

**Exploring unintentional drifts in finger force production and muscle activity:
A study of finger independence**

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A study of finger independence**

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Abstract

Human beings cannot move or produce force with their fingers independently from each other. Finger independence is constrained by the central nervous system which coordinates force production via multi-finger synergies, among additional mechanical and peripheral neural factors. Finger interdependencies represented in the central nervous system rely on integrating tactile, proprioceptive, and visual feedback on task performance. The primary purpose of this thesis was to explore drifts in finger interdependencies in the absence of visual feedback. Twenty right-handed participants (10 females and 10 males, aged 18-29 years) performed a series of isometric, single finger flexion and extension exertions with digits II-V. The right arms of the participants were braced in a mid-prone position, with their right wrist at 0° flexion and digits II-V secured to uniaxial force transducers. The activity of flexor digitorum superficialis (FDS) 2-5 and extensor digitorum communis (EDC) 2-5 were recorded via surface electromyography. Participants performed 30 second static, single finger flexion and extension exertions at 15% and 30% of their maximum voluntary contraction (MVC) with digits 2-5. A single repetition of each exertion was performed in two conditions: (1) with continuous visual force feedback, and (2) with visual feedback removed following 10 s. When feedback was given for the whole trial, the uninstructed fingers drifted towards greater involuntary force production (~4% MVC between the four fingers) while FDS and EDC activity generally increased over time. Removing visual feedback on the instructed finger induced consistent downward force drifts in its force production at 15% and 30% MVC flexion and 30% MVC extension, along with decreased extrinsic finger muscle activity. In the flexion conditions, removing feedback also eliminated the upward uninstructed finger force drifts.

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Contents

List of Tables..... 1

List of Figures..... 3

List of Abbreviations..... 5

Chapter 1: Introduction..... 6

Chapter 2: Literature Review..... 9

 2.1. Review of the Anatomy..... 9

 2.2. Factors Limiting Finger Independence 13

 2.2.1 Mechanical Factors..... 14

 2.2.2 Neural Factors..... 17

 2.3. Unintentional Force Drifts in Finger Pressing 20

 2.3.1 Referent Control of Motor Actions..... 21

 2.3.2 The Origin of Finger Force Drifts 24

 2.4 Summary 26

Chapter 3: Manuscript..... 27

 3.1 Abstract..... 28

 3.2. Introduction 30

 3.3. Methods 34

 3.3.1. Participant Characteristics 34

 3.3.2. Set-up..... 34

 3.3.3. Experimental Protocol..... 37

 3.3.4. Data Processing..... 39

 3.3.5. Statistical Analysis 39

 3.4 Results 42

 3.4.1. Instructed Fingers - Force..... 42

 3.4.2. Uninstructed Fingers - Force 45

 3.4.3. EMG 49

 3.5. Discussion 55

 3.6. Conclusions 59

 3.7. References 61

 3.8 Supplementary Tables 64

Chapter 4: Thesis Discussion..... 67

 4.1 Contributions..... 67

4.2 Rationale for Methods	67
4.3 Future Directions	69
References	71
Appendix A – Letter of Informed Consent	76

List of Tables

Table 3.1: Electrode locations for the EDC and FDS compartments. Adapted from May & Keir, (2018)

Table 3.2: Participant (random) slope effects and model estimated [95% confidence interval] slopes (%MVC/Time (s)) for each instructed finger during the final 20 seconds (10 s – 30 s) of the feedback removed trials. Separate models were run for both flexion (left) and extension (right), at 15% MVC (top) and 30% MVC (bottom). Fixed effects of fingers are not presented as they were fixed at the target force. Model estimates, t, and p-values were derived from mixed effects models of the instructed finger forces. The uninstructed fingers are analyzed separately (See Table 3.3).

Table 3.3: Model estimated F[DFn, DFd] effects and effect sizes (η^2) of instructed finger (index, middle, ring, little), magnitude (15% MVC, 30% MVC) and feedback (feedback given, feedback removed) on the total uninstructed finger force drift (% MVC). Drifts in the uninstructed finger force ($\overline{\Delta F}_{Unins}$) were calculated as the difference in the mean force produced by the three uninstructed fingers pre-drift (5-10 s) and post-drift (25-30 s): $\overline{\Delta F}_{Unins} = \sum |\overline{F}_{Finger}[25 - 30s]| - \sum |\overline{F}_{Finger}[5 - 10s]|$. A separate instructed finger (4) \times magnitude (2) \times feedback (2) repeated measures ANOVA was computed for finger flexion (left) and extension (right).

Table 3.4: Estimated effects of muscle (FDS2, FDS3, FDS4, FDS5, EDC2, EDC3, EDC4, EDC5), and feedback (pre-drift, post-drift) on muscle activity (%MVE). Estimates F[DFn, DFd], effect sizes (η^2), and p-values were derived from a separate muscle (8) \times Time (2) repeated measures ANOVA run for each finger and direction (8 total models). Pre-drift and post-drift muscle activations were calculated as the average muscle activity recorded the second before feedback was removed (9-10 s) and in the final second (29-30 s) of each trial in the **feedback given condition**.

Table 3.5: Estimated effects of muscle (FDS2, FDS3, FDS4, FDS5, EDC2, EDC3, EDC4, EDC5), and feedback (pre-drift, post-drift) on muscle activity (%MVE). Estimates F[DFn, DFd], effect sizes (η^2), and p-values were derived from a separate muscle (8) \times Time (2) repeated measures ANOVA run for each finger and direction (8 total models). Pre-drift and post-drift muscle activations were calculated as the average muscle activity recorded the second before feedback was removed (9-10 s) and in the final second (29-30 s) of each trial in the **feedback removed condition**.

Table S1: Pairwise comparisons (Tukey's method) of the uninstructed finger force drifts (%MVC) for each instructed finger between the feedback given and feedback removed conditions (left). Beside the comparison of each instructed finger, the estimated marginal mean [95% confidence interval] uninstructed finger force drift in the feedback given (center) and feedback removed (right) conditions are presented.

Table S2: Pairwise comparisons (Tukey's method) of the main effect of time in separate muscle (8) \times time (2) repeated measures ANOVA run for each finger and direction (8 total models). Comparisons show the mean muscle compartment activity pre-drift (5-10 s) and post-drift (25-30

s) [95% CI]. Estimated mean differences (% MVE) for each instructed finger, direction, and magnitude are also presented for the feedback given condition (left) and the feedback removed condition (right).

Table S3: Pairwise comparisons (Tukey's method) of the activity measured in each muscle compartment (% MVE) pre-drift (9-10 s) and post-drift (29-30 s) in the feedback removed condition. Estimated mean differences (% MVE) within each muscle compartment are presented for each instructed finger (left to right) in both flexion (top) and extension (bottom). Differences are based on a separate muscle (8) \times Time (2) repeated measures ANOVA run for each finger and direction (8 total models).

List of Figures

Figure 2.1: Posterior view of a right hand. The DIP, PIP, and MCP joints of the 5th digit, and the IP and MCP joints of the 1st digit are labeled. (Schuenke et al., 2020)

Figure 2.2: (A) Anterior view of right arm with FDL and FDP labelled. (B) Posterior view of right arm with ED, ED tendons, and the extensor mechanism labelled. (C) Anterior view of right hand with lumbricals and 1st dorsal interosseus labelled. (D) Anterior view of right hand with 1st – 4th dorsal interossei and 1st – 3rd palmar interossei labelled. (Schuenke et al., 2020)

Figure 2.3: (A) Dorsal view of a cadaveric hand, depicting the juncturae tendineii between the ED tendons (von Schroeder et al., 1990). (B) Schematic illustrating a contracting muscle (top) exerting force on an inactive muscle (bottom) via the myofascial connective tissue (Yoshitake et al., 2018).

Figure 2.4: (A) The force-length relationship of active muscle force production. The dependence between muscle active force, F , and length, L . A change in the length parameter λ can lead to a change in muscle force by shifting length (L_1) of the muscle along the force-length curve. (B) The referent coordinate (RC) of any effector can be described by two elements (λ_{AG} and λ_{ANT}) which describe a single muscle equivalent of the agonist and antagonist muscle groups. The effector force characteristic is shown with the bold line. (C) Commands sent to any effector can be described by the coordinates $\{R; C\}$ defined at the task level. This low dimensional set of coordinates maps onto sequentially higher dimensional sets corresponding to of individual joints $\{r, c\}$ and muscles (λ). (D) An infinite number of $\{R; C\}$ combinations can be used to produce the same motor action. C-commands translate into slopes and R-commands translate into intercepts of the force coordinate. (Adapted from Abolins & Latash, 2021)

Figure 3.1: The experimental apparatus depicting the forearm braced in a mid-prone position. The wrist and MCP joints are held in neutral postures by the wrist brace and finger cuffs. Force transducers are mounted on a sliding 3D printed plate.

Figure 3.2: Electrode placements for the compartments of (A) FDS and (B) EDC (locations adapted from May & Keir (2018)).

Figure 3.3: An example of instructed index finger force during a 30% MVC (A) force feedback trial and (B) feedback removed trial.

Figure 3.4: Mean force produced by the instructed finger (solid line) and the sum of the three uninstructed fingers (dashed line) over time (s) (x axis) in the feedback removed condition at 15% MVC (A-D) and 30% MVC (E-H). Each panel shows the flexion (red) and extension (blue) conditions for a single instructed finger. The shaded regions represent one standard deviation above the mean force (between participants). The horizontal thin dashed line marks the target instructed finger force, while the vertical line marks the moment when visual feedback was removed (10 s).

Figure 3.5: Mean force (% MVC) produced by each finger from (A) 5-10 seconds (i.e., pre-drift) and (B) 25-30 seconds (i.e., post-drift) for each participant. Plots are grouped by task magnitude

(15%, 30%) and task direction (flexion, extension). Boxes are grouped by the instructed finger for a given task. The three lines on each box show the 25th percentile, median and 75th percentile with error bars representing the minimum and maximum forces. In this figure, forces in the opposite direction to the target force are labelled as negative forces.

Figure 3.6: Mean muscle activity (% MVE) produced by each finger in the **feedback given condition** for (A) flexion and (B) extension. Each set of four plots presents the average muscle activity recorded in compartment (FDS 2-5, EDC 2-5) from 5-10 seconds (top plots) and 25-30 seconds (bottom plots) force targets of 15% MVC (left plots) and 30% MVC (right plots). Box plots are coloured according to the instructed finger. The three lines on each box show the 25th percentile, median and 75th percentile with error bars representing the minimum and maximum activations excluding outliers.

Figure 3.7: Mean muscle activity (% MVE) produced by each finger in the **feedback removed condition** for (A) flexion and (B) extension. Each set of four plots presents the average muscle activity recorded in compartment (FDS 2-5, EDC 2-5) from 5-10 seconds (top plots) and 25-30 seconds (bottom plots) force targets of 15% MVC (left plots) and 30% MVC (right plots). Box plots are coloured according to the instructed finger. The three lines on each box show the 25th percentile, median and 75th percentile with error bars representing the minimum and maximum activations excluding outliers.

List of Abbreviations

(In order of appearance)

M1 – Primary motor cortex

FDS – Flexor digitorum superficialis

EDC – Extensor digitorum communis

MVC – Maximum voluntary contraction

RC – Referent coordinate

MCP – Metacarpophalangeal

PIP – Proximal interphalangeal

DIP – Distal interphalangeal

IP – Interphalangeal

FDP – Flexor digitorum profundus

FPL – Flexor pollicis longus

CIS – Common input strength

AC – Actual coordinate

S1 – Primary somatosensory cortex

Chapter 1: Introduction

The human hand is specialized in performing a wide array of motor tasks requiring both individuated and synchronous use of the fingers. Flexible control of single and multi-finger actions is achieved through the coordination of mechanical and neural structures which consequently impose limitations on finger independence. When a person moves or produces voluntary force with a single instructed finger, involuntary movement or force is produced by the uninstructed fingers (May & Keir, 2018; Sanei & Keir, 2013; Van Beek et al., 2018; Zatsiorsky et al., 2000). Finger independence is limited by mechanical structures in the hand and forearm and neural factors, which potentially reflect neuromuscular control strategies used to coordinate finger movements. Mechanical factors limiting finger independence include passive force transfers via myofascial connections between the extrinsic finger muscles, connective tissue surrounding neurovascular tracts, and intertendinous connections known as *juncturae tendineae* (Huijing et al., 1998; Leijnse, 1997; Maas et al., 2024; Von Schroeder et al., 1990). Neurally, finger independence is suggested to be limited by overlapping cortical regions representing the fingers and common corticospinal pathways which diverge onto pools of motor units spanning multiple extrinsic finger muscles (Ejaz et al., 2015; Keen & Fuglevand, 2004; McIsaac & Fuglevand, 2007; Sanei & Keir, 2013; Schieber & Hibbard, 1993). Delineating between the contributions of these different factors is at the crux of finger independence research and is necessary to understand how finger movements are coordinated by the central nervous system.

