average, in all groups and tasks, the nondominant preceded the dominant hand.

The greatest difference in onset times for all groups occurred when grasp force was produced by the nondominant hand in grasp-pinch tasks. During these tasks, onset time differences in all age groups were approximately twice those found in dominant grasp-nondominant pinch tasks.

Table 3.4. Mean ms (+/- 1 SE) Difference in Dominant (D) and Nondominant (N) Hand Onset Time by Age and Task

Age	Grasp-Grasp	D grasp-N pinch	N grasp-D pinch
Young	52.0 ± 6.3	120.0 ± 25.9	366.4 ± 104.2
Old	168.1 ± 39.2	164.8 ± 40.5	350.3 ± 45.7
Old-Old	71.2 ± 33.4	211.3 ± 43.2	402.0 ± 70.7

In young adults, onset times were most tightly coupled during tasks in which both hands produced grasp-grasp force with a significant difference found between grasp-grasp and nondominant grasp-dominant pinch tasks ($p < .05$). In

old adults, a similar finding was found, with significant differences between onset times in grasp-grasp and nondominant grasp-dominant pinch ($p < .05$), but not dominant grasp-nondominant pinch tasks. In old-old adults, grasp-pinch onset times were significantly different than those for the grasp-grasp task, regardless of whether the dominant ($p < .02$), or nondominant ($p \leq .001$) hand produced grasp force.

3.2. Experiment Two: Sequential Bilateral Submaximal Grasp Force Coordination

Twelve young (22-27 y) and twelve old (75-87y) healthy, right-handed, community-dwelling females participated in the study. There was no difference in handedness between the two age groups, $t(22) = .33$, $p = 0.74$. Mean age, standard deviation and laterality are summarized in Table 3.5.

Table 3.5. Age and Laterality of Adults in Experiment Two

Characteristics	Young (n = 12)	Old (n = 12)
Age (y) mean (SD)	21.9 (3.5)	78.2 (2.7)
Range	18-27	75-85
Laterality mean (SD)	90.8 (9.6)	89.1(15.5)
Range	75-100	57-100

3.2.1. Peak Force Magnitude

As shown in Figure 3.8 and Table 3.6, young compared to old adults produced significantly greater maximum forces in each hand, $F(1,21) = 23.6$, $p < .0001$. In addition, there was a significant interaction between hand and age during maximum force production, $F(1,21) = 10.525$, $p < .01$, with greater

maximum force differences observed between the dominant and nondominant hands in young but not old adults.

Given the instruction to produce a grasp force similar to “a firm handshake” (firm force) or “squeezing an uncooked egg without breaking it” (light force), individuals within each age group produced fairly constant force magnitudes, as can be seen by the relatively small standard errors for each force produced. Additionally, each age group was able to consistently produce approximately the same firm or light force magnitude across all tasks and in both hands.

A main effect for age, $F(1,21) = 7.279$, $p = .013$, and hand, $F(1,21) = 18.110$, $p < .001$, was found in peak force magnitude when either unilateral or bilateral simultaneous firm force was produced. Firm force production was significantly less in old compared to young adults in both unilateral, $F(1,22) = 6.77$, $p < .02$, and bilateral, $F(1,22) = 7.58$, $p < .02$, tasks. When light tasks were examined, no significant differences between young and old adults in any unilateral, bilateral simultaneous or bilateral sequential light task were observed.

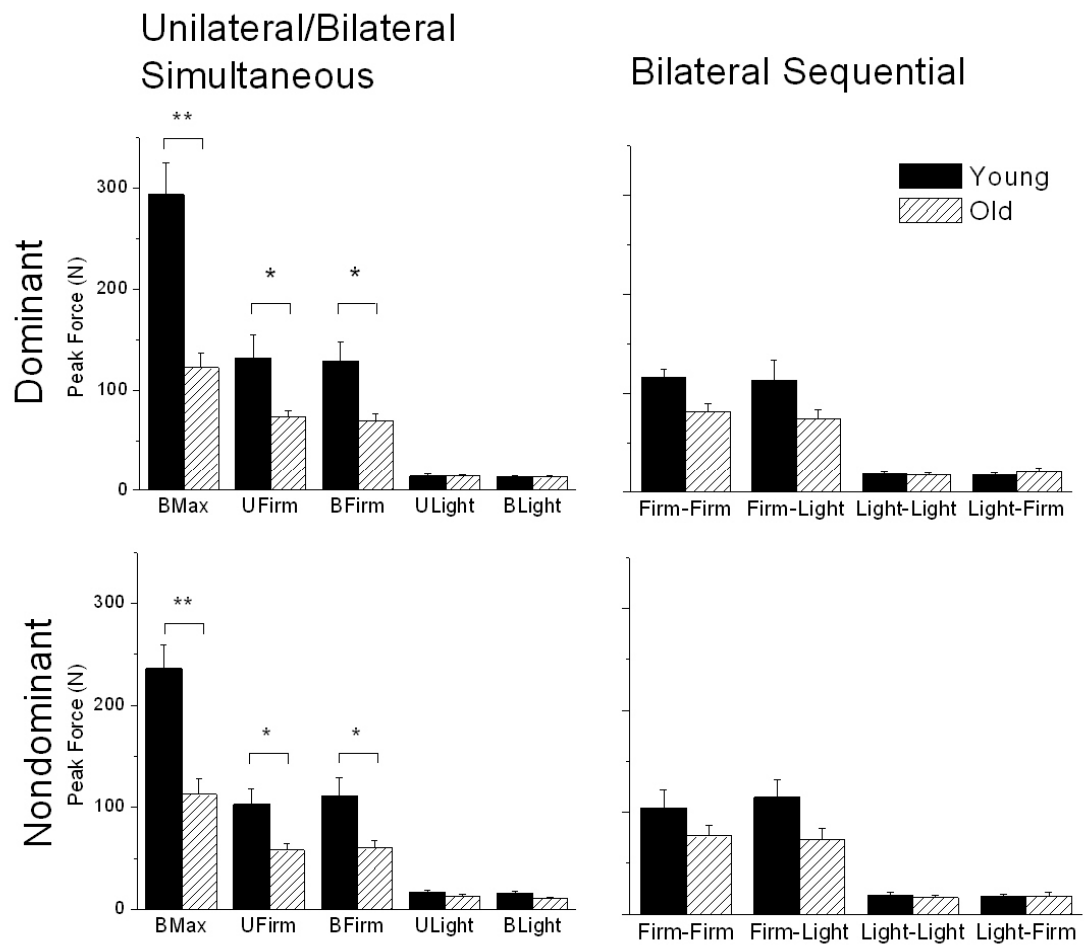


Figure 3.8. Mean (\pm 1SE) peak force magnitude for young and old adults. BMax = bilateral simultaneous maximum; UFirm = unilateral firm; BFirm = bilateral simultaneous firm; ULight = unilateral light; BLight = bilateral simultaneous light; Firm-Firm = bilateral sequential static firm-transient firm; Firm-Light = bilateral sequential static firm-transient light; Light-Light = bilateral sequential static light-transient light; Light-Firm = bilateral sequential static light-transient firm.

* $p < 0.05$, ** $p < 0.01$.

Table 3.6. Peak force (N) in Unilateral, Bilateral Simultaneous and Bilateral Sequential Tasks

Task	Young Dominant	Young Nondominant	Old Dominant	Old Nondominant
Bilateral Simultaneous Maximum	293.3 (32.2)	235.5 (23.6)	122.5 (14.4)	112.6 (15.4)
Unilateral Firm	131.5 (23.1)	102.3 (15.8)	73.6 (6.3)	58.0 (6.5)
Bilateral Simultaneous Firm	127.9 (19.5)	110.9 (18.1)	69.7 (6.8)	60.0 (7.0)
Unilateral Light	14.0 (2.0)	15.8 (3.0)	14.3 (1.2)	12.6 (1.7)
Bilateral Simultaneous Light	13.0 (1.7)	15.2 (2.3)	12.8 (1.8)	10.6 (1.3)
Bilateral Sequential Firm – Firm	116.7 (19.4)	104.4 (17.4)	82.1 (8.2)	76.8 (10.1)
Bilateral Sequential Firm – Light	113.3 (20.4)	114.6 (17.8)	75.0 (8.7)	73.5 (10.6)
Bilateral Sequential Light – Light	17.8 (2.3)	19.0 (2.4)	16.9 (2.2)	16.1 (2.1)
Bilateral Sequential Light – Firm	16.7 (2.7)	17.9 (2.0)	20.39 (4.2)	17.8 (3.6)

Values are mean N (± 1 SE). Static hand values are given for bilateral sequential trials (Firm-Firm, Firm-Light, Light-Light, Light-Firm).

3.2.2. Consistency of Self-Selected Grasp Force Values

Both young and old adults were able to produce consistent absolute forces regardless of task or hand, as shown in Figure 3.9. Dominant and nondominant hand data were combined within each age group, as there were no significant differences between them in either age group. Furthermore, no differences were found when bilateral and unilateral force magnitudes were compared for either age group.

When expressed as a percent of maximum force, old compared to young adults produced significantly greater forces in all tasks, $F(1,21) = 8.66$, $p < .01$.

The percentage of maximum force for firm forces in bilateral simultaneous tasks was approximately 40 and 60 percent for young and old adults, respectively.

In bilateral sequential tasks, however, firm force production in old adults increased further to approximately 70 percent, with increased variability, while firm forces in young adults remained approximately the same. A similar trend was found between simultaneous and sequential tasks in the percent of bilateral maximum force when light force was produced, but significance was not found. Whereas light force in young adults was approximately 7 percent of their maximum force, in old adults a light force was approximately 15 percent in bilateral simultaneous tasks and 20 percent in bilateral sequential tasks.