Most studies quantifying interdependencies between the fingers compare the force or movement produced by the instructed finger(s) to the involuntary force or movement in the uninstructed fingers during brief (< 5 seconds) movement or force production tasks. However, a series of studies have identified drifts towards lower finger independence which occur during

prolonged pressing without visual force feedback (Ambike et al., 2015; Cuadra et al., 2018; Hirose et al., 2020; Vaillancourt & Russell, 2002). When a person performs isometric flexion with a finger or subset of fingers at a target force level and visual feedback is removed, the instructed finger rapidly drifts to lower force magnitudes, decreasing by up to 40% of the initial target force (Ambike et al., 2015). If these drifts towards lower instructed finger forces represent a drift in finger force production at the task level (i.e., full hand), then parallel drifts in the uninstructed finger forces towards less involuntary force production should occur. However, when visual feedback is used to hold the instructed finger(s) at a target force, the uninstructed fingers are found to drift towards greater magnitudes, resulting in increased force sharing between the fingers (i.e., less finger independence) (Hirose et al., 2020). These drifts occur over a period of ~10 – 20 seconds and are not consciously perceived by the actor.

Recent studies explain unintentional finger forces drifts using the motor control theory of spatial referent coordinates (Abolins & Latash, 2021; Ambike et al., 2015; Hirose et al., 2020). Referent control asserts that fingertip forces are produced by a set of internal spatial referent coordinates (RC) representing the hand at the task level, the individual fingers, and the muscles. These RCs are arranged hierarchically, with voluntary movements produced at the task level projecting onto lower dimensional sets of RCs controlling the fingers and muscles. The RC representing the instructed finger is suggested to gradually drift towards the actual coordinate of the finger when visual feedback is removed, decreasing the instructed finger force over time. When the instructed finger force is fixed, the spread of cortical excitation creates drifts in the RCs of the uninstructed fingers resulting in greater force production.

Unintentional force drifts provide evidence that finger interdependencies produced by the central nervous system are less robust than previously suggested (Zatsiorsky et al., 2000).

Therefore, a thorough investigation of these drifts is required to understand how neural interdependencies between the fingers change during prolonged finger force production. Drifts in the force production of a given finger likely result from complex changes in activity across multiple co-contracting muscles. However, no study has measured the changes in muscle activity responsible for unintentional finger force drifts. Finger force drifts have also solely been measured in static finger flexion. Finger extension is found to be less independent than finger flexion and may be affected differently by unintentional force drifts (May & Keir, 2018; McIsaac & Fuglevand, 2007). The purpose of this thesis is to investigate the relationship between instructed and uninstructed finger force drifts and the changes in muscle activity underlying these drifts in static single finger flexion and extension.

Chapter 2: Literature Review

2.1. Review of the Anatomy

The hand consists of the thumb (digit 1) and four fingers (digits 2-5). Digits 2-5 consist of four bone segments: metacarpal, proximal phalanx, middle phalanx, and distal phalanx; and three joints: metacarpophalangeal (MCP), proximal interphalangeal (PIP), and distal interphalangeal (DIP). Digit 1 does not have a middle phalanx and only has a single interphalangeal joint (IP) (Figure 2.1).

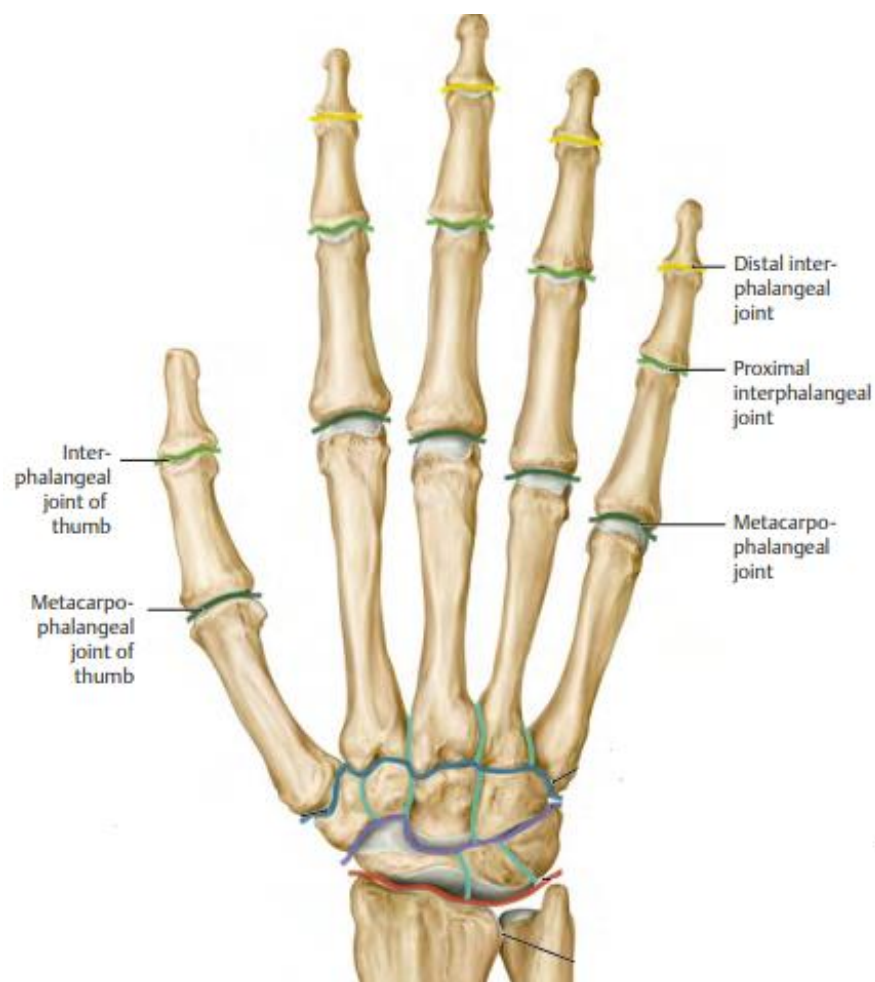


Figure 2.1: Posterior view of a right hand. The DIP, PIP, and MCP joints of the 5th digit, and the IP and MCP joints of the 1st digit are labeled. (Schuenke et al., 2020)

Finger movements are controlled by both extrinsic and intrinsic muscles. The extrinsic finger muscles originate in the forearm and transmit force through the wrist via tendinous structures, while the intrinsic muscles originate within the hand. The extrinsic flexors include flexor digitorum superficialis (FDS), flexor digitorum profundus (FDP), and flexor pollicis longus (FPL) (Figure 2.2A). FDS inserts onto the middle phalanx of digits 2-5, flexing the MCP, PIP, and wrist joints. FDP inserts onto the distal phalanx of digits 2-5, flexing the DIP, MCP, PIP, and wrist joints. FPL inserts onto the distal phalanx of the thumb and flexes the MCP and IP joint. The primary extrinsic finger extensor muscle is extensor digitorum (ED) (Figure 2.2B). ED inserts onto the extensor mechanism on the dorsum of the hand; a tendinous network that distributes forces generated by the extrinsic extensors and intrinsic muscles along the dorsal surface of each finger (Garcia-Elias et al., 1991; Keen & Fuglevand, 2003; Lee et al., 2008; MacIntosh & Keir, 2017). The ED extends the three joints of each finger and the wrist. Finger movements are also controlled by intrinsic muscles such as the dorsal and palmar interossei and lumbricals. Lumbricals (Figure 2.2C) and interossei (Figure 2.2D) insert into the extensor mechanism of each finger and they flex the MCP as well as extend the PIP and DIP joints. The palmar and dorsal interossei also adduct and abduct the MCP respectively.

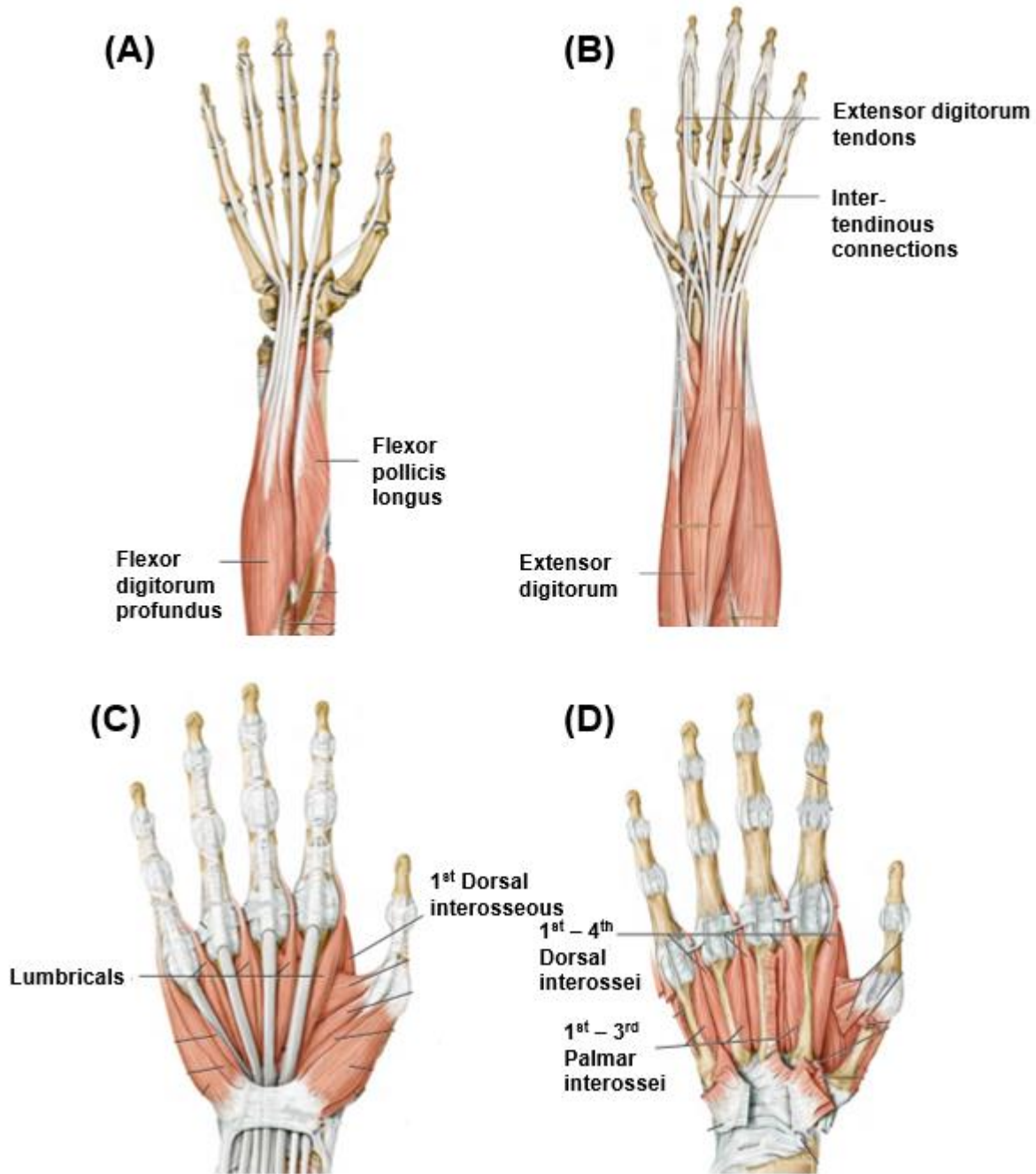


Figure 2.2: (A) Anterior view of right arm with FDL and FDP labelled. (B) Posterior view of right arm with ED, ED tendons, and the extensor mechanism labelled. (C) Anterior view of right hand with lumbricals and 1st dorsal interosseous labelled. (D) Anterior view of right hand with 1st – 4th dorsal interossei and 1st – 3rd palmar interossei labelled. (Schuenke et al., 2020)

Multiple passive connective tissue structures also influence and limit finger movement. The network of extensor tendons on the dorsum of the hand are interconnected by connective tissues known as *juncturae tendineii* (Figure 2.3A). *Juncturae tendineii* functions to stabilize the ED tendons and maintain the spacing between them, but is also known to transfer force between the extensor tendons of the digits (Garcia-Elias et al., 1991; Keen & Fuglevand, 2003; Lee et al., 2008; MacIntosh & Keir, 2017; Von Schroeder et al., 1990). The proximal myofascial connective tissue between the bellies of the extrinsic finger flexors and extensors are also capable of transferring force between the fingers. During shortening contractions, force can be transferred passively to adjacent muscles through this connective tissue (Figure 2.3B) (Huijing et al., 1998, Maas & Huijing, 2005, Maas et al., 2003).

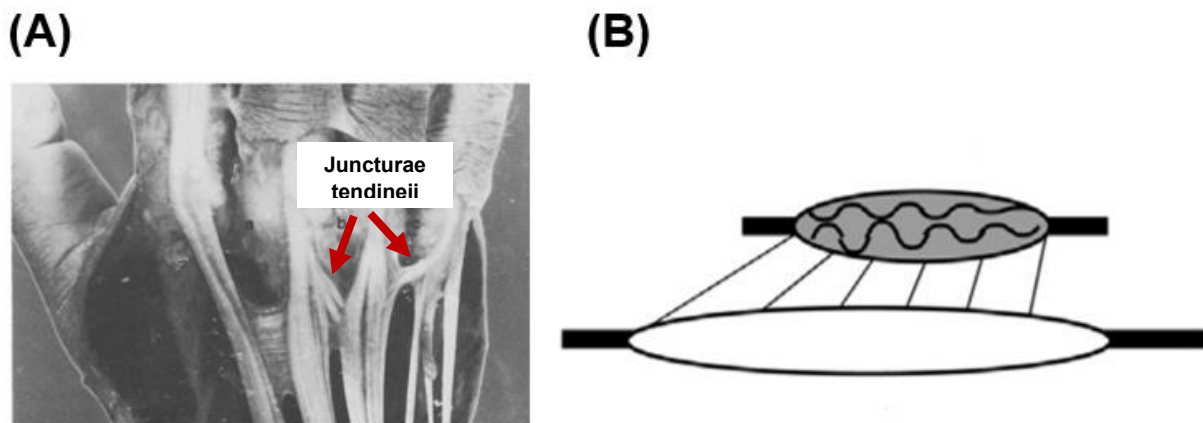


Figure 2.3: (A) Dorsal view of a cadaveric hand depicting the *juncturae tendineii* between the ED tendons (von Schroeder et al., 1990). (B) Schematic illustrating a contracting muscle (top) exerting force on an inactive muscle (bottom) via the myofascial connective tissue (Yoshitake et al., 2018).

2.2. Factors Limiting Finger Independence

The fingers are incapable of moving or producing force with complete independence. When a voluntary movement is produced by a finger or subset of fingers (instructed fingers), involuntary movement also occurs in the uninstructed fingers. Similarly, during isometric single or multi-finger pressing, involuntary fingertip forces are produced by the uninstructed fingers. This phenomenon has come to be known as “finger enslaving,” with the instructed fingers being referred to as the “master fingers,” and the uninstructed fingers referred to as the “slave fingers” (Zatsiorsky et al., 2000). However, in recognition of the harm done and historical significance of the descriptors “master” and “slave” to marginalized groups, this work will utilize more neutral terminology in their place.

The index finger is the most independent finger in both flexion and extension exertions, while the ring finger is the least independent (Sanei & Keir, 2013; Zatsiorsky et al., 2000). But the degree of dependence in each uninstructed finger also depends on which finger is instructed. The fingers adjacent to the instructed finger produce greater unintentional forces and movements than the non-adjacent fingers. Additional variables influencing finger interdependence include contraction mode/strength, wrist posture, relative finger posture, and movement frequency (Häger-Ross & Schieber, 2000; May & Keir, 2018; Mirakhorlo et al., 2017).

Finger interdependencies are attributed to both mechanical and neural factors. Neural factors include overlapping cortical regions representing the fingers and cross-muscle/compartments motor unit synchronization (Abolins & Latash, 2021; Keen & Fuglevand, 2003; Sanes et al., 1995; Schieber & Hibbard, 1993). Mechanical factors include extrinsic myofascial connections and passive intertendinous connections between the tendons controlling the fingers (Huijing et al., 1998; Leijnse, 1997; Maas et al., 2024; Mirakhorlo et al., 2017; Von

Schroeder et al., 1990). As studies disagree on the extent to which these mechanical and neural factors influence finger independence, the following sections will describe the evidence for the contribution of each factor.

2.2.1 Mechanical Factors

Finger independence is limited by mechanical coupling of the fascia surrounding the extrinsic finger muscles and force transfers via juncturae tendineae between the extrinsic finger extensor tendons. In a cadaveric study, von Schroeder & Botte (1993) pulled the individual extensor tendons and observed involuntary MCP, PIP, and DIP extension in the adjacent digits. Following the removal of these juncturae tendons, involuntary movements were eliminated. The influence of passive tendinous force transfers between the extrinsic finger flexors is less substantiated. Kilbreath & Gandevia (1994) passively rotated the DIP joints of participants with anesthetized forearms and found no involuntary movement in adjacent digits. Force is also transmitted passively between the fingers by myofascial connective tissue between the bellies of the extrinsic finger muscles (Huijing et al., 1998; Maas et al., 2003, 2024; Maas & Huijing, 2005). In a study of rat EDL muscles, Huijing et al., (1998) removed the distal tendons of EDL compartments 2-4, preventing direct myotendinous force transmission. If force was only transferred by myotendinous connections, the force exerted by the intact EDL 5 muscle would be expected to decrease according to the physiological cross-sectional area of the disconnected muscle. However, during electrical stimulation of the tibial nerve, the remaining EDL 5 muscle produced 84% of the initial force of the intact muscle, suggesting large force transfers through the shared proximal aponeurosis of EDL. Due to the invasive nature of measuring myofascial force transmission, no study has identified passive myofascial force transfer in human arms in vivo. Bojsen-Møller et al., (2010) identified tissue displacement in the soleus muscle during

localized electrical stimulation of the medial gastrocnemius using ultrasonography, but the magnitude of the force transfer was not quantified.

Although the presence of mechanical factors limiting finger independence is well substantiated, their influence relative to neural factors is debated. Keen & Fuglevand (2003) quantified the force distribution in the muscles using a “selectivity index” based on the extension forces produced by each finger following localized intramuscular electrical stimulation of the ED muscle. The selectivity index of 1 indicates that forces generated from weak intramuscular stimulation were transmitted only to one finger, whereas an index of 0 represents an equal distribution of force across the four fingers. They found a mean selectivity index of 0.71 suggesting that forces were primarily transmitted to a single finger and juncturae tendineii probably only played a minor role in force distribution across the fingers. These findings are contrasted by Van Beek et al., (2018a; 2018b) who found that during voluntary finger flexion, force transfers through mechanical linkages contribute substantially to uninstructed finger movements. A series of full range unrestricted flexion tasks were completed for fingers 2-5, while the uninstructed fingers were left unrestrained. The FDS tendon displacement of the index, middle, and ring finger was measured using 2D ultrasound. The activity of FDS and EDC were measured using a grid of surface electrodes and kinematics were tracked using inertial measurement units. No correlation was found between the movement pattern of the uninstructed fingers and the activity pattern of the corresponding muscle regions, suggesting intertendinous and myofascial (passive) connections played a major role in producing uninstructed finger movements. However, the researchers later concluded that the relative role of neural and mechanical factors in finger independence change with age (Van Beek et al., 2019). When the younger group (22–29 years) from Van Beek et al (2018a; 2018b) were compared to a group of

older adults (68–84 years), they found a more evenly distributed muscle activation pattern over the finger-specific FDS and ED muscle regions during single finger flexion.

The degree to which intertendinous connections limit finger independence is affected by both finger and wrist posture. May & Keir (2018) measured uninstructed finger force during isometric flexion and extension exertions with the wrist held in 30° flexion, neutral, and 30° extension. Wrist posture significantly affected uninstructed finger force, with the greatest extensor force produced in the 30° extended wrist posture, where passive agonist tendons and mechanical connections were in positions of decreased tension. In these positions of decreased tension, increased muscle activity was measured in the uninstructed compartments of the ED muscle, suggesting that neural factors played a primary role in the increased uninstructed forces. The role of posture dependent tendon tension was elucidated by Mirakhorlo et al., (2017), who recorded the isometric flexion force of the uninstructed fingers during a static phase (1 s of voluntary isometric index finger flexion at a constant force) and dynamic phase (~1.35 s of index MCP isotonic flexion at ~ 30 °/s; performed immediately after the static phase). The authors found an ~300 ms delay between the initiation of the dynamic phase and an increase in force by the uninstructed fingers. Following this delay, mechanical force transfers played a major role in uninstructed finger force production. At neutral wrist postures with the finger flexor tendons relaxed, the fingers are found to act independently over a small range of flexion (on average 13–61% of the finger's range of motion) (Van Den Noort et al., 2016). However, these findings were highly variable and asymmetric between the hands. It is plausible that these findings reflect the delay required to take up the slack in the flexor tendons as the flexion movements were brief and continuous. The movement of the uninstructed fingers may have also been restricted by the increased antagonist muscle activity required for wrist stability.

2.2.2 Neural Factors

Neural factors limiting finger independence are typically identified as involuntary firing of extrinsic finger muscle fibers in compartments controlling the uninstructed fingers.

Involuntary muscle activity in uninstructed compartments is considered a result of a shared neural drive to muscles controlling multiple fingers. Using intramuscular electrodes, Kilbreath & Gandevia (1994) found activation of FDP compartments controlling the uninstructed fingers during finger flexion. Involuntary activation of uninstructed muscle compartments is also shown to increase with greater activation of the instructed compartment (Sanei & Keir, 2013).

The concept of a shared neural drive constraining finger independence is further substantiated by studies identifying synchronous motor unit activity across multiple compartments of the extrinsic finger muscles. Synchronous motor unit activity is quantified by the common input strength index (CIS) (Nordstrom et al., 1992). The value of the CIS index (ranging from 0-1) represents the percentage of synchronous discharges for a motor-unit pair observed above a 'chance' level. Keen & Fuglevand (2003) found high levels of motor unit synchronization in motor unit pairs within a compartment of ED (CIS = 0.7 ± 0.3) and moderate synchronization (CIS = 0.4 ± 0.22) between motor units in different compartments. Less synchronization is observed between motor unit pairs between compartments of FDS (CIS = 0.23 ± 0.19), suggesting less neural coupling in finger flexion than extension (McIsaac & Fuglevand, 2007). The potential functional role of cross-compartment motor unit synchronization was highlighted further by a study observing the greatest degree of synchronization between the index finger compartment of FDP and FPL (CIS = 0.49 ± 0.03) (Winges & Santello, 2004). The strong degree of neural coupling between the index finger and

thumb flexors may reflect their large force contributions during grasping tasks (Ergen & Oksuz, 2020).

Traditionally, finger interdependence has been viewed as a flaw in the functioning of the hand and fingers, which is desirable to decrease or eliminate. Increased finger interdependence is observed in studies of patients with neurological disorders (Brandauer et al., 2012; Lang & Schieber, 2004; Latash et al., 2002; Park et al., 2012). The view that finger interdependence exists as a detriment to performance is further substantiated by practice effects. Lower indices of interdependence are observed in people possessing specialized hand skills such as professional musicians (Slobounov et al., 2002; Winges & Furuya, 2015). Short term practice effects are also shown to improve individuated finger movements. Furuya et al. (2014) observed a decrease in movement covariation across fingers in novice musicians following just four days of piano practice. This decrease in movement covariation was most pronounced at the ring and little fingers, which are shown to have the poorest independent control prior to practice.