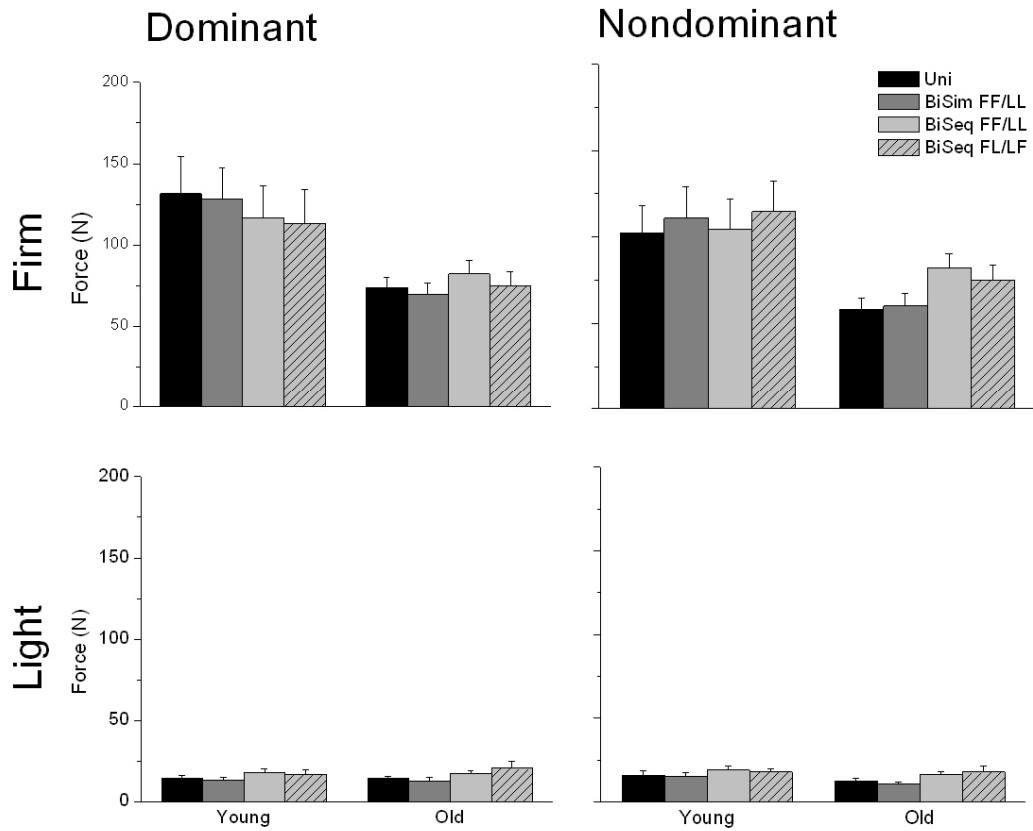


Figure 3.9. Consistency in peak force production across task. Mean (+ 1SE) absolute peak force values (N) in young and old adults for firm and light tasks. Uni = unilateral, BiSim FF/LL = bilateral simultaneous firm-firm or light-light, BiSeq FF/LL = Bilateral sequential firm-firm or light-light, BiSeq FL/LF = bilateral sequential firm-light or light-firm.

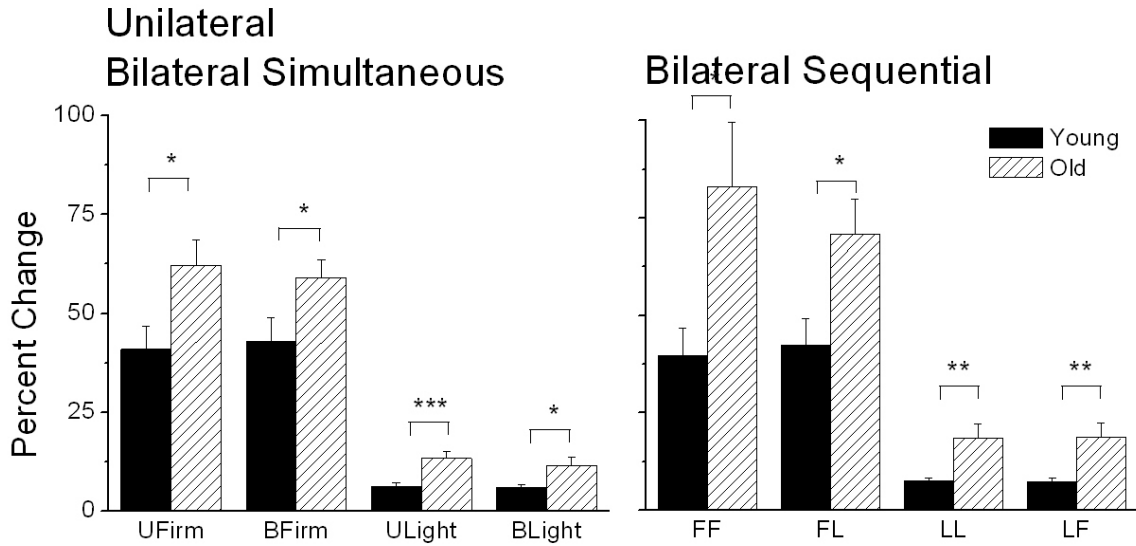


Figure 3.10. Percent change in peak force from bilateral maximum force values by age and task. Dominant and nondominant hand data for each age group are combined as they were not significantly different. UFirm = unilateral firm; BFirm = bilateral simultaneous firm; ULight = unilateral light; BLight = bilateral simultaneous light; FF = bilateral sequential firm static/firm transient; FL = bilateral sequential firm static/light transient; LL = Bilateral sequential light static /light transient; LF = Bilateral sequential light static/firm transient. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 3.7. Mean (+1SE) Percent Force Change from Bilateral Maximum for Firm and Light Tasks

Task	Young	Old
Unilateral Firm	40.9 (5.7)	62.1 (6.6)
Bilateral Simultaneous Firm	42.8 (6.0)	59.0 (4.6)
Sequential Firm-Firm	39.7 (7.0)	83.0 (16.6)
Sequential Firm-Light	42.3 (6.8)	70.8 (9.1)
Unilateral Light	6.3 (0.8)	13.3 (1.6)
Bilateral Simultaneous Light	5.9 (0.7)	11.6 (2.0)
Sequential Light-Light	7.5 (1.0)	18.5 (3.6)
Sequential Light-Firm	7.3 (1.1)	18.7 (3.7)

Dominant and nondominant hand data are combined for each task as they were not significantly different.

3.2.3. Effect of Transient Hand on Static Hand Force Maintenance

In all bilateral sequential tasks, a temporary decline in static force at the time of transient force onset and relaxation was found in both young and old adults, as shown in Figure 3.11. (Also see Figure 3.15 for a typical record showing the time period associated with the decline.) Overall, the decline in static force for both dominant and nondominant hands was greater in old compared to young adults during both transient onset, $F(1,23) = 6.03, p < .05$, and transient relaxation, $F(1,23) = 8.710, p < .01$. This greater decline in static force at transient relaxation compared to onset was also shown in both young, $t(11) = 7.588, p < .001$, and old, $t(11) = 7.898, p < .001$, age groups.

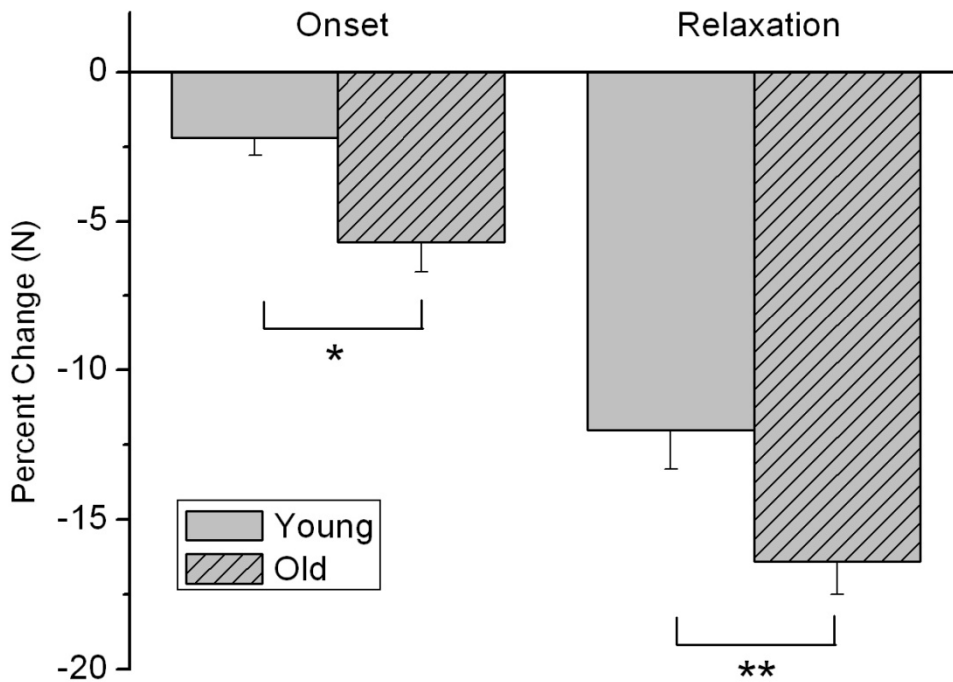


Figure 3.11. Mean (+1SE) of percent change of force in the static hand at the time of transient onset and relaxation. Hand and task data are combined.

* $p < .05$, ** $p < .01$.

Data were examined in more detail, considering the effect on static hand force of task (light-light, firm-firm, firm-light or light-firm), hand (dominant or nondominant) and time period (during transient hand onset or relaxation), as shown in Figure 3.12. In all but the light static-firm transient (LF) tasks, a decline in static force during both transient force onset and relaxation was observed in both young and old subjects. In the LF task, an increase in static force occurred in the young group while, in old adults, a very small decline was observed.

During transient force relaxation greater declines in static force occurred in all tasks regardless of which hand produced the force. While the decline in static force tended to be greater in LF tasks, differences were not statistically different across tasks or hand.