Contrasting the view of finger interdependence as purely detrimental, numerous studies suggest it may be functionally important and contributes to the stability of movements (Beringer et al., 2020; Dupan et al., 2018; Zatsiorsky et al., 2000). In a study of isometric finger flexion tasks, Dupan et al., (2018) observed widespread activation of the antagonist ED muscle. Since the wrist was not braced, the authors concluded that antagonistic muscle activation is necessary to provide wrist stability at neutral postures, despite its contribution to unintentional finger force production. The role of uninstructed extrinsic finger muscle activation in stabilizing the wrist is corroborated by studies of the effects of non-neutral wrist posture on finger independence. May & Keir (2018) found that during extension of the index and ring fingers, muscle activity of the uninstructed ED compartments was significantly higher with the wrist extended at 30° ($17.7 \pm$

2.1% MVE). These findings agree with Beringer et al., (2020) who reported a 70% increase in finger extensor activity during unrestricted MCP movements across the range of motion when the wrist was extended, although the exact wrist posture was not reported. It is plausible that when the wrist is rotated in the direction of the agonist muscle group, increased agonist muscle activity is required to maintain the wrist posture, resulting in activation of extrinsic finger muscle compartments controlling uninstructed fingers.

Shared input to extrinsic finger muscles is suggested to be rooted in the corticospinal system. Schieber & Hibbard (1993) analyzed the spatial distribution of neuronal activity for the hand region in M1 of a rhesus monkey, during single finger flexion-extension performed using each digit. Most neurons in the M1 hand area were activated during the movement of each finger, which suggest that the cortical regions representing the fingers overlap. The importance of the somatotopic organization of the M1 hand area in humans was confirmed by Sanes et al. (1995), who discovered substantial overlap of the activated M1 regions during single finger flexion-extension movements, using functional magnetic resonance imaging.

Recent findings indicate the neural contribution to finger interdependence is unstable. Force drifts to lower magnitudes in the instructed finger have been observed during steady isometric force production tasks following the removal of visual force feedback (Ambike et al., 2015; Vaillancourt & Russell, 2002). These force drifts are very large and can reach up to 40% of the initial force level. They are also potentially accompanied by drifts in the uninstructed fingers to higher force magnitudes. Studies of unintentional force drifts attribute these findings to a spread of cortical excitation in the M1 area and analyze the phenomenon using the motor control theory of spatial referent coordinates (Abolins & Latash, 2021). The following sections

will review and question the robustness of this framework, ultimately seeking to test the validity of its assertions using biomechanical principles.

2.3. Unintentional Force Drifts in Finger Pressing

Finger independence in static pressing tasks is usually evaluated at fixed force magnitudes and maintained with the help of visual force targets (Dupan et al., 2018; May & Keir, 2018; Sanei & Keir, 2013; Zatsiorsky et al., 2000). These experimental setups are not representative of natural conditions in finger pressing tasks during which visual force feedback is absent. Finger forces in natural hand use are generated by the excitation of the hand area of the M1 cortex, influenced by a combination of visual feedback and afferent feedback from muscle spindles, golgi tendon organs, and mechanoreceptors in the skin (Feldman, 2015). Following the removal of visual feedback during single finger static pressing tasks, the instructed finger force rapidly drifts to lower magnitudes, up to 40% lower than the initial force over a relatively short period of time (8-20s) (Ambike et al., 2015; Cuadra et al., 2018; Vaillancourt & Russell, 2002).

A series of recent studies have investigated the impact of visual feedback manipulation on unintentional force drifts in instructed and uninstructed fingers (Abolins & Latash, 2021; Cuadra et al., 2018; Hirose et al., 2020; Ricotta et al., 2021). In a study by Hirose et al., (2020) subjects were asked to meet a force target with a cursor on a screen by pressing with a pair of instructed fingers. The visual feedback was either representative of the force produced by the instructed pair or the uninstructed pair, which the participants were unaware of due to adjustments in feedback gain. Visual feedback on the force produced by the instructed fingers led to a 30% drift in the force produced by the uninstructed fingers toward higher magnitudes. However, when visual feedback on the uninstructed finger force was presented, the instructed finger force drifted to lower magnitudes. Both conditions led to increased interdependency

indices. Taken together, these findings suggest that in the absence of visual feedback, instructed finger force will drift to lower magnitudes while uninstructed finger force drifts to higher magnitudes. The authors of the most recent studies of force drifts and finger interdependence interpret these force drifts through the framework of spatial referent coordinates (Abolins & Latash, 2021).

2.3.1 Referent Control of Motor Actions

The theory of spatial referent control of neuromuscular action originates from Feldman's (1986) equilibrium point hypothesis (Abolins & Latash, 2021; Cuadra et al., 2021; Reschechtko & Latash, 2017). The equilibrium point hypothesis describes the neural control of a muscle as reflecting time changes in the threshold (λ) of the stretch reflex, which can be expressed in mechanical variables (i.e., the length at which muscle activity begins during slow stretch). The amount of force (F) produced by the muscle at lengths $(L) > \lambda$ depends on the $F(L)$ characteristics of the muscle and the external load applied. In the absence of an external load, the muscle will shorten until it reaches length λ (Figure 2.4A). Therefore, the action of a joint crossed by two or more muscles can be described using a pair of spatial coordinates λ_{AG} and λ_{ANT} which represent single muscle equivalents of the agonist and antagonist muscles.

The force coordinate characteristics of the opposing muscle groups sum up to produce the joint force (and moment) coordinate characteristics. Shifting λ_{AG} and λ_{ANT} in the same direction will cause the joint to rotate (or translate along the spatial axis X) and shifting λ_{AG} and λ_{ANT} in opposite directions will result in coactivation (or joint stiffness). Therefore, the spatial characteristics of a joint (or any effector) can be summarized using a lower dimensional set $\{r, c\}$, which is compared to the actual coordinate (AC) of the effector (Figure 2.4B). Each effector's $\{r, c\}$ commands are projected onto an even lower dimensional set $\{R, C\}$ which

describes an entire movement or body position at the task level. The hierarchical structure of these referent commands is depicted in Figure 2.4C. The reciprocal command (R) represents the coordinate at which the resultant force or moment is zero, and the coactivation command (C) is the range where the two opposing muscle groups are active simultaneously (Figure 2.4D). To produce a target force with an effector, an infinite combination of R and C commands can be used. Changing R or C independently will result in a change in force at the effector (Figure 2.4D). In finger pressing tasks, the {R, C} of the effector can be described as penetrating the surface it is contacting. The amount of pressing force produced at the fingertip is described in terms of how deeply the referent position penetrates the surface, and the C-coordinate which determines the co-contraction.

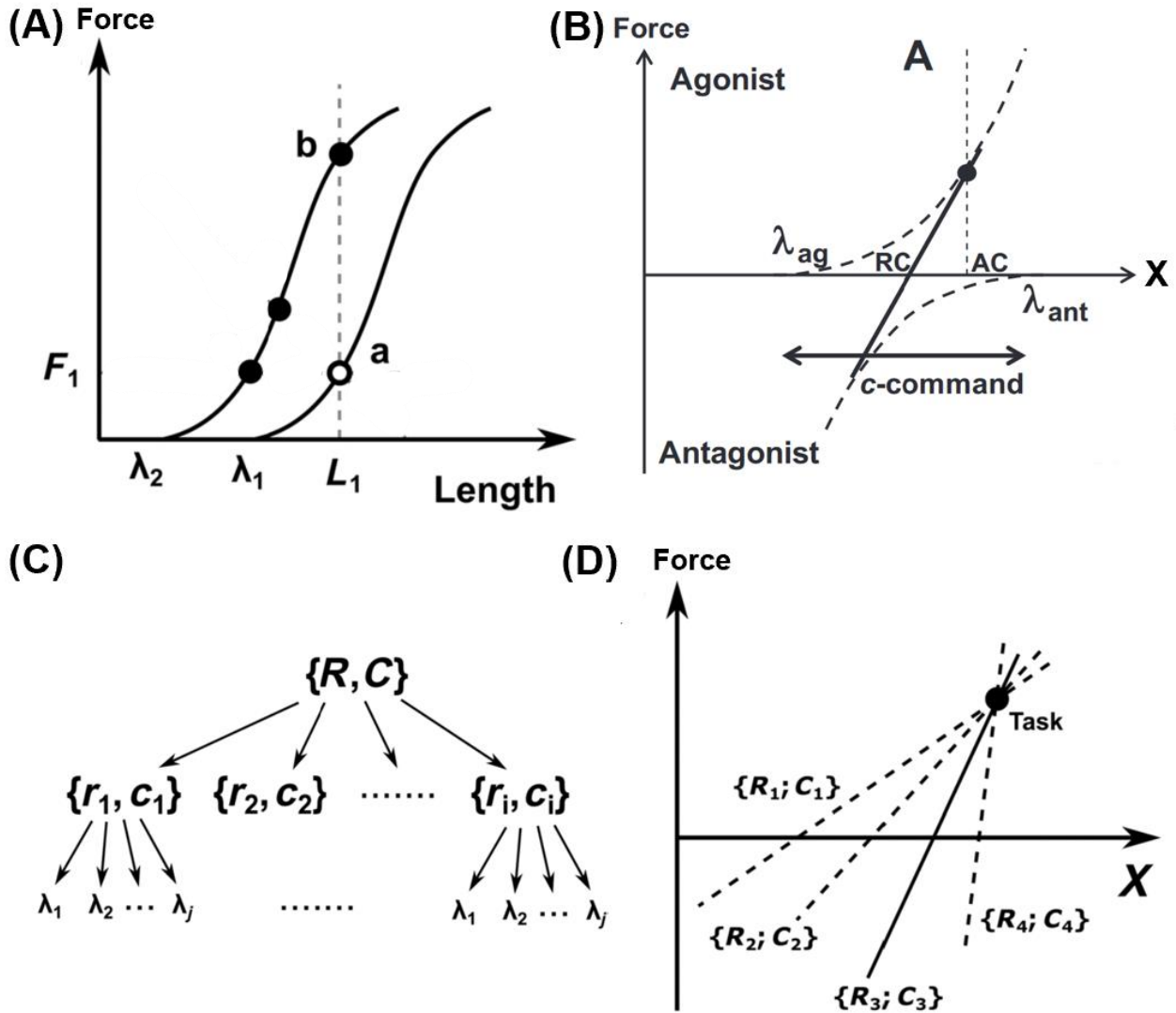


Figure 2.4: (A) The force-length relationship of active muscle force production. The dependence between muscle active force, F , and length, L . A change in the length parameter λ can lead to a change in muscle force by shifting length (L_1) of the muscle along the force-length curve. (B) The referent coordinate (RC) of any effector can be described by two elements (λ_{AG} and λ_{ANT}) which describe a single muscle equivalent of the agonist and antagonist muscle groups. The effector force characteristic is shown with the bold line. (C) Commands sent to any effector can be described by the coordinates $\{R; C\}$ defined at the task level. This low dimensional set of coordinates maps onto sequentially higher dimensional sets corresponding to of individual joints $\{r, c\}$ and muscles (λ). (D) An infinite number of $\{R; C\}$ combinations can be used to produce the same motor action. C-commands translate into slopes and R-commands translate into intercepts of the force coordinate. (Adapted from Abolins & Latash, 2021)

2.3.2 The Origin of Finger Force Drifts

Unintentional force drifts in instructed and uninstructed fingers are described by Abolins & Latash (2021) as resulting from two phenomena: (1) drifts in the RC coordinate of the instructed finger towards the AC of the finger, and (2) spread of cortical excitation resulting in larger RC commands to uninstructed fingers. Drifts towards larger magnitudes observed in the uninstructed fingers are interpreted as primarily reflecting a drifts in the C command, indicating more muscle coactivation (Abolins et al., 2020; Cuadra et al., 2021; Reschechtko & Latash, 2017). In the absence of visual feedback, λ_{ANT} starts to drift toward the actual muscle length resulting in less instructed finger force, which is measured as joint stiffness (Reschechtko and Latash, 2017). However, this assertion is incongruent with the finding that the instructed fingers drift towards lower force magnitudes in the absence of visual feedback, as decreased antagonistic extensor activity would produce greater finger pressing forces in both the instructed and uninstructed fingers. Abolins & Latash (2021) assert that a spread of cortical excitation is the cause of the contrasting drifts towards higher force magnitude in the uninstructed fingers, but little explanation is offered for what is causing the uninstructed fingers not to drift back to lower magnitudes. Based on the findings of Zatsiorsky et al., (2000), the minimization of the wrist pronation-supination moment produced by the normal forces of all the fingers of the hand is suggested (Hirose et al., 2020). Under the explanation of spatial referent control, the referent position of the entire upper limb would hierarchically supersede the {r, c} commands of the individual fingers, causing them to drift away from the AC of the fingers. The point of saturation where the force drifts in the instructed and uninstructed fingers end would then represent the equilibrium point of the wrist pronation-supination command. However, this hypothesis has yet to be demonstrated empirically.

The explanation of spatial referent control theory for unintentional force drifts observed in studies of finger independence is subject to several additional limitations. In recent studies of finger force drifts, finger stiffness (relating to the C-command) is determined by applying small linear translations to the force transducers along the axis of the applied force which is called the ‘inverse piano’ technique (Ambike et al., 2016; Cuadra et al., 2021; Hirose et al., 2020; Martin et al., 2011). The temporary increase in force is used to compute the agonist and antagonist force, typically at two points before and after the visual feedback manipulation. This approach is limited in its ability to characterize neuromuscular changes that occur continuously throughout unintentional force drifts. Exclusively measuring end effector characteristics also does not allow for differentiation between intrinsic and extrinsic finger muscle activation. A more thorough investigation of finger flexor and extensor muscle activation using EMG is required to clarify the relationship between motor control of finger pressing tasks and end effector force output. Additionally, no study has characterized changes in finger muscle co-contraction during force drifts in the instructed and uninstructed fingers simultaneously. Studies assessing changes in finger stiffness using the inverse piano technique do so in multi-finger instructed finger tasks only (Abolins et al., 2020; Cuadra et al., 2021; Hirose et al., 2020). The neuromuscular cause of force drifts in uninstructed fingers remains largely inferred. Finally, a wide range of instructed force magnitudes have yet to be examined in studies of unintentional force drifts following visual feedback manipulation. Hirose et al. (2020) use instructed force magnitudes of 7-25% MVC, but the effects of instructed finger force levels >25% remain unexplored.

2.4 Summary

Independent finger control is required for performing dexterous manual tasks. Constraints on independent finger movements are imposed by both mechanical and neural factors. Recent studies on unintentional force drifts in instructed and uninstructed fingers suggest that neural influences on finger interdependence are highly unstable and drift towards greater levels of force sharing in the absence of visual feedback. The authors of these studies explain drifts towards higher levels of finger interdependence using the framework of spatial referent coordinates. However, this framing lacks experimental evidence of the neuromuscular mechanisms driving unintentional force drifts in studies of finger interdependence. Studies of instructed and uninstructed finger force drifts should measure extrinsic finger flexor and extensor activity across both flexion and extension tasks and a wide range of force magnitudes to improve our understanding of finger control from a biomechanical perspective.

Chapter 3: Manuscript

Exploring unintentional drifts in finger force production and muscle activity:

A study of finger independence

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3.1 Abstract

Recent findings indicate that the fingers become less independent during prolonged finger flexion due to drifts towards greater uninstructed finger force. These force drifts may indicate that neural factors significantly limit finger independence during prolonged force production. However, finger force drifts have solely been studied in flexion through changes in fingertip force over time, rather than at the level of the muscle through electromyography (EMG). Our study sought to quantify the phenomenon of unintentional finger force drifts in digits 2-5, performing both single-finger flexion and extension.

Twenty right-handed participants (10F and 10M, age 18-29) performed a series of isometric, single finger flexion and extension exertions with digits 2-5. The activity of flexor digitorum superficialis (FDS) 2-5 and extensor digitorum communis (EDC) 2-5 were recorded via surface EMG. Participants performed 30 s static single finger flexion and extension exertions at 15% and 30% of their maximum voluntary contraction (MVC) with digits 2-5. A single repetition of each exertion was performed in two conditions: (1) with continuous visual force feedback, and (2) with visual feedback removed following 10 s of feedback. In the feedback removed condition, significant downward drifts in the instructed finger force were observed at both flexion magnitudes (0.6-8.4% MVC), and at 30% MVC extension (1.4-5.2% MVC). When feedback was given, we measured small drifts towards greater involuntary force production (0.5-3.9% MVC) by the uninstructed fingers over the final 20 seconds of the trial. These drifts were eliminated in the feedback removed condition. Drifts in the instructed fingers towards lower force production were associated with decreased finger muscle activity, which was identified during 30% MVC flexion of the index, middle, and little fingers. Decreased extrinsic muscle activity coupled with our

findings regarding the uninstructed fingers suggest that drifts towards lower finger force may be occurring at the task level, reflecting an overall decline in force production by the hand.

3.2. Introduction

Individuated finger control is essential to perform activities of daily living including typing and writing, as well as skilled manual tasks such as playing musical instruments or specialized tool use. However, the fingers also need to operate synchronously to perform prehensile tasks and multi-finger pressing. The intricate mechanical structure of the hand and the neural structures controlling finger movement are specialized to perform both types of manual tasks, imposing limitations on purely independent finger control. When a voluntary movement or pressing force is produced by a finger or subset of fingers, involuntary movement or fingertip forces are observed among the uninstructed fingers (May & Keir, 2018; Sanei & Keir, 2013; Van Beek et al., 2018; Zatsiorsky et al., 2000)

Finger independence is limited by both direct mechanical connections between the fingers and underlying neural constraints. Mechanical factors limiting individuated finger control include myofascial and intertendinous connections between the extrinsic finger muscles and connective tissue surrounding synergistic muscle groups and neurovascular tracts (Finni et al., 2023; Huijing et al., 1998; Leijnse, 1997; Von Schroeder et al., 1990). In addition to mechanical factors, finger interdependencies also arise from hard-wired neural pathways which constrain our ability to independently activate the extrinsic finger muscles. Common spinal interneurons are suggested to project onto groups of multiple muscles, distributing common neural inputs across different motoneuron pools (Keen & Fuglevand, 2003; McIsaac & Fuglevand, 2007). Independent recruitment of the extrinsic finger muscles may be further constrained by overlapping regions of the M1 cortex representing the fingers (Sanes et al., 1995; Schieber & Hibbard, 1993).

Until recently, constraints on finger independence in the central nervous system have been thought of as a relatively rigid set of hypothetical control variables, also known as synergies, representing weighted commands to all five of the digits (Feldman, 2015). However, a series of recent studies have called into question the robustness of a purely synergistic model of finger interdependencies by identifying short term changes in finger independence associated with the well known phenomenon of unintentional force drifts (Ambike et al., 2015; Hirose et al., 2020; Vaillancourt & Russell, 2002). In the absence of visual feedback, instructed finger flexion forces are found to follow a downward exponential curve proportional to the initial force magnitude, reaching saturation after ~20 seconds (Ambike et al., 2015). These unintentional force drifts are large, decreasing by up to 40% of the initial force magnitude and are reportedly unperceived by the actor. When visual feedback is used to hold the instructed finger at a constant force magnitude, contrasting upward drifts in the involuntary force produced by the uninstructed fingers are also measured, indicating a general decrease in finger independence (Hirose et al., 2020). However, these unintentional force drifts have not been identified in isometric finger extension.

Researchers interpret drifts towards less finger independence under the framework of internal spatial referent control, an extension of the equilibrium point hypothesis (Feldman, 1985). Spatial referent control theory asserts that voluntary finger movements arise from internal spatial referent coordinates. These control variables dictate the position in space an effector will move towards in the absence of external force. Spatial referent coordinates are hierarchical, with a relatively low dimensional set of coordinates at the task level (i.e., multi-finger synergies) projecting onto a lower dimensional set of coordinates representing the individual fingers, which then project onto an even lower dimensional set controlling individual muscles via the stretch

reflex length threshold. Voluntary movements are produced at the task level, with lower-level control variables arising parametrically within an allowed solution space (Abolins & Latash, 2021).

Drifts in the activation of a multi-finger synergy should cause parallel force drifts in the instructed and uninstructed fingers towards greater or less total force. Instead, the forces produced by the instructed and uninstructed fingers converge, suggesting these drifts are at the level of the individual fingers rather than multi-finger synergies (Hirose et al., 2020). However, these two sets of drifts (instructed and uninstructed) have not been measured simultaneously (i.e., no visual feedback on any fingers), so their relationship remains somewhat indeterminate. It is plausible that the central nervous system employs a different set of multi-finger synergies during prolonged pressing compared to brief force production, showing a preference for greater force sharing between the fingers. Holding the instructed finger(s) at a constant force magnitude through visual feedback may attenuate the effects of these synergies, as any increase in the uninstructed finger force would increase the total task force, which is consciously avoided by the participants in these studies. It also remains unclear what changes are occurring at the muscle level of control, with no study quantifying changes in muscle activity associated with these unintentional force drifts. If the instructed fingers drift towards less force production independently of the uninstructed fingers, this drift should be reflected by decreased agonist activity or increased antagonist activity specific to the instructed finger.

The primary purpose of this study was to explore drifts in finger independence at all three levels of hierarchical control (i.e., muscle, finger, multi-finger synergy). We aimed to answer three specific research questions: (1) How does the instructed finger force drift after removing visual force feedback? (2) How does the instructed finger force drift after removing visual force

feedback during single finger isometric pressing? (3) How does extrinsic finger muscle activity drift with and without visual feedback on the instructed finger? We quantified drifts in the instructed and uninstructed finger forces and the associated changes in extrinsic finger muscle activity during a wide range of single finger isometric force production tasks. These tasks were performed in both flexion and extension. By performing tasks with and without visual force feedback on the instructed finger, we also aimed to clarify the relationship between force drifts in the instructed and uninstructed fingers. We hypothesized that removing visual feedback on the instructed finger would increase the magnitude of the drifts in the uninstructed fingers. We also expected the downward instructed finger force drifts to be associated with a significant decrease in agonist muscle activity (i.e., FDS2 activity decreases along with index finger force).

3.3. Methods

3.3.1. Participant Characteristics

Twenty right-handed participants (10 male, 10 female; age: 21.7 ± 3.4 years; height: 170.7 ± 7.3 cm; mass: 69.3 ± 11.1 kg) were recruited from the McMaster University student population. Individuals were excluded from the study if they reported any upper extremity injuries in the past year. This study was approved by the McMaster Research Ethics Board and written consent was provided by all participants prior to data collection.

3.3.2. Set-up

Participants were seated in an upright posture on a height adjustable stool, with their right elbow and wrist strapped into a custom-built adjustable brace. The right arm was braced in a mid-prone position (i.e., thumb pointing up), with their wrist braced in a neutral posture (0° flexion) (Figure 3.1). The brace was affixed to a height adjustable table, with the elbows of the participants flexed to 90° and the shoulder slightly abducted. Digits 2-5 were held straight (0° metacarpophalangeal joint flexion) by a set of plastic finger cuffs (diameter: 13-20 mm) fit snugly around the middle phalanges. Each cuff was attached to a uniaxial force transducer (MLP50, Transducer Techniques, Temecula, CA, USA) mounted on a baseplate which could be adjusted to accommodate a wide variety of finger lengths. Each element of the apparatus was 3D printed and mounted on an adjustable aluminum frame to accommodate a wide range of anthropometrics.