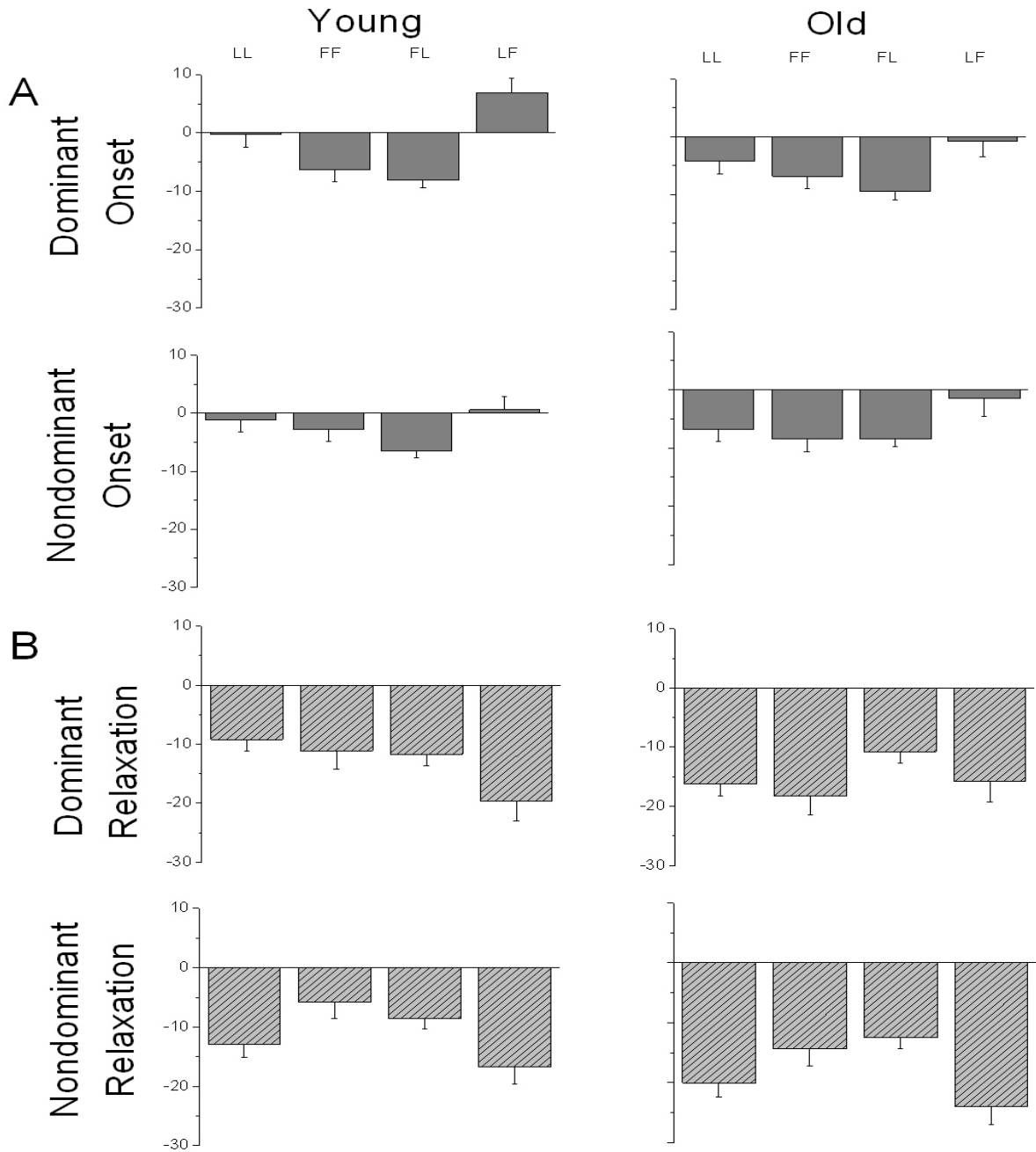


Figure 3.12. Mean (+1SE) percent force change in static hand force at the time of transient hand onset (A) and relaxation (B) in bilateral sequential tasks. LL = light static-light transient; FF = firm static-firm transient; FL = firm static-light transient; LF = light static-firm transient.

3.2.4. Rate of Change of Force

The rate of change of force was analyzed in both the static and transient hands during force rise and relaxation, as shown in Figure 3.13.

During force rise to peak force in unilateral and bilateral trials, a significantly faster rate of change of force was found in young compared to old adults ($p < .05$), except during firm-firm force development in either hand. During sequential trials, in both static and transient force rise, the rate of change of force was similar between the two groups, with a rate of change that was decreased in young and increased in old adults as compared to simultaneous trials.

Across all force relaxation tasks, a slower rate of change of force was observed in old compared to young adults during force relaxation $F(1,22) = 5.19$, $p = .03$, and in simultaneous ($p < .05$) and sequential ($p < .01$) trials. This change in force rate was greater in young compared to old adults during all firm force tasks except the transient firm-static firm task. When light force was produced, the rate of change of force was slightly greater in old compared to young adults during static and transient light-light tasks. The greatest rate of change of force in both young and old adults during light force relaxation occurred in the transient light-firm task.

No significant differences were found between the dominant and nondominant hands; therefore, data were combined for analyses. At the individual task level, the significant effect during relaxation was observed primarily in firm $F(5,75) = 2.93$, $p = .02$ task relaxation, as shown in Figure 3.13 and Table 3.8.

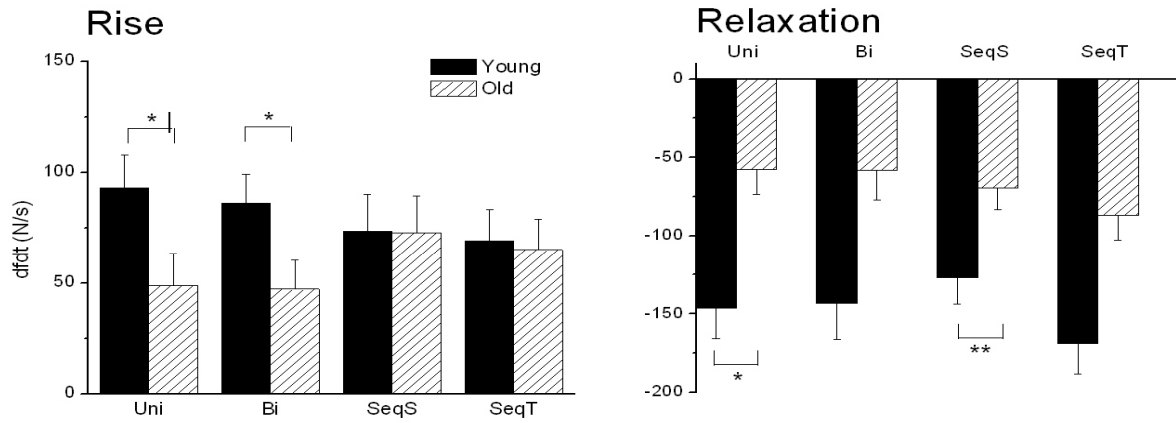
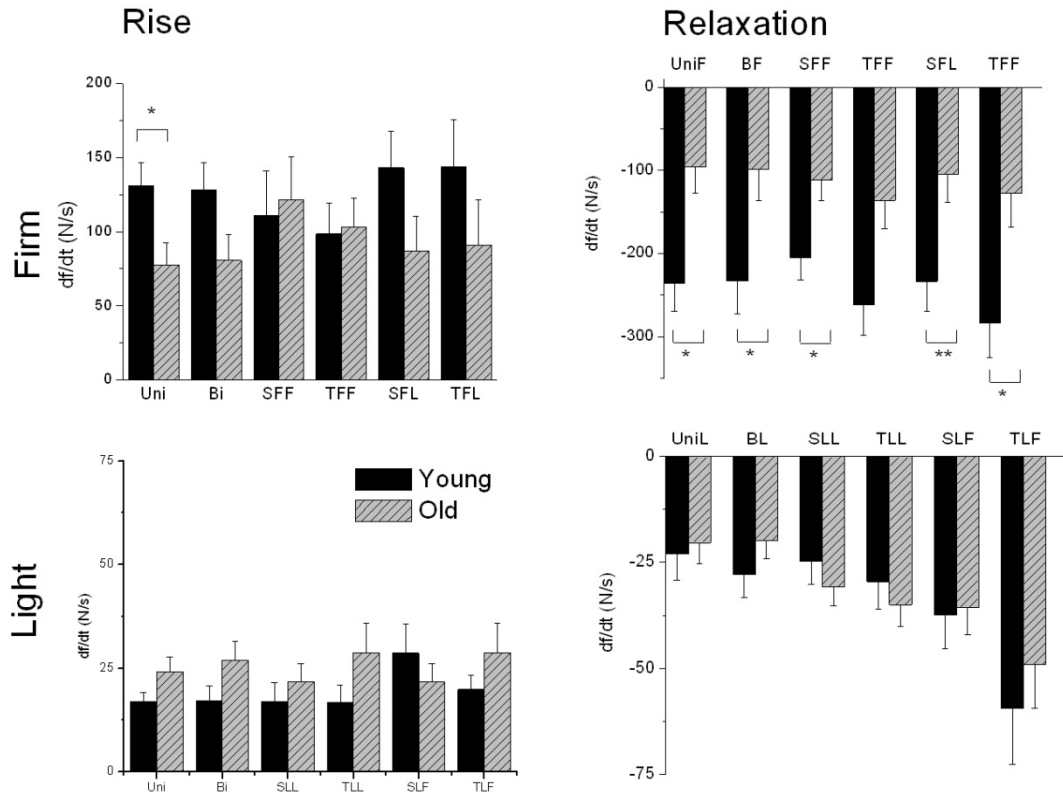


Figure 3.13. Rate of change of force during force rise to peak and force relaxation (mean \pm 1 SE). Uni = unilateral; Bi = bilateral simultaneous; SeqS = bilateral sequential tasks performed with the static hand; Seq T = bilateral sequential tasks performed with the transient hand. * $p < .05$, ** $p < .01$.



Note: Scales differ for firm graphs. The light graphs have similar scales.

Figure 3.14. Rate of change of force ($\Delta f/\Delta t$) by task. Mean (± 1 SE). UL = unilateral light, BL = bilateral light, UF = unilateral firm, BF = bilateral firm; S = static hand; T = transient hand; LL = light static-light transient; LF = light static-firm transient; FF = firm static-firm transient; FL = firm static-light transient.

* $p < .05$, ** $p < .01$.

Table 3.8. Rate of Change of Force for Static and Transient Tasks by Age

	Onset		Drop	
	Young df/dt (SE)	Old df/dt (SE)	Young df/dt (SE)	Old df/dt (SE)
FF Static	110.7 (30.3)	121.4 (29.0)	-205.0 (26.9)	-111.1 (25.3)
FF Transient	98.3 (20.6)	102.9 (19.7)	-261.4 (36.2)	-136.1 (34.1)
FL Static	143.1 (24.3)	87.1 (23.3)	-233.6 (35.6)	-105.0 (33.6)
FL Transient	143.8 (31.8)	90.8 (30.5)	-283.2 (42.3)	-127.8 (40.0)
LL Static	17.0 (4.6)	21.8 (4.3)	-24.7 (5.5)	-30.8 (4.4)
LL Transient	16.7 (4.3)	28.8 (7.0)	-29.5 (6.5)	-35.0 (5.2)
LF Static	28.6 (7.0)	21.8 (4.3)	-37.4 (8.0)	-35.7 (6.3)
LF Transient	19.9 (3.4)	28.8 (7.0)	-59.5 (13.2)	-49.1 (10.4)

Values are N/s (\pm 1SE). Dominant and nondominant values are combined. $\Delta f/\Delta t$ = rate of change of force; FF = firm static-firm transient; FL = firm static-light transient; LL = light static-light transient; LF = light static-firm transient.