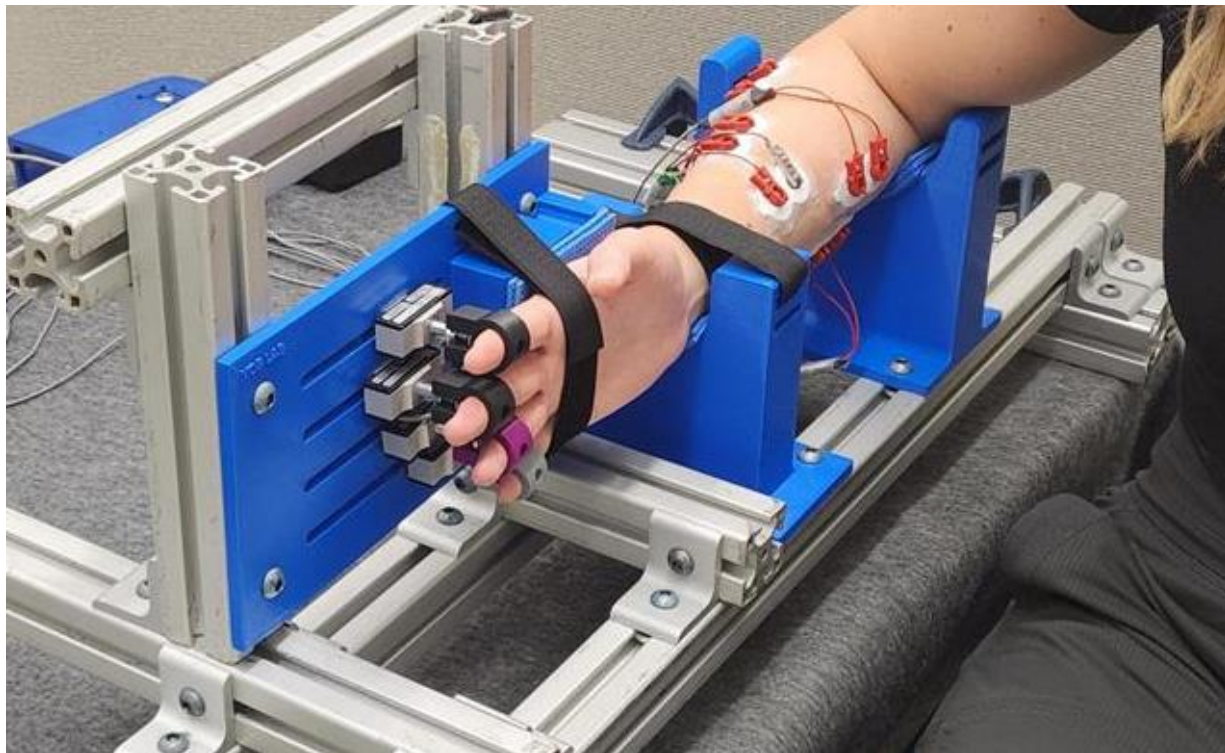


Figure 3.1: The experimental apparatus depicting the forearm braced in a mid-prone position. The wrist and MCP joints are held in neutral postures by the wrist brace and finger cuffs. Force transducers are mounted on a sliding 3D printed plate.

The activity of each extensor digitorum communis (EDC) and flexor digitorum superficialis (FDS) muscle compartment was recorded using bipolar surface electrodes with a fixed interelectrode distance of 2 cm (SEMG/NCV Electrodes, Natus Neurology Inc., WI, USA). For each compartment of EDC and FDS, electrode sites on the skin were shaved and cleansed with isopropyl alcohol before placing the electrodes over the muscle belly parallel to the fibre direction (Figure 3.2). Electrode locations were based on literature (Leijnse et al., 2008; May & Keir, 2018; Sanei & Keir, 2013) (Table 3.1) and confirmed using manual palpation. EMG signals were differentially amplified (CMRR > 115 dB, input impedance ~ 10 G Ω) and bandpass filtered (10-1000 Hz) (AMT-8, Bortec Biomedical Ltd, AB, CA). EMG and force signals were sampled synchronously at 2000 Hz (16 bit, USB-6229, National Instruments, TX, USA) and collected using a custom-designed program (LabView 2016, National Instruments, TX, USA).

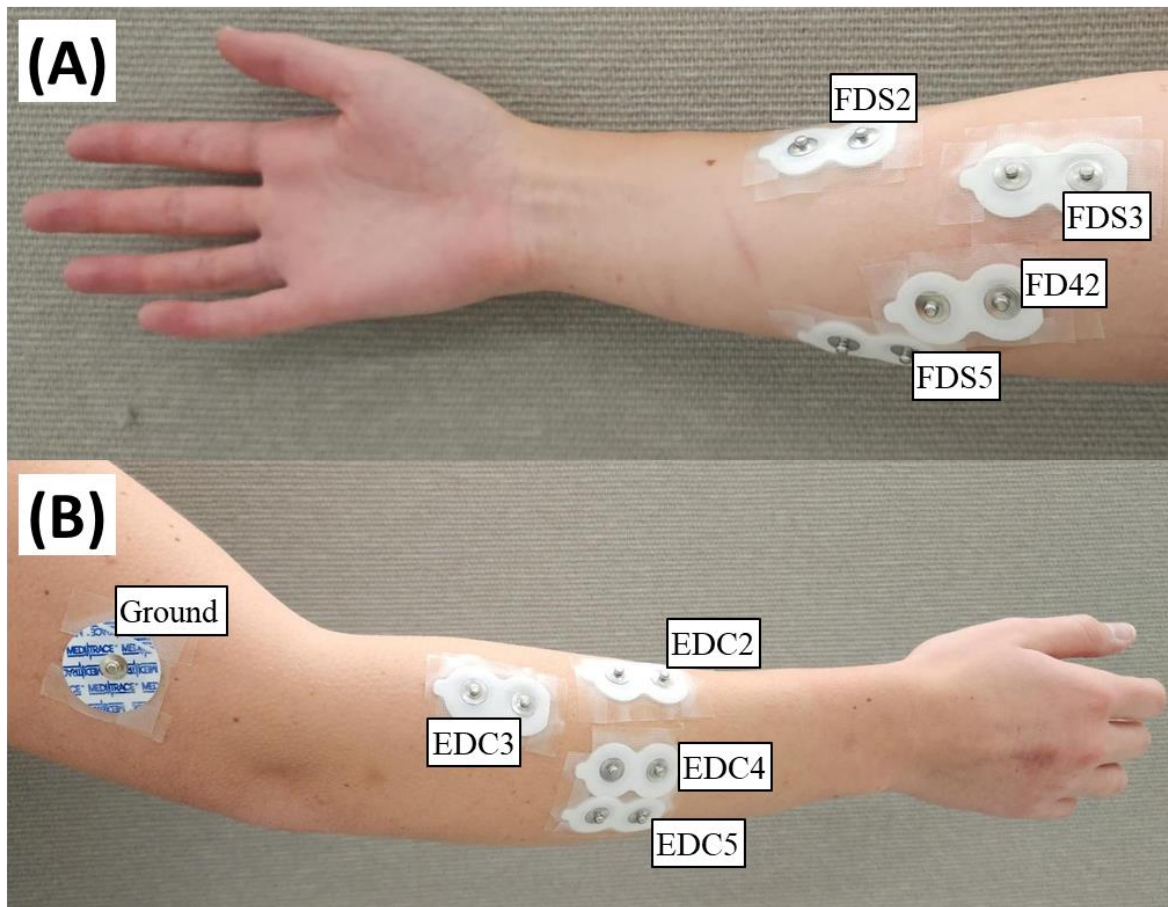


Figure 3.2: Electrode placements for the compartments of (A) FDS and (B) EDC (locations adapted from May & Keir (2018)).

Table 3.1: Electrode locations for the EDC and FDS compartments. Adapted from May & Keir, (2018)

Muscle	Electrode location
EDC2	Approximately half the radial length of the forearm, on the medial border of the ED
EDC3	Just distal to the humeroradial joint at the midline of ED
EDC4	Distal to ED3, parallel to ED2 at the ulnar border
EDC5	Mid-forearm (or more distal with to palpation), medial and distal to ED4 electrodes
FSD2	Approximately half the length of the forearm, on the lateral border of the radius
FDS3	Medial and proximal to FDS2, on the medial border of the radius
FDS4	Medial and proximal to FDS3, on the lateral border of the ulna
FDS5	Medial and distal to FDS4, on the medial border of the ulna

3.3.3. Experimental Protocol

An initial 10 second quiet trial was performed to debias the force and EMG signals. During this trial, the participant was strapped into the apparatus but instructed not to produce any force with their fingers. Following the quiet trial, participants performed two 10 second maximum voluntary contraction (MVC) trials in both flexion and extension with digits 2-5 (i.e., index middle, ring, little), for a total of 16 exertions (4 digits \times 2 directions \times 2 trials). The order of these trials was randomized across the 8 task conditions. Prior to performing MVC trials, participants were instructed to gradually ramp up to the maximum force they could produce with their instructed fingers, while ignoring any forces produced by the uninstructed fingers. A third MVC trial was added to a task condition if the peak forces from the first two trials differed by more than 10%. One minute of rest was given between each MVC. The highest force achieved during the MVC trials was used as the maximal force for a given finger and direction (100% MVC) and used to normalize the force and EMG during the submaximal trials.

Participants performed a series of submaximal (15% and 30% MVC) isometric single finger flexion and extension exertions with their index, middle, ring, and little fingers. All submaximal trials were 30 seconds long, during which participants were instructed to produce force only with the instructed fingers and to avoid producing force with the uninstructed fingers. Submaximal exertions were performed under two conditions: (i) *force feedback condition* followed by (ii) *feedback removed condition*. In the force feedback condition, participants were instructed to exert force with the instructed finger towards a visual target represented by a horizontal line on a display and to maintain the target force until the end of the 30 second trial. In the feedback removed trial, participants once again began exerting force with the instructed finger towards a visual target. Ten seconds into the trial, the visual force feedback was removed and the participant was instructed to maintain the target force level for the remaining 20 seconds of the trial (Figure 3.3). Trials were grouped based on the instructed finger, exertion direction, and target force creating 16 total combinations (4 digits \times 2 directions \times 2 magnitudes). For each finger, direction, and magnitude combination, a single force feedback trial followed by a force removed trial was performed (32 submaximal trials in total). Participants were given 30 seconds of rest between each submaximal trial or more if they reported discomfort or fatigue. Participants were informed of the task conditions (i.e., finger, magnitude, feedback) prior to each upcoming trial.

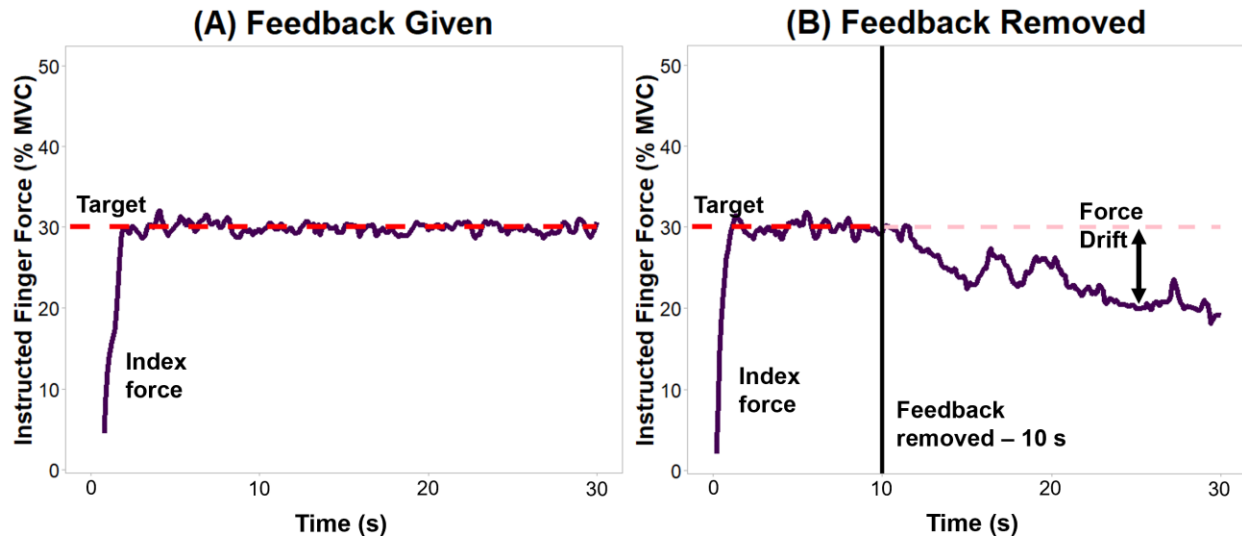


Figure 3.3: An example of instructed index finger force during a 30% MVC (A) force feedback trial and (B) feedback removed trial.