3.2.5. Variability of Maintained Force

The variability of maintained force was analyzed before, during and after transient hand grasp and release. A representative profile is shown in Figure 3.15 with maintenance intervals identified by the shaded areas. When light force was produced in the static hand, significantly greater force variability was found, with all adults combined, in light compared to firm force tasks, $F(1,21) = 26.69$, $p < .0001$, as shown in Figure 3.15. While a greater variability was observed in old compared to young adults before, during and after transient hand force production, it did not reach statistical significance. Overall, a large increase in variability was found in following transient hand force production in all light, $F(1,21) = 9.36$, $p < .01$, and firm tasks, $F(2,44) = 15.21$, $p < .0001$. This increase in variability following transient hand force production was seen especially in old adults, while young adults showed a similar increase only in light-firm tasks.

When firm force was produced in the static hand, variability generally decreased slightly across all tasks for both young and old groups. A similar pattern of increased static force variability was observed in firm-firm tasks for both age groups, but variability was relatively constant during firm-light tasks for both young and old adults. The hand used to produce force was not significant for either firm, $F(1,21) = .14, p = .71$, or light, $F(1,21) = .14, p = .72$, forces.

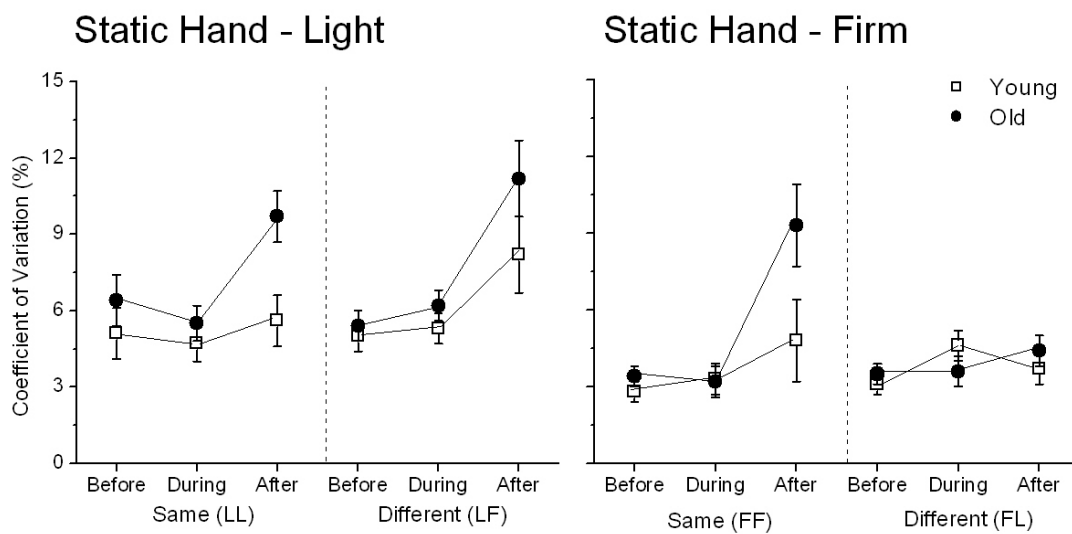


Figure 3.15. Variability of static force maintenance for young and old adults before, during and after transient grasp force production. Data for the dominant and nondominant hand was pooled as they were not significantly different.

Table 3.9. Coefficient of Variation (%) of Static Force Maintenance by Age

	Before		During		After	
	Young	Old	Young	Old	Young	Old
	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
UF	2.2 (.6)	3.9 (.5)	3.6 (.4)	4.9 (.7)		
BF	2.9 (.3)	4.4 (.7)	3.7 (.5)	5.2 (.8)		
UL	5.2 (.6)	6.0 (.7)	6.4 (.9)	6.9 (.9)		
BL	6.1 (1.1)	8.0 (.6)	6.8 (1.5)	8.3 (.9)		
FF	2.8 (.4)	3.4 (.3)	3.3 (.6)	3.2 (.6)	4.8 (.8)	9.3 (2.0)
LL	5.1 (.5)	6.4 (1.0)	4.7 (.6)	5.5 (.7)	5.6 (.6)	9.7 (.1.3)
FL	3.1 (.4)	3.5 (.5)	4.6 (.6)	3.6 (.7)	3.7 (.5)	4.4 (.7)
LF	5.1 (.5)	5.4 (.7)	5.3 (.6)	6.2 (.6)	8.2 (1.6)	11.2 (1.9)

The coefficient of variation after transient hand force production was not computed in unilateral and bilateral trials. UF = unilateral firm, BF = bilateral simultaneous firm, UL = unilateral light, BL = bilateral simultaneous light, FF = firm static–firm transient, LL = light static–light transient, FL = firm static–light transient, LF = light static–firm transient.

3.2.6. Response Time

Response time was defined as the time period between the tone and force onset or relaxation. In both age groups, there was no hand effect in either force onset, $F(1,19) = 2.43$, $p = .14$, or relaxation, $F(1,5) = .61$, $p = .47$; therefore, dominant and nondominant hands were combined in further analyses.

Overall, old compared to young adults were significantly faster in their response times during onset and relaxation, $F(1,22) = 5.20$, $p = .03$, as shown in Figure 3.16. Onset times were most similar between the two age groups during unilateral and bilateral firm and light tasks. In both young and old adults, relaxation response time was faster than onset response time, $F(1,22) = 57.13$, $p < .0001$. When the two age groups, were compared, however, old compared to young adults were significantly faster in initiating force relaxation, $t(22) = 2.89$, $p < .01$, but not onset.



Figure 3.16. Mean (± 1 SE) response times for static hand onset and relaxation. Data for onset and relaxation have been combined from all sequential sources.

There were no significant differences between young and old adults for either firm or light tasks, as shown in Figure 3.17. However, an interaction between task and age was found in onset response time for firm forces, $F(5,22) = 2.82$, $p = .02$. Old adults responded more quickly with either the static ($p < .05$) or transient ($p = .05$) hand compared to the unilateral hand in the firm-firm task. Light force response times differed by task but not age, with faster responses shown in unilateral compared to bilateral simultaneous tasks ($p < .05$). Further, response times were faster for both the dominant and nondominant hand ($p < .05$) in sequential compared to bilateral simultaneous tasks.

The response time in relaxation of old compared to young adults was faster during both firm, $F(1,14) = 6.712, p = .02$, and light, $F(1,14) = 6.201, p = .03$, tasks. No difference by individual task was found during firm relaxation response time, while an age and task interaction, $F(3,42) = 3.45, p = .03$, was found in light relaxation responses.

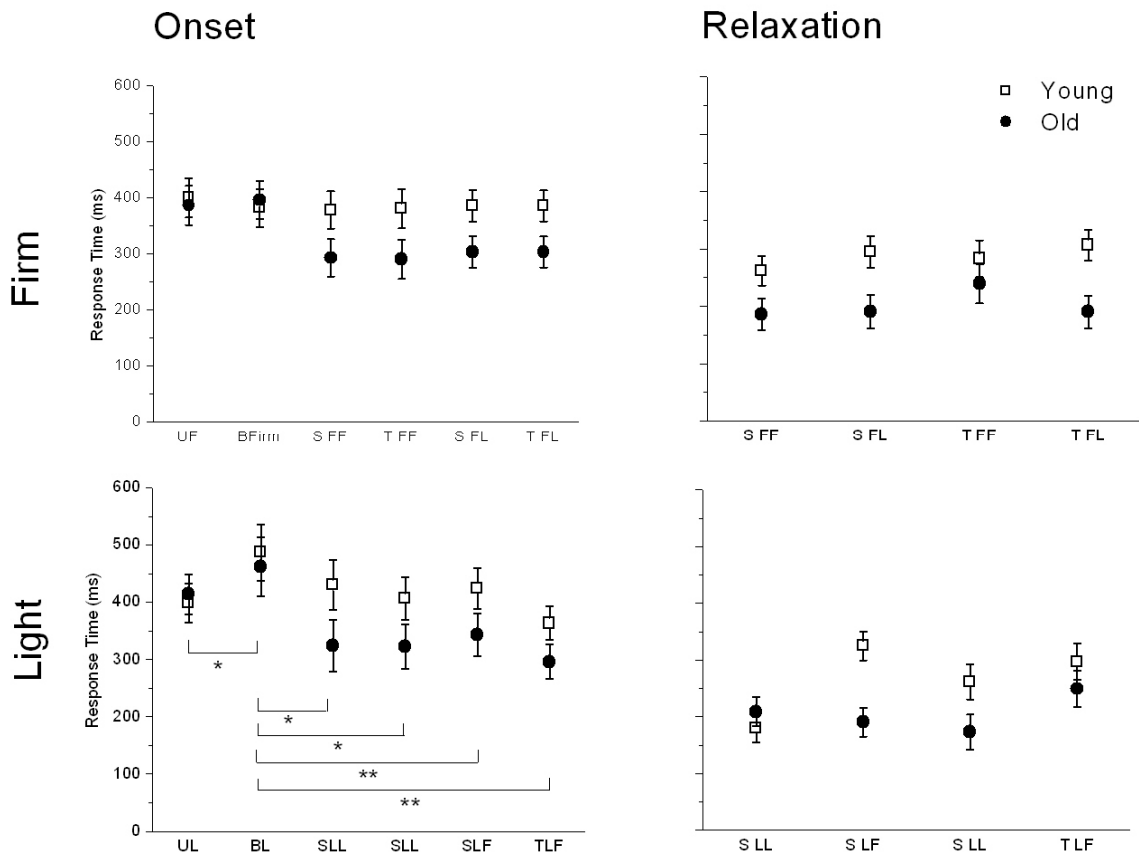


Figure 3.17. Mean ($\pm 1SE$) onset and relaxation response times (ms) in static and transient hand. UF = unilateral firm; UL = unilateral light; BF = bilateral firm; BL = bilateral light. S = static hand; T = transient hand; FF = firm static-firm transient; FL = firm static-light transient (FL); LL = light static-light transient; LF = light static-firm transient. Unilateral and bilateral response times were available for onset only. * $p < .05$, ** $p < .01$

When response times were examined for individual tasks in both static and transient force production, a faster response time was found, in general, for old compared to young adults. Onset times were most similar between the two age groups during unilateral and bilateral firm and light tasks. In light tasks, a greater response time was observed in both young and old adults, resulting in significant differences with all other tasks. During relaxation, no significant differences were observed between any tasks.