3.3.4. Data Processing

Raw forces were debiased and low pass filtered (4th order Butterworth, 4 Hz cutoff). Forces during submaximal trials were normalized to participants MVC and down sampled to 10 Hz for analysis. The three uninstructed finger forces in each trial were analyzed as a group and added together at each frame. Uninstructed forces were summed as absolute values to avoid obscuring forces in opposite directions within a single trial. Raw EMG signals in each muscle compartment were debiased by subtracting the mean activity measured during the quiet trial. The debiased EMG signals were then full wave rectified and low pass filtered using a 4 Hz dual pass critically damped second order filter. All data processing was performed using Python (Version 3.2).

3.3.5. Statistical Analysis

To quantify drifts in instructed finger forces following the removal of visual feedback, we evaluated how these forces changed over the final 20 seconds of each submaximal trial. For each force magnitude (15%, 30% MVC) and exertion direction combination (flexion, extension),

a separate linear mixed effects model was generated (4 models in total). Each model included a main effect of time, a main effect of instructed finger, and an interaction term between time and finger. The dependent variable was instructed finger force. To account for differences in finger force drifts between participants, a random (participant) slope term was included in each model. A random intercept term was not included because the intercepts were fixed at the target force magnitude when feedback was removed.

In our mixed effects models, the “reference” finger was the index finger. Thus, the main effect of time was used to evaluate the drift in the index finger (i.e., slope of force over time). The interaction between finger x time describes whether the drifts of the non-index fingers (middle, ring, and little) over time are significantly different compared to the index finger. The model coefficients (main effects of time, interaction between finger x time) are expressed in % MVC / seconds. Thus, a main effect coefficient of -0.1 would indicate that the change in index finger force is, on average, decreasing by 0.1 % MVC over each second. Consequently, if the model coefficient for the interaction between middle finger x time is -0.04, this would indicate that the middle finger has a drift that is -0.14 % MVC / s (or -0.04 % MVC / s less than the index finger [-0.1 % MVC / s]).

We calculated the drift in uninstructed finger force (ΔF_{Unins}) as the difference in the mean force produced by the three uninstructed fingers *pre-drift* (5-10 s) and *post-drift* (25-30 s) in both the feedback given and feedback removed conditions (Equation 1). To determine whether the uninstructed finger force drifts depended on the feedback and magnitude conditions of the instructed fingers, we used a 4 (instructed finger) \times 2 (force magnitude) \times 2 (feedback) repeated measures analysis of variance (ANOVA). Separate models were generated for flexion and extension.

$$\Delta F_{Unins} = \sum |\bar{F}_{finger}[25 - 30s]| - \sum |\bar{F}_{finger}[5 - 10s]| \quad (1)$$

Drift in the mean muscle activity of each compartment was calculated between the same *pre-drift (5-10 s)* and *post-drift (25-30 s)* windows used for the uninstructed finger force data. To determine whether significant drifts in muscle activity occurred under the feedback removed condition, we computed a 2 (time) \times 8 (muscle compartment) repeated measures ANOVA of the dependent measure of muscle compartment activity. Separate models were computed for each instructed finger in each combination of direction (i.e., flexion, extension), magnitude (i.e., 15% MVC, 30% MVC), and feedback (feedback given, feedback removed) for a total of 32 models. The drift in the mean muscle activity across each compartment of FDS 2-5 and EDC 2-5 was represented as the main effect of time (pre-drift vs. post-drift) in the models. Significant main effects of time and interactions between time \times muscle compartment were followed up with pairwise comparisons to identify significant drifts within a single muscle compartment.

All statistical tests were performed in R (Version 4.3.2). Assumptions of mixed effects models and ANOVAs were verified through visual inspection, using the *performance* package. Alpha values for all tests were set at $\alpha = 0.05$. Statistically significant effects identified in ANOVAs were followed up with pairwise comparisons using Tukey's HSD post-hoc analysis. Sphericity was violated in two out of the eight uninstructed finger force drift ANOVAs and was corrected using the Greenhouse-Geiser method.

3.4 Results

3.4.1. Instructed Fingers - Force

Continuous drifts by each instructed finger are described by the mixed effects model estimated slopes [95% confidence interval] (Table 3.2). The mean force (\pm standard deviation) produced by both the instructed fingers and the sum of the three uninstructed fingers during the feedback removed condition are displayed in Figure 3.4. In the flexion conditions, the instructed finger consistently drifted to significantly lower force magnitudes over the duration of the feedback removed trials (Figure 3.4, red lines). Under the 15% MVC flexion condition (Figure 3.4, top set of plots), the index finger drifted downward significantly when visual feedback was removed (Time [Index]: -0.12 [$-0.17, -0.06$] % MVC / s, $p < 0.001$), averaging a 2.4% MVC decrease over the remaining 20 seconds of the trial. Relative to the index finger, at 15% MVC, the middle finger experienced smaller (but still downward) drifts (Time \times Middle: 0.07 [$0.05, 0.09$] % MVC / s, $p < 0.001$), while the little finger drifted downward to an even greater extent (Time \times Little: -0.09 [$-0.11, -0.06$] % MVC / s, $p < 0.001$). Significant differences in force drifts between the index finger and ring finger were not found (Time \times Ring: 0.01 [$-0.02, 0.03$] % MVC / s, $p = 0.663$). In the 30% MVC flexion condition (Figure 3.4, bottom set of plots), downward force drifts were measured in all four instructed fingers. These drifts were the greatest when the index finger was the instructed finger (Time [Index]: -0.42 [$-0.51, -0.32$] % MVC / s, $p < 0.001$), amounting to an average 8.4% MVC decrease over the last 20 seconds of the feedback removed condition. Compared to the index finger, smaller downward force drifts were measured in the middle (Time \times Middle: 0.06 [$0.01, 0.11$] % MVC / s, $p = 0.032$), ring (Time \times Ring: 0.13 [$0.08, 0.18$] % MVC / s, $p < 0.001$), and little (Time \times Little: 0.06 [$0.01, 0.11$] % MVC / s, $p = 0.019$) fingers. The interparticipant variability of these drifts is described by the random (participant) slope effect of our mixed effects models, which indicates the

standard deviation of the main effect of time on the index finger force (% MVC / s) (Table 3.2). Drifts were more variable in the 30% MVC condition (0.20 % MVC / s) than at 15% MVC (0.12 % MVC / s).

In the extension conditions, drifting behaviour varied greatly between the instructed fingers (Figure 3.4, blue lines). During the 15% extension condition (Figure 3.4, top set of plots), no consistent force drifts were observed in the index finger (Time [Index]: -0.02 [-0.12, 0.08], $p = 0.690$) or the middle finger (Time \times Middle: $p = 307$). In contrast, the ring (Time \times Ring: 0.12 [0.09, 0.16] % MVC / s, $p < 0.001$) and little (Time \times Little: 0.25 [0.21, 0.28] % MVC / s, $p < 0.001$) fingers drifted towards greater force production when visual feedback was removed. In the 30% extension condition (Figure 3.4, bottom set of plots), we observed downward force drifts by the index finger (Time [Index]: -0.26 [-0.38, -0.15] % MVC / s, $p < 0.001$). This slope indicates an average downward index finger extension force drift of 5.2% MVC when feedback was removed. Significantly smaller downward force drifts were measured in the middle (Time \times Middle: 0.06 [0.01, 0.12] % MVC / s, $p < 0.031$), ring (Ring \times Time: 0.13 [0.08, 0.19] % MVC / s, $p < 0.001$), and little (Little \times Time: 0.19 [0.13, 0.24] % MVC / s, $p < 0.001$) fingers. Similar random slope (participant) effects were observed at both magnitudes (15% MVC = 0.22% MVC; 30% MVC = 0.25% MVC), although the random slope effect was proportionally greater relative to the target force at 15% MVC (Table 3.2).

Table 3.2: Participant (random) slope effects and model estimated [95% confidence interval] slopes (%MVC/Time (s)) for each instructed finger during the final 20 seconds (10 s – 30 s) of the feedback removed trials. Separate models were run for both flexion (left) and extension (right), at 15% MVC (top) and 30% MVC (bottom). Fixed effects of fingers are not presented as they were fixed at the target force. Model estimates, t, and p-values were derived from mixed effects models of the instructed finger forces. The uninstructed fingers are analyzed separately (See Table 3.3).

Direction Magnitude	Parameter	Flexion			Extension		
		Estimate [95% CI]	t	p	Estimate [95% CI]	t	p
15% MVC							
	Random [Participant × Time]	0.12			0.22		
	Intercept	14.21 [13.41, 15.00]	35.05	< 0.001	15.23 [14.30, 16.16]	32.10	< 0.001
	Time [Index]	-0.12 [-0.17, -0.06]	-4.24	< 0.001	-0.02 [-0.12, 0.08]	-0.40	0.690
	Middle × Time	0.07 [0.05, 0.09]	5.90	< 0.001	-0.02 [-0.05, 0.02]	-1.02	0.307
	Ring × Time	0.01 [-0.02, 0.03]	0.44	0.663	0.12 [0.09, 0.16]	6.80	< 0.001
	Little × Time	-0.09 [-0.11, -0.06]	-7.33	< 0.001	0.25 [0.21, 0.28]	13.57	< 0.001
30% MVC							
	Random [Participant × Time]	0.20			0.25		
	Intercept	28.02 [25.82, 30.23]	24.93	< 0.001	26.67 [24.90, 28.43]	29.57	< 0.001
	Time [Index]	-0.42 [-0.51, -0.32]	-8.46	< 0.001	-0.26 [-0.38, -0.15]	-4.41	< 0.001
	Middle × Time	0.06 [0.01, 0.11]	2.16	0.032	0.06 [0.01, 0.12]	2.16	0.031
	Ring × Time	0.13 [0.08, 0.18]	4.95	< 0.001	0.13 [0.08, 0.19]	4.54	< 0.001
	Little × Time	0.06 [0.01, 0.11]	2.34	0.019	0.19 [0.13, 0.24]	6.30	< 0.001