CHAPTER IV

DISCUSSION

These studies examined the coordination of simultaneous and sequential bilateral grasp force production in young and old adults. In the first experiment, simultaneous force production was assessed in both grasp-grasp and grasp-pinch tasks at maximum force levels. The first purpose of this study was to determine if old adults exhibit a force deficit during simultaneous maximum and submaximum grasp force tasks. A force deficit has been reliably shown in one or both hands during bilateral maximum grasp force production in young adults, but the effect of bilateral maximum force production during grasp has not been ascertained in old adults. The second purpose was to determine if young and old adults exhibit a force deficit when one hand produces maximum grasp force and the other produces maximum pinch force. As similar hand muscles are activated in both grasp and pinch, but with a different number of involved fingers, this may be considered a more complex task than simultaneous grasp-grasp tasks.

In the second experiment, submaximum force was produced by young and old adults in a sequential grasp force task. In this task, one hand maintained grasp force while the other hand developed and relaxed a transient grasp force, as occurs in many daily tasks, such as opening a jar. The purpose of this study was to determine the effect of transient hand force production on maintained force in both young and old adults.

4.1. Bilateral Simultaneous Force Production

4.1.1. Effect of Age

4.1.1.1. Young Adults

Young adults showed a reduction in force during maximum bilateral grasp relative to single hand grasp performance. This phenomenon has been reliably found in both the upper (Henry & Smith, 1961; Kroll, 1965a; Li, Zatsiorsky, Li, Danion, & Latash, 2001; Oda & Moritani, 1994, 1995b; Ohtsuki, 1981a, 1983, 1994; Shinohara, Scholz, Zatsiorsky, & Latash, 2004; Taniguchi, 1997; Van Dieën, Ogita, & De Haan, 2003) and lower (Howard & Enoka, 1991; Kawakami, Sale, MacDougall, & Moroz, 1998; Kawakami, Sale, & MacDougall, 1995; Owings & Grabiner, 1998; Secher, Rube, & Elers, 1988; Taniguchi, 1998; Vandervort, Sale, & Moroz, 1984) extremities. The results of the current study concur with the presence of a force deficit during bilateral maximum grasp in young adults. Furthermore, the force decline of approximately eight percent is within the range of values (up to 14 percent) found in previous studies of grasp (Oda & Moritani, 1995b; Ohtsuki, 1981a; Taniguchi, 1997).

The force difference in the current study was significantly less than zero (deficit) in the dominant hand of young adults. However, the mean of the nondominant hand force difference was not significantly less than zero (see Table 3.3 and Figure 3.5). The absence of a deficit in the nondominant hand was also found in an early study by Henry and Smith (1961). This finding differs from other studies of the force deficit in grasp-grasp tasks, as most have found that the deficit occurs in both hands during bilateral tasks (Gatev, Gavrilenko, &

Kolev, 2001; Morehouse, Szeligo, & DiTommaso, 2000; Oda & Moritani, 1994; Ohtsuki, 1981a, 1981c).

Examination of the individual young adult data for the nondominant hand (see Figures 3.6 and 3.7) found that most but not all participants showed a force deficit during the bilateral task, while a one or two participants exhibited a large force facilitation. Participants who exhibit a bilateral facilitation exert their maximum voluntary force during bilateral tasks, while participants demonstrating a bilateral deficit exert their maximum force during single grasp tasks. The finding that some but not all participants exhibit a bilateral deficit concurs with other studies (Howard & Enoka, 1991; Schantz, Moritani, Karlson, & Johansson, 1989; Secher, 1975) and suggests that interlimb interactions during maximum contractions exist along a continuum ranging from a bilateral deficit to a bilateral facilitation.

4.1.1.2. Old and Old-Old Adults

The effect of aging was examined in two ten-year age groups, on the basis of known ongoing declines in strength (Brooks & Faulkner, 1994; Krampe, 2002; Mathiowetz et al., 1985) and bilateral coordination (Christou & Carlton, 2001, 2002; Stelmach, Amrhein, & Goggin, 1988) throughout the aging process. Given these ongoing declines in strength and coordination, it was anticipated that age-related changes would be greater in old-old compared to old adults. As expected, maximum isometric grasp forces in both old and old-old adults in the current study were significantly less than those recorded for young adults (see

Figure 3.4), regardless of hand. However, while a further force decline occurred with increased age in old-old adults, this decline was relatively small. Consequently, maximum force means of the dominant and nondominant hands in both old and old-old adults were not significantly different from each other (see Table 3.3 and Figure 3.5). The absence of a force deficit in the two old age groups is in agreement with three studies by Häakinen and colleagues (1995, 1996, 1997), who found no evidence of a bilateral deficit in studies of isometric knee extension in old men (mean ages of approximately 70 years in each study). As a force deficit was found in young but not old or old-old adults, any neural mechanism of the force deficit must be able to account for this age-related difference. Changes in callosal structure with aging are suggested to best explain the presence of a force deficit in young but not old adults.

The results of the current study differ from other studies of maximum bilateral grasp-grasp force, which raises a question about the potential source of that difference. The subjects in each study were comparable in age and dominance, as were the methods for computing the force deficit. All grasp paradigms required a step paradigm that requires relatively fast development of force. However, while other studies have required rigid upper limb restraints, restraints were not used in the current study. Rather than restraint, the forearm, wrist and hand were carefully positioned in the current study but not rigidly restrained, in order to replicate more natural grasp force production. This lack of restraint may have allowed a slight wrist extension of approximately three to five degrees during natural maximum grasp development, resulting in a slight

decrease in muscle length and biomechanical enhancement of grasp force (Johanson & Murray, 2002). In contrast, both Oda and Moritani and Ohtsuki rigidly restrained the forearm and wrist, to prevent any limb movement during grasp force development.

A second possible reason for the differences observed may be found in the pattern of data observed. One or two individuals in each age group showed a large force facilitation in the bilateral task, which contributed to the group force variabilities found in this study. Examination of the individual trials for these participants found consistent and comparable responses; thus the mean was not skewed by a unusually strong single trial for any individual. Further, when facilitation was observed, the magnitude of the facilitation effect was larger than that of the inhibition effect. This variability of individual response was also identified by Enoka et al. (1991), who found both force deficits and force facilitations among trained and untrained adults. Therefore, as the maximum force in the three trials were consistent for all participants, and to avoid bias in data analysis, all data was included. Information about individual fitness and frequent activities were examined to better understand why some but not others show a force facilitation in the bilateral condition, but these factors were not found to provide an explanation for these differences.

4.1.2. Effect of Tasks

4.1.2.1. Maximum Grasp-Grasp and Grasp-Pinch Tasks

While age was found to be a significant factor in the examination of maximum bilateral force production, the two maximum grasp tasks resulted in remarkably similar results in each age group. In both the grasp-grasp and grasp-pinch tasks, a significant force deficit was found in the dominant but not the nondominant hand when young adults produced maximum grasp force. There was no evidence of a force deficit in either hand in the old and old-old age groups during grasp-grasp and grasp-pinch tasks.

The grasp-pinch task may be considered a more complex, asymmetrical force task, as similar effectors are activated but the hand configuration and maximum force capabilities differ in the two tasks. During both grasp and pinch force production, intrinsic and extrinsic flexor muscles are activated, although in differing proportions for the two tasks. At the same time, intrinsic thumb flexors and adductors produce force in opposition to the finger flexors (Hepp-Reymond et al., 1996). The hand configuration varies in that whole-hand grasp involves all four fingers and the thumb, whereas pinch involves only one or two fingers and the thumb. The smaller number of fingers involved in pinch results in absolute pinch force values that are generally smaller than grasp values by a factor of at least four. Increased task complexity can, therefore, be examined during bilateral simultaneous grasp and pinch maximal force tasks, as the requirement for maximum force production is the same for both tasks but the hand configurations vary.

When maximum grasp force is produced concurrently with maximum pinch force, greater demands are placed on force coordination. When maximum force requirements are the same in the two limbs, the same force program can be sent to the motoneuron pools of both hands (Kelso, Southard, & Goodman, 1979). However, in an asymmetrical force task such as in the current study, different maximum forces must be programmed for each hand. Thus, the grasp-pinch task also can be considered a more complex task than a grasp-grasp task from a motor programming standpoint. The fact that a force deficit was found in young but not old or old-old adults in either grasp-grasp and grasp-pinch tasks suggests that motor programming for maximum force production is independent of task complexity.

While there was no difference in the force deficit between the two tasks in any age group, there were task-related differences in onset time between the two hands. These onset time differences varied primarily as a function of task and not age. Young and old-old adults produced roughly synchronous bilateral force onset times during grasp-grasp tasks, with old adults showing slightly greater differences in onset time than young and old-old adults. However, all participants showed large temporal differences between onset times for each hand during grasp-pinch tasks, regardless of which hand produced pinch force (see Table 3.4). The differences found in all adults during the grasp-pinch task suggest that, in the presence of a more complex force task, all adults initiated force in each hand individually. When movement is produced in response to an external stimulus, corticospinal tract neurons have been shown to discharge from 60ms to

several hundred ms prior to movement (Evarts, 1974). A delay greater than 300 ms between force onsets in each hand suggests that there was sufficient time for each force to be developed separately rather than simultaneously.

Onset asynchrony was examined by Vint and Hinrichs (1997), in a study of bilateral force production in young adults. They suggested that the absence of a force deficit could be due to an asynchronous onset of bilateral force during rapid force development, arguing that the asynchrony would allow for two separate rather than simultaneous motor commands. The current findings support this suggestion, but only for tasks involving homologous muscle activation. In bilateral maximum same-force tasks, onset synchrony was present, and a force deficit was found in young adults in the dominant hand, as predicted by Vint and Hinrichs. However, in bilateral maximum tasks in which different absolute forces were produced and different hand configurations were required, onset of the two hands was asynchronous, yet a force deficit was still found in young adults in the dominant hand. This finding suggests that, when two different tasks are performed (i.e., grasp and pinch), programming of separate motor commands occurs regardless of the degree of temporal synchrony between the two hands.

4.1.2.2. Submaximum Grasp-Grasp Task

A bilateral deficit was not observed in young or old adults during either bilateral submaximum (firm or light) same-force grasp task. This finding differs

from the limited number of other studies involving submaximum forces (Hernandez et al., 2003; McLean, Vint, & Stember, 2006; Seki & Ohtsuki, 1990). A bilateral deficit was found when bilateral force was examined at 25, 50, and 75 percent of maximum voluntary force during grasp tasks in young adults (Seki & Ohtsuki, 1990), and elbow flexion tasks in young and old adults (Hernandez, Nelson-Whalen, Franke, & McLean, 2003; McLean, Vint, & Stember, 2006).

The primary difference between the present study and prior submaximum studies is the way in which submaximum force values were identified. In the three submaximum force studies (Hernandez et al., 2003; McLean et al., 2006; Seki & Ohtsuki, 1990), participants were asked to produce force to match a percentage of their maximum force, following either one (Hernandez et al., 2003) or no (McLean et al., 2006; Seki & Ohtsuki, 1990) practice trials with feedback. It has been shown that healthy young adults can accurately exert unilateral submaximum forces when expressed as a percentage of maximum force (Jackson & Dishman, 2000).

In contrast, participants in the current study were asked to develop forces comparable to those used with common objects, i.e., to squeeze an uncooked egg or shake a person's hand, rather than to develop a specific percentage of maximum force. This was selected to more closely approximate real-life tasks, and to reduce any additional perceptual or cognitive costs of force level selection during bilateral tasks. McLean et al. (2006) found a perceptual/cognitive cost during submaximum force production and suggested that, especially during submaximum as compared to maximum bilateral force tasks, a variable and

conscious cognitive component must be considered in addition to the constant neurophysiological mechanism.

All adults in the present study were able to use common objects to develop appropriate force levels. Furthermore, while a wide range of force levels were acceptable, young and old participants produced approximately the same forces across all trials (see Figures 3.7 and 3.8). This suggests that young and old adults are able to develop common object-related force levels in unilateral and bilateral force tasks.

It has been shown that both young and old adults can generate motor images of movement (Skoura, Papaxathis, Vinter, & Pozzo, 2005). The *a priori* assumption made by Skoura et al. was that common objects were universally familiar, and that the grasp tasks had been performed naturally by participants throughout adulthood. Using common objects may involve using sensorimotor memory (Johansson & Westling, 1984) or perceptual priming (Gordon, Westling, Cole, & Johansson, 1993; Tulving & Schacter, 1990), which is suggested to link visual or memory identification of an object with its associated force requirements. As a result of lifelong practice, then, object-related sensorimotor memories may be well-rehearsed and task specific, thereby decreasing the perceptual/cognitive cost (Quaney, Nudo, & Cole, 2005). This decrease in cost, associated with use of object- rather than percentage-related force levels, is proposed to account for the absence of a force deficit during submaximum tasks in young and old adults in the current study.

4.1.3. Mechanism

The mechanism underlying the force deficit must be able to account for the presence of a force deficit in young but not old or old-old adults, and for the presence of a force deficit in the dominant but not nondominant hand of young adults. It must also account for similar findings in the more complex grasp-pinch task. Furthermore, it must also account for the absence of a force deficit in young and old adults during submaximum grasp-grasp force.

Activity of the motor cortex in one hemisphere has been shown to reduce the maximum motor outflow in the homologous area of the opposite cortex, possibly through transcallosal inhibition (Ferber et al., 1992; Oda & Moritani, 1995b). Mutual interhemispheric inhibition during bilateral tasks, through connections within the corpus callosum, has been verified in functional magnetic resonance imaging (Kultz-Buschbeck et al., 2001) and movement-related cortical potential (Oda & Moritani, 1996) studies, as well behavioral studies of reaction and movement time (Kelso, Southard, & Goodman, 1979; Marteniuk, MacKenzie, & Baba, 1984; Ohtsuki, 1981b). Activation of the motor cortex appears to result in an early facilitation of the contralateral motor cortex, probably through transcallosal mechanisms. However, inhibition has been shown to occur with greater intensity of effector activation or spread of cortical activation within each hemisphere (Asunama & Okuda, 1962; Ferbert et al., 1992; Meyer, Roricht, Graf von Einsiedel, Kruggel, & Weindl, 1995; Meyer, Roricht, & Woiciechowsky, 1998; Salerno & Georgesco, 1996; Ugawa, Hanajima, & Kanazawa, 1993), as is found when maximum force is produced. As the callosum is composed of

excitatory fibers, inhibition is thought to occur through excitatory influences on inhibitory interneurons, resulting in an overall inhibitory response (Hoy, Fitzgerald, Bradshaw, Armatas, & Georgiou-Karistianis, 2004).

Bilateral coordination between the two hemispheres is also required during submaximum bilateral force development. However, as the force is less than maximal, the neural signal and area of cortical activation can be expected to be less as well. It may be that, in this instance, callosal inhibition does not occur or inhibition is lessened. With the absence or minimization of inhibition, bilateral force magnitudes would approximate those found during unilateral tasks. Thus a force deficit would not be observed at any age, as found in the current study. While this is in contradiction to other studies, it is proposed that the paradigm used in the present study allows a more definitive examination of the force deficit than has previously occurred, through the use of object-related force levels. A reduction in perceptual/cognitive costs can be assumed as the use of object-related force magnitudes, which occurs through the unconscious use of well-established sensorimotor memories, can be expected to have fewer costs than the conscious determination of a given percentage of maximum voluntary force. As these additional neural costs decrease, interference with force production can be expected to decline, resulting in bilateral force magnitudes that are approximately equal to the forces produced during unilateral tasks. Therefore, no force deficit would be expected.

Callosal transmission has been shown to be asymmetric. In right-handed individuals, there is stronger inhibition of the left compared to the right motor

cortex (Ferber et al., 1992; Netz, Ziemann, & Hömberg, 1995). This asymmetry could account for the presence of a force deficit in the dominant but not nondominant hand of young adults.

In aging, the naturally occurring decrease in callosal size and demyelination of callosal fibers is thought to lead to inefficient transcallosal functioning, resulting in a loss of inhibition (Bodwell, Roderick, Waddle, Price, & Cramer, 2003; Hoy, Fitzgerald, Bradshaw, Armatas, & Georgiou-Karistianis, 2004). The loss of inhibition would increase the likelihood that force magnitude would be unchanged in unilateral and bilateral tasks in aging, i.e., neither a force deficit nor a force facilitation would be present. In a functional magnetic resonance imaging study of 76 healthy elderly adults (ages 65-95y), age-related atrophy of the anterior and middle sections of the corpus callosum was found in females but not males. The loss shown in females was approximately 20 percent of the total corpus callosum and 10 percent of the anterior callosum (Salat et al., 1997). The anterior area of the callosum, identified by labeling studies in the monkey, project fibers to the prefrontal area, premotor area, supplementary motor area, and primary motor cortex while the middle area provides projections to the primary and secondary somatosensory cortices (Aboitiz et al., 1996; Pandya & Seltzer, 1986). As a result of this fiber loss especially in the anterior area of the callosum, inhibition of motor neurons during bilateral tasks is lessened, increasing the likelihood that a force deficit will be absent.

A bilateral deficit has been found not only in force production but also in cortical activity (Taniguchi, Burle, Vidal, & Bonnet, 2001). Taniguchi et al.

examined motor cortical activity during both a bilateral simultaneous and a sequential reaction time paradigm using maximum isometric index finger flexion. They found a bilateral deficit in cortical activity related to the motor command, as well as a force deficit during bilateral tasks. Their conclusion was that the presence of the force deficit was due to a reduction of the motor command, and suggested the deficit may be due to transcallosal inhibitory activity.

4.1.3.1. Alternative Mechanisms

4.1.3.1.1. Motor unit activation

The focus of early studies of the force deficit was to identify whether fast or slow motor units were inhibited during bilateral contractions. Failure to achieve full motor unit activation during maximum voluntary bilateral force production was found to be due to an inability to activate the large motor units innervating fast muscle fibers (Belanger & McComas, 1981; Vandervort, Sale, & Moroz, 1984), as expected according to the size principle. In aging, it has been shown that older individuals have fewer motor units, and that there are a greater proportion of slow units in the composition of remaining units (Brooks & Faulkner, 1994; Faulkner & Brooks, 1995; Grimby, 1986; Lexell, 1995). While this finding may provide a partial explanation for decreased force production capability in aging, it does not adequately address the loss of force in a bilateral but not unilateral task as both tasks should demonstrate equal force declines.

The modification of force during maximum bilateral contractions has been shown, through the use of movement-related cortical potentials, to be neurally

mediated. These cortical potentials are generated by neural circuits involved in movement preparation and execution. (Oda & Moritani, 1995b; Taniguchi, Burle, Vidal, & Bonnet, 2001). Oda and Moritani observed a significant correlation between reduced movement-related cortical potentials and a force deficit during bilateral grasp tasks. Taniguchi et al. found a similar correlation between changes in the cortical potential and a simple reaction time task. Both Oda and Moritani (1995b) and Taniguchi et al. (2001) attributed this effect to transcallosal inhibition, resulting in decreased neural activation of fast motor units. Given these findings, it is suggested that the force deficit during bilateral tasks is best accounted for by central neural changes mediated through corpus callosal fibers. This can also partially explain the presence of a bilateral deficit in the dominant but not nondominant hand of young adults. Transcallosal inhibition has been shown to be asymmetric in right dominant individuals, with greater inhibition to the left hemisphere (Netz, 1995). This would result in greater force deficit in the right compared to left hand, as was found in the current study.

4.1.3.1.2. Training/Habitual Use

A basic question to be considered is whether training in young adults is equivalent to a lifetime of habitual use in elderly adults, and can therefore account for the absence of the bilateral deficit in old and old-old adults. In young adults, Howard and Enoka (1991) found that long-term deliberate exercise of bilateral homologous muscles in young adults led to a facilitation effect during bilateral muscle exertion in some participants. In the current study, no participant

reported deliberate exercise of maximum hand grasp, nor was maximum grasp force required for daily tasks. Further, routine daily hand use occurs at typically low force levels (Napier, 1956), with only infrequent use of maximum forces. The current study, involving maximum force production, cannot, therefore, answer the question of the effect of training or habitual use on the bilateral deficit.

4.1.3.1.3 Attention Allocation

A difficulty in attention allocation has been shown not to be a primary cause of the force deficit. Ohtsuki (1983) found no bilateral deficit in a study of simultaneous contraction of elbow extension and contralateral elbow flexion, and suggested that division of attention may not provide a complete explanation for the simultaneous bilateral force deficit. Furthermore, Taniguchi et al. (2002) found no difference between early and late motor-related cortical potentials in unilateral and bilateral tasks. As the late phase of a cortical potential is considered to reflect an attentional component of the task (Tecce & Hamilton, 1973; Tecce, Savignano-Bowman, & Meinbresse, 1979; Tecce & Scheff, 1969), Taniguchi et al. suggested that a division of attention is unlikely to be the primary factor mediating the force deficit. However, as attention is known to affect motor production in bilateral tasks (Monno, Temprado, Zanone, & Laurent, 2002), further study of the effect of attention on bilateral force production is warranted.

4.1.3.1.4. Spinal Reflexes and Coactivation of Antagonist Muscles

Ohtsuki (1983) suggested that a reflexive inhibition, occurring through double reciprocal innervation, might be related to the force deficit, as maximum voluntary activation of one limb could result in sensory input to the spinal cord and inhibition of motoneurons of the contralateral limb. However, the findings of Howard and Enoka (1991) contradict this theory. They found that electrical stimulation of one leg caused facilitation of force in the opposite leg., with the degree of facilitation related to the unilateral or bilateral nature of the task. They argued that the increased force observed was mediated by sensory feedback effects associated with the stimulation, and not the removal of inhibition to the motoneurons. Co-activation of antagonist muscles is also no longer considered a cause of the bilateral deficit, as the level of antagonist activation has been shown to be identical in both bilateral and unilateral conditions over a range of force levels (Jakobi & Cafarelli, 1998; Koh, Grabiner, & Clough, 1993).

4.1.4. Summary: Bilateral Simultaneous Force Production

In summary, the aim of the current experiment was to examine the coordination of bilateral simultaneous force production in young and old adults. During bilateral maximum grasp-grasp and grasp-pinch tasks, a force deficit was found in the dominant but not nondominant hand of young adults, while there was no evidence of a bilateral force deficit in either old or old-old adults. These findings are best accounted for through the neural mechanism of transcallosal inhibition, with a decline in inhibitory effects present with aging. No force deficit

was found during bilateral submaximum grasp-grasp tasks in any age group. The concomitant decrease in cortical activation is suggested to result in a decline in transcallosal inhibition, and a mitigation of any force deficit.

4.2. Bilateral Sequential Force Production

Bilateral tasks may be considered more complex than unilateral tasks because both within- and between-hand forces must be coordinated by the nervous system. Among bilateral tasks, sequential tasks are more complex than simultaneous tasks, as more cortical resources are necessary during planning and execution, and greater degrees of motor and working memory are required. In the current study, for example, during a sequential task, the participant needed to remember, over the course of each trial, both the onset and relaxation order of the hands as well as the required force levels. This suggests that, during sequential force production, neural circuits for bilateral force production, attention and working memory need to be interconnected.

A temporary decline in grasp force maintenance in one hand was observed when a transient force was produced or released in the other hand, for young and old participants, all force magnitudes, and each hand. It was found during transient force onset and during relaxation. Dissimilar combinations of forces, such as light grasp with firm pinch, resulted in a similar temporary decline in maintained force as when both hands produce firm grasp force. This finding therefore agrees with studies that have shown that the cortical costs of cognitive

dual tasks in both young and old adults were not modulated by task difficulty (for review, see Verhaeghen & Cerella, 2002).

Transient hand relaxation in the current experiment is compatible with the concept of withdrawal of input to the motor cortex rather than active inhibition of input. It has been shown that withdrawal of cortical input forms the basis for relaxation of isometric forces (Rothwell, Higuchi, & Obeso, 1998). Rothwell et al. found that cortical potentials preceding relaxation in an isometric pinch task were smaller than at onset. They further found that the release task was considered simple by participants, while electromyographic activity showed that the release of force was achieved by decreasing activity in hand and forearm muscles simultaneously. Additionally, the cortical potential was confined to a smaller cortical area than at onset. Cortical areas activated at release included the supplementary motor area and the cingulate area but not the primary motor area, indicating the withdrawal of input. Rothwell et al. suggested that, as no activity is observed in the primary motor cortex during simple relaxation in an isometric task, release requires no motor preparation. In addition, Rothwell and colleagues suggested that the cortical activity found in the midline structures could reflect timing or other attentional processes.

Age-related declines in force were found in the present experiment, as expected. This force decline is associated with age-related degeneration in the primary motor cortex, supplementary motor area and the cingulate area. There is strong support for the activation of both the supplementary motor area (Cramer et al., 2002; Kazennikov et al., 1999; Tanji, Okano, & Sato, 1987) and primary

motor cortex (Cardoso de Oliveira, 2002; S. Cardoso de Oliveira, Gribova, Donchin, Bergman, & Vaadia, 2001; Donchin, Gribova, Steinberg, Bergman, & Vaadia, 1998; Gribova et al., 2002) in bilateral coordination. Degeneration in the supplementary motor area may be associated with bimanual task incoordination and difficulty in effectively using internal feedback, resulting in greater reliance on external feedback. While less is known about the cingulate area, aging of the cingulate cortex has been associated with decreased working memory (Nordahl et al., 2006a) and an inability to suppress irrelevant stimuli (Heuninckx, Wenderoth, Debaere, Peeters, & Swinnen, 2005b). Both of these abilities were required in the present experiment.

4.2.1. Mechanisms

4.2.1.1. Attention Allocation

In a bilateral sequential grasp task, the neuromotor system must select and execute a motor command for one hand while continuing to provide activation to muscles of the other hand. This is a different paradigm than that used in movement studies, where an alternating pattern is commonly used. The current experiment showed that, during the four-second period of transient force development, maintenance and relaxation, force declined in the hand maintaining force. The most cogent explanation for this finding is that attention is reallocated during these brief periods.

Attentional allocation is operationally assessed through a dual-task paradigm. The basic assumption of the dual task paradigm is that one task,

typically the second task, will interfere with the original task, or that resource allocation will differ between the two tasks. Attention is thought to generally reflect the intensity of neural programming required to maintain a motor pattern (Monno, Temprado, Zanone, & Laurent, 2002). Studies of bimanual coordination have found that interference occurs in young adults during bilateral motor tasks. For example, in a study requiring both in-phase and anti-phase movement patterns simultaneously (Kelso, 1984), interference of the in-phase movement on the anti-phase movement was found. Dual-task interference in force production has also been found in young adults. In a dual-task paradigm involving isometric force production and choice reaction time (Zijdewind, van Duinen, Zileman, & Lorist, 2006), force production provided significant interference on cognitive performance in young adults. Data from the current study indicate that onset and relaxation of transient force interfered with maintained force production. Thus interference was shown by the second motor task on the first motor task, and supports the concept of dual-task interference in young adults.

Accumulating evidence supports a growing interdependence between sensory and motor functions and cognition in aging (Cabeza, 2002; Cabeza et al., 1997; Heuninckx et al., 2005; Li & Lindenberger, 2002; Logan, Sanders, Snyder, Morris, & Buckner, 2002; Reuter-Lorenz, 2002). With aging, sensory losses and impaired motor performance occur, while at the same time cognitive processes are increasingly less able to support or enhance performance needs (Lindenberger, Marsiske, & Baltes, 2000). Changes in the basal ganglia and dopamine receptors, especially in the nigrostriatal region (Wong, Young, Wilson,

Meltzer, & Gjedde, 1997) have been correlated with both motor and cognitive declines seen in aging. In addition to known age effects of motor slowing and increased reaction times (Darling, Cooke, & Brown, 1989; Dubrowski, Roy, Black, & Carnahan, 2005; Stelmach, Amrhein, & Goggin, 1988; Vaillancourt, Mayka, Thulborn, & Corcos, 2004), decreased dopamine availability has been linked to cognitive declines (Nieoullon, 2002), decreased attention (Li & Sikström, 2002) and impaired matching of efferent copies of movement with proprioceptive feedback (Toffano-Nioche, Beroule, & Tassin, 1998). Each of these factors may have contributed to the larger temporary declines in maintained force found in old compared to young adults.

In the presence of age-related degeneration of neural structures, old adults increase activation in additional neural structures. Heuninckx et al. (2005) used functional magnetic resonance imaging to study brain activation patterns in young and old adults during cyclical hand and foot movements. Multilimb coordination resulted in increased activation of the cerebellum and the ventral premotor cortex in both young and old adults. Old adults, however, additionally activated the presupplementary motor area, the dorsal premotor area, the rostral cingulate cortex and the prefrontal cortex. The rostral cingulate cortex, in particular, was activated during inhibition of distractors. Heuninckx and colleagues have suggested that this pattern is consistent with an increased reliance in old adults on higher-level processing and the integration of auditory and somatosensory information, while young adults rely more on automatized internal movement generation. As a result of these increased neural processing

demands, Heuninckx and colleagues, in concert with other studies (Cabeza, 2002; Logan, Sanders, Snyder, Morris, & Buckner, 2002; Reuter-Lorenz, 2002) have suggested that there are greater attentional costs of motor performance in aging.

The effect of these attentional costs in aging has been examined in a dual task involving isometric force tracking and a computational task (Voelcker-Rehage, Stronge, & Alberts, 2006). Young and old adults were able to successfully complete each task when performed individually. However, when the two tasks were performed at the same time, errors in force tracking occurred in old adults. Furthermore, these errors increased, as did force variability, immediately after a computational error. Young adults, in contrast, exhibited consistent and accurate force tracking profiles during the dual task, even when making errors in the computational task. These findings suggest that, while old adults are able to successfully complete a single motor task, there may be insufficient attentional resources for the successful completion of two concurrent motor tasks. Data from the current study indicate that onset and relaxation of transient force interfered temporarily with maintained force production in old adults, and is consistent with the findings of Voelcker-Rehage and colleagues, and with the concept of attentional reallocation.

4.2.1.2. Anterior Cingulate Area

The anterior cingulate area is suggested as a potential site for the integration of motor control and cognition needed in bilateral tasks, based on

anatomical and experimental findings. The cingulate cortex is located deep in the brain on the medial surfaces of the frontal and parietal cortices, just above the corpus callosum. Dense projections from the anterior cingulate cortex to the motor cortex and spinal cord suggest a role for this structure in motor control at the spinal level. There are also reciprocal corticocortical connections with the lateral prefrontal cortex, which supports a possible role in cognition. Studies in nonhuman primates have shown that prefrontal neurons converge in the cingulate sulcus (Bates & Goldman-Rakic, 1993; Picard & Strick, 1996), where input is also received from the primary motor cortex, premotor cortex and supplementary motor area (Dum & Strick, 1991). Fibers from this area then give rise to corticospinal projections to the spinal cord (Dum & Strick, 1991). Intracortical microstimulation in nonhuman primates has revealed that these corticospinal projections are clearly distinguished from the dorsally located supplementary motor area (Luppino, Matelli, Camarda, Gallese, & Rizzolatti, 1991). As a result, the cingulate cortex is anatomically positioned to interconnect with cortical motor planning areas. The importance of the cingulate cortex to movement has been demonstrated by positron emission tomography. Paus (2001) showed activation of the cingulate cortex during voluntary key presses with the right hand (Paus, 2001).

The anterior cingulate cortex is also important in the integration of sensation. There are extensive neurons from thalamic and brainstem nuclei to the anterior cingulate cortex. (Paus, 2001). Midline thalamic and brainstem neurons, involved in the regulation of arousal and integration of sensation, are

connected with all levels of the anterior cingulate cortex. Additionally, there is extensive availability of dopamine, important for both motor and cognitive function. In the human cortex, the highest density of dopamine-related fibers is found in the anterior cingulate cortex (Paus, 2001). Lesion studies have shown that damage to the cingulate cortex results in deficits in spontaneous initiation of movement and speech and/or difficulty suppressing externally triggered motor subroutines. For example, adult expression of the grasp reflex (De Renzi & Babieri, 1992; Hashimoto & Tanaka, 1998; Stephan et al., 1999; Turkan & Swick, 1999) and verbal perseveration (Shahani, Burrows, & Whitty, 1970) are often found after unilateral lesions of the frontal lobe, including the anterior cingulate cortex.

Degeneration of the anterior cingulate cortex with aging can also account for the greater declines found in the present study in old compared to young adults. Degeneration of the cingulate cortex with aging has been shown by functional magnetic resonance imaging (Dirnberger et al., 2000; Nordahl et al., 2006b) and has been associated with an inability to initiate movement and suppress irrelevant stimuli. The present findings of a greater decline in maintained force at the time of transient force onset and relaxation for old adults are compatible with an interpretation of difficulty suppressing irrelevant stimuli, which may be at least partially mediated by degeneration of the cingulate cortex.

4.2.2. Alternative Mechanism

Neural cross-talk between homotopic areas of the motor cortex has been posited to occur during bilateral movement of homologous muscles, especially when forces are different or movements are complex (Swinen, Jardin, Meulenbroek, Dounskaia, & Hofkens-Van Den Brandt, 1997). Spatial coupling observed during bimanual movement, as can be observed in mirror movements, is considered to be evidence of neural cross-talk (Addamo, Farrow, Hoy, Bradshaw, & Georgiou-Karistianis, 2007; Walshe, 1923).

There are three explanations for neural cross-talk as shown occasionally in adults during either strong contraction of or complex movements by the opposite hand. The first explanation suggests cross-talk occurs as a result of activity of the uncrossed corticospinal projection from the motor cortex controlling the voluntarily activated hand (Nass, 1985). This explanation is generally unsatisfactory as ipsilateral axons are thought to activate primarily axial and proximal upper limb muscles. Additionally, reports of bilateral motor evoked potentials in hand muscles are rare (Brinkman & Kuypers, 1973; Netz, Lammers, & Homberg, 1997; Quarterone, Di Lazzaro, Oliviero, & Rothwell, 1996). The second explanation suggests that corticospinal axons from one motor cortex may branch and innervate left and right homologous motor neuron pools. This occurs most commonly found in Klippel-Feil syndrome (Carr, Harrison, Evans, & Stephens, 1993; Farmer, Ingram, & Stephens, 1990), and thus is unlikely as an explanation for healthy adults. Bilateral cortical activity during unilateral movement is proposed as a third explanation for children (Mayston, Harrison, &

Stephens, 1999). The disappearance of mirror movements after approximately age ten years is posited as a result of myelination of callosal fibers, allowing the suppression of activation from the contralateral hemisphere (Ferbert et al., 1992; Meyer et al., 1995).

If neural cross-talk can occur during bilateral tasks, it might be supposed that force approximation would occur during activation of bilateral homologous muscle groups in which different forces are produced. This was not found in the current study, as firm and light forces were distinct and consistent across bilateral tasks involving both similar and different forces. It is, therefore, unlikely that neural cross-talk provides a full explanation for the current findings.

4.3. Summary

The purpose of these experiments was to examine the coordination of simultaneous and sequential bilateral grasp force production in young and old adults. During bilateral simultaneous maximum grasp-grasp and grasp-pinch tasks, a force deficit was observed in the dominant but not nondominant hand of young adults, and there was no evidence of a deficit in either old or old-old adults. These findings are consistent with the mechanism of transcallosal inhibition and degeneration of the corpus callosum in aging.

During bilateral grasp tasks performed sequentially with one hand maintaining force while the other hand produces a transient grasp, maintained force decreased during the times of transient force onset and relaxation in both young and old adults, regardless of force magnitudes used in each hand. The

decline was greater in old than in young adults at both onset and relaxation. Divided attention was suggested to account for the decline in maintained force, with the anterior cingulate cortex posited as the locus for the integration of bilateral force production and attention.

4.4. Limitations

4.4.1. Determination of Maximum Force Capability

In studies of the force deficit during maximum force tasks, where the maximum force exerted in the bilateral task is compared to that exerted in a unilateral task, the question of whether voluntary activation of all appropriate motor units during maximum force production is relevant. Techniques used to investigate this question include the use of supramaximal tetanic stimulation (Bigland & Lippold, 1954b) or twitch interpolation techniques (Vandervort, Sale, & Moroz, 1984). It has been shown that, on average, approximately 25 percent of all attempts to achieve maximum voluntary contraction attain full motor unit activation (Herbert & Gandevia, 1996; Jakobi & Cafarelli, 1998). However, Van Dieën and colleagues suggest that full activation may be achieved by highly motivated and/or well-trained participants (Van Dieën, Ogita, & De Haan, 2003).

Since neither supramaximal tetanic stimulation nor twitch interpolation techniques were used in the present study, it is not possible to demonstrate that full motor unit activation was achieved. Motivation also was not objectively assessed, however, physical signs of effort, such as sweating and slight shaking of the limb with great effort, were routinely observed. Intertrial consistency of force magnitude was used to indicate maximum force, based on the assumption that inconsistency would indicate different levels of motor unit activation. It was found that forces produced in the three trials were consistent for each participant.

4.4.2. Fitness effects in old adults

The high level of fitness of the elderly participants in these studies may not be representative of the general population. As a result, the findings may not apply to less fit elderly individuals. All elderly participants expressed active and ongoing voluntary participation in aerobic fitness activities. Fitness training has been shown to positively affect a wide variety of tasks and cognitive abilities in elderly adults. Positive effects are largest for tasks involving executive control, such as working memory, interference control and task coordination, which have been shown to decline with aging (Kramer, Bherer, Colcombe, Dong, & Greenough, 2004). However, these skills have been shown to be amenable to fitness training in old adults, as shown by the meta-analysis of Colcombe and Kramer (2003). A further study by Black and colleagues (Black, Isaacs, Anderson, Alcantara, & Greenough, 1990) observed rats provided with either forced exercise, access to voluntary activity, nonaerobic skill task use, or handling. Results showed that while aerobic activity increased brain vasculature, voluntary learning resulted in increased formation of synapses. Brain scans have also shown that older adults who had better cardiovascular fitness, i.e., participated actively in aerobic fitness tasks, showed less tissue loss in the frontal, parietal and temporal cortices as a function of age (Colcombe et al., 2003). As the participants in these experiments were actively involved in fitness activities, they therefore may not reflect the general aging population.

4.4.3. Other Limitations

While twelve participants were identified as appropriate in number by power analysis, and were of comparable or larger size than most studies of the bilateral deficit (Gatev et al., 2001; Hakkinen et al., 1996; Häkkinen et al., 1995; Koh et al., 1993; Oda & Moritani, 1994; Ohtsuki, 1983; Taniguchi et al., 2001), a larger sample size may have further strengthened current findings or revealed new results.

Finally, while it is impossible to rule out fatigue as a factor, it seems unlikely. Ample rest was provided between trials, in order to avoid fatigue. Furthermore, analysis showed there was no order effect in force magnitude for any participant in the first experiment requiring maximum force production. If fatigue had been present, a decline in force would have been anticipated between the first and third trial, resulting in an order effect.

4.5. Future Directions

In future experiments, both male and female participants will be included. All will be fully right-handed according the Edinburgh Laterality survey, and stratification on the basis of current levels of physical activity and hand-intensive activity, will occur.

The first experiment provided minimal positioning constraints during unilateral and bilateral maximum grasp force production. A direct comparison of this positioning with more constrained limb and hand postures (for example, forearm and wrist casting as was used by Ohtsuki (1981a)) could identify the extent, if any, to which positioning constraints modify the bilateral deficit in young and old adults. This is an important step

in the process of understanding the presence or absence of the bilateral deficit in the context of daily life.

A second experiment could further explore the effect of object-related compared to percent-based force development in unilateral and bilateral submaximum grasp force production. If object-related forces reduce the perceptual or cognitive load, as was argued in this dissertation, then a deficit should be associated with percent-based force development and should be absent or significantly minimized with object-related force production. This study would require that both paradigms be examined for each participant, with appropriate counterbalancing of trials to avoid bias.

To more specifically assess the effect of attention on bilateral sequential force production, expansion of the test paradigm will occur to encompass the modulation of visual attention. Young and old participants will complete the same bilateral sequential force paradigm with auditory tones as in the current study. Visual feedback of the force level generated will be differentially provided in the following conditions: no vision, vision of the static hand response only, vision of the transient hand only, and vision of both the static and transient hand. If attention is the source of the observed decline, it is expected that the decline in maintenance force will be the least when visual feedback of the static hand alone occurs. Vision has been used effectively in a comparable force development study (Voelcker-Rehage, Stronge, & Alberts, 2006) , and is expected to facilitate rather than degrade performance when the static hand response is viewed. Conversely, maintenance performance is expected to worsen when the transient hand response is displayed.

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