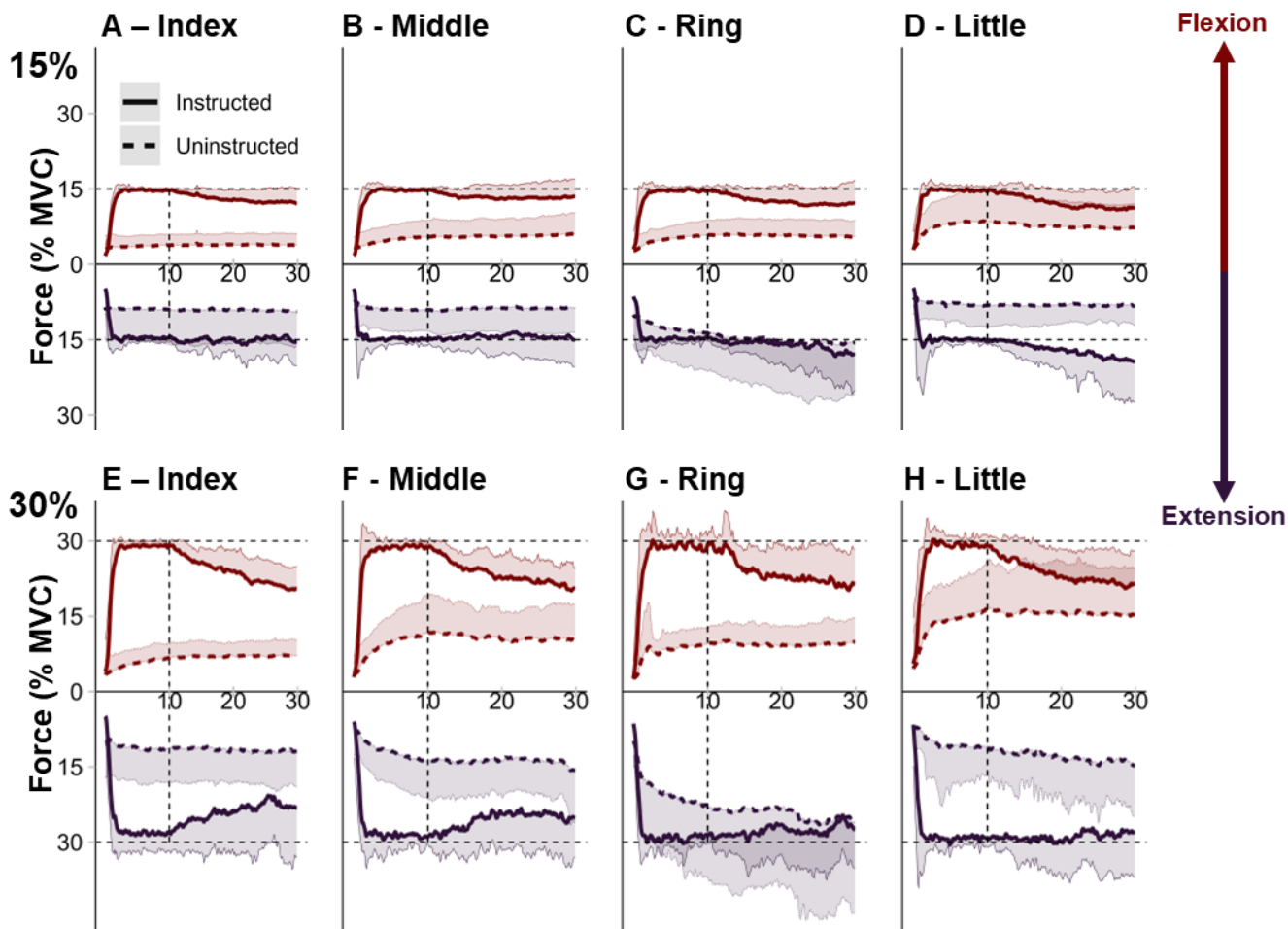


Figure 3.4: Mean force produced by the instructed finger (solid line) and the sum of the three uninstructed fingers (dashed line) over time (s) (x axis) in the feedback removed condition at 15% MVC (A-D) and 30% MVC (E-H). Each panel shows the flexion (red) and extension (blue) conditions for a single instructed finger. The shaded regions represent one standard deviation above the mean force (between participants). The horizontal thin dashed line marks the target instructed finger force, while the vertical line marks the moment when visual feedback was removed (10 s).

3.4.2. Uninstructed Fingers - Force

The forces produced by each finger before and after removing visual feedback on the instructed finger are presented in Figure 3.5. The main effects and interactions between the four instructed fingers, two force magnitudes, and whether instructed finger feedback was removed are described by the repeated measures ANOVA estimates presented in Table 3.3. In the flexion

conditions, we found a significant magnitude \times feedback interaction ($F[1,19] = 12.2, p = 0.002$). At 15% MVC, the uninstructed fingers drifted by 0.9 [0.4, 1.4] % MVC when feedback was given compared to -0.1 [-0.6, 0.4] % MVC when feedback was removed. Under the 30% MVC flexion condition, the effect of removing feedback on the uninstructed finger force drifts was greater, with the three uninstructed fingers drifting by 3.9 [2.3, 5.6] % MVC in the feedback given condition and 0.3 [-0.8, 1.4] % MVC in the feedback removed condition. The attenuation of the uninstructed force drifts in the flexion conditions are observed in Figure 3.5A where the uninstructed fingers drift minimally after feedback is removed (top vs bottom plots). Differences in the uninstructed finger force drifts between the four instructed fingers also depended on the feedback condition (Feedback \times Instructed: $F[3,57] = 4.66, p = 0.006$). In the feedback given condition, upward uninstructed finger force drifts were observed for all four instructed fingers (index = 1.2% MVC [0.7, 1.7] % MVC; middle = 2.1 [0.9, 3.3] % MVC; ring = 2.6 [1.2, 4.0] % MVC; little = 3.8 [1.4, 6.3] % MVC). In the feedback removed condition, the uninstructed finger force drifts were nearly eliminated. Very small uninstructed finger force drifts were measured when the middle (0.14% MVC [-1.0, 1.3]), ring (0.29% MVC [-0.49, 1.07]), and little (-0.51% MVC [-2.1, 1.1]) fingers were instructed.

The extension model found no significant interactions and no significant main effect of the instructed finger ($F [3, 57] = 1.95, p = 0.130$) or the feedback condition ($F [1, 19] = 1.9, p = 0.130$) on the uninstructed finger force drifts. Pairwise comparisons of the instructed \times feedback interaction and visual inspection of the data suggest this is likely due to high interparticipant variability (Figure 3.5B) (e.g., Ring [Feedback given] - Ring [Feedback removed] = 1.4% MVC, standard error = 1.6) (Table S1). The uninstructed fingers drifted significantly more in the 30%

MVC extension condition (2.6 [1.5, 3.8] % MVC) than in the 15% MVC condition (0.3 [-0.1, 1.3] % MVC).

Table 3.3: Model estimated F[DFn, DFd] effects and effect sizes (η^2) of instructed finger (index, middle, ring, little), magnitude (15% MVC, 30% MVC) and feedback (feedback given, feedback removed) on the total uninstructed finger force drift (% MVC). Drifts in the uninstructed finger force ($\overline{\Delta F}_{Unins}$) were calculated as the difference in the mean force produced by the three uninstructed fingers pre-drift (5-10 s) and post-drift (25-30 s): $\overline{\Delta F}_{Unins} = \sum |\bar{F}_{Finger}[25 - 30s]| - \sum |\bar{F}_{Finger}[5 - 10s]|$. A separate instructed finger (4) \times magnitude (2) \times feedback (2) repeated measures ANOVA was computed for finger flexion (left) and extension (right).

Direction Term	Flexion					Extension		
	DFn	DFd	F	η^2	p	F	η^2	p
Instructed	3	57	0.55	0.15	0.647	1.95	0.03	0.130
Magnitude	1	19	10.49	0.63	0.004	26.22	0.03	< 0.001
Feedback	1	19	34.90	< 0.01	< 0.001	1.64	0.01	0.216
Instructed \times Magnitude	3	57	1.81	0.04	0.155	0.41	0.00	0.743
Instructed \times Feedback	3	57	4.66	0.36	0.006	1.70	0.00	0.176
Magnitude \times Feedback	1	19	12.24	0.00	0.002	0.92	0.05	0.348
Instructed \times Magnitude \times Feedback	3	57	1.07	0.32	0.368	1.29	0.56	0.287

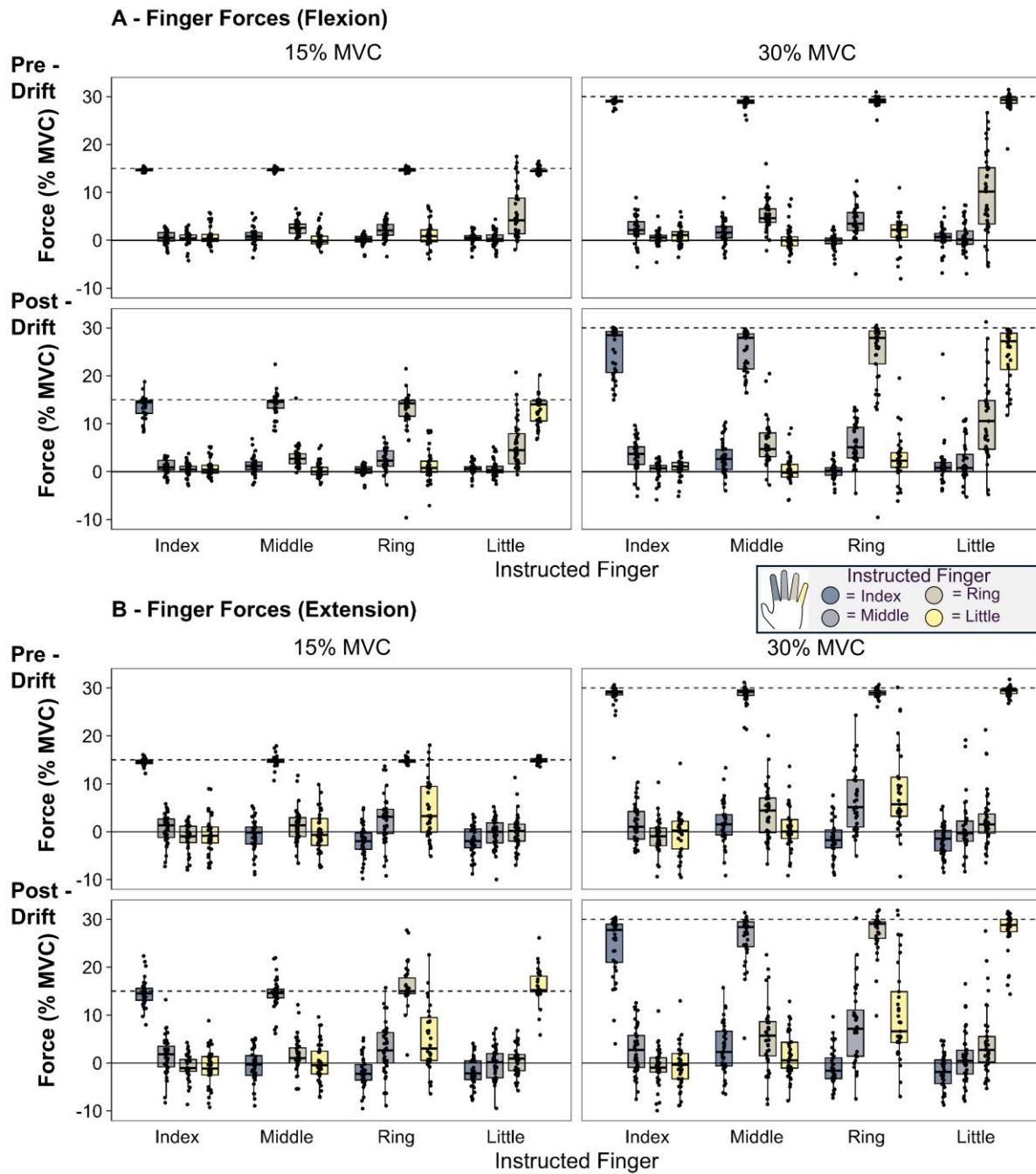


Figure 3.5: Mean force (% MVC) produced by each finger in the *feedback removed* condition in (A) flexion and (B) extension. Each set of four plots presents the average force produced by each finger from 5-10 seconds (top plots) and 25-30 seconds (bottom plots) at 15% MVC (left plots) and 30% MVC (right plots). Boxes are grouped by the instructed finger for a given task. The three lines on each box show the 25th percentile, median and 75th percentile with error bars representing the minimum and maximum forces. In this figure, forces in the opposite direction to the target force are labelled as negative forces.

3.4.3. EMG

Muscle activity recorded from FDS 2-5 and EDC 2-5 in the feedback given condition are presented in Figure 3.6. Each panel shows the mean activity of the eight muscle compartments for each instructed finger condition. Substantial coactivation is observed across all muscle compartments, regardless of which finger was instructed. Visual inspection suggests this coactivation is relatively invariant among antagonist muscles (Figure 3.6 A, EDC 2-5, Figure 3.6 B, FDS 2-5) compared to agonist muscles (Figure 3.6 A, FDS 2-5, Figure 3.6 B, EDC 2-5). This finding makes sense, as the antagonist muscle compartments play a similar stabilizing role in finger force production, regardless of the instructed finger. Significant Muscle x Time interactions were found for the index ($F[7, 133] = 2.4, p = 0.026$), middle ($F[7, 133] = 2.5, p = 0.018$), and ring fingers ($F[7, 133] = 2.4, p = 0.022$) at 15% MVC extension, and the middle finger ($F[7, 133] = 2.9, p = 0.008$) at 30% MVC extension (Table 3.4). However, follow-up pairwise comparisons found no significant changes in muscle activity within compartments in any of our models, indicating this interaction is a manifestation of changes in the activity difference between muscle compartments. Additionally, drifts in gross muscle activity were observed as significant main effects of time on muscle activity for all four instructed fingers at 15% MVC flexion (index: $F[1, 19] = 17.9, p < 0.001$, middle: $F[1, 19] = 10.2, p = 0.005$, ring: $F[1, 19] = 8.1, p = 0.011$, little: $F[1, 19] = 15.1, p < 0.001$) and the ring finger at 15% MVC extension ($F[1, 19] = 8.1, p = 0.01$). Pairwise comparisons of these significant effects indicate that muscle activity always increased, ranging between 0.5% MVE and 1.6% MVE depending on the condition.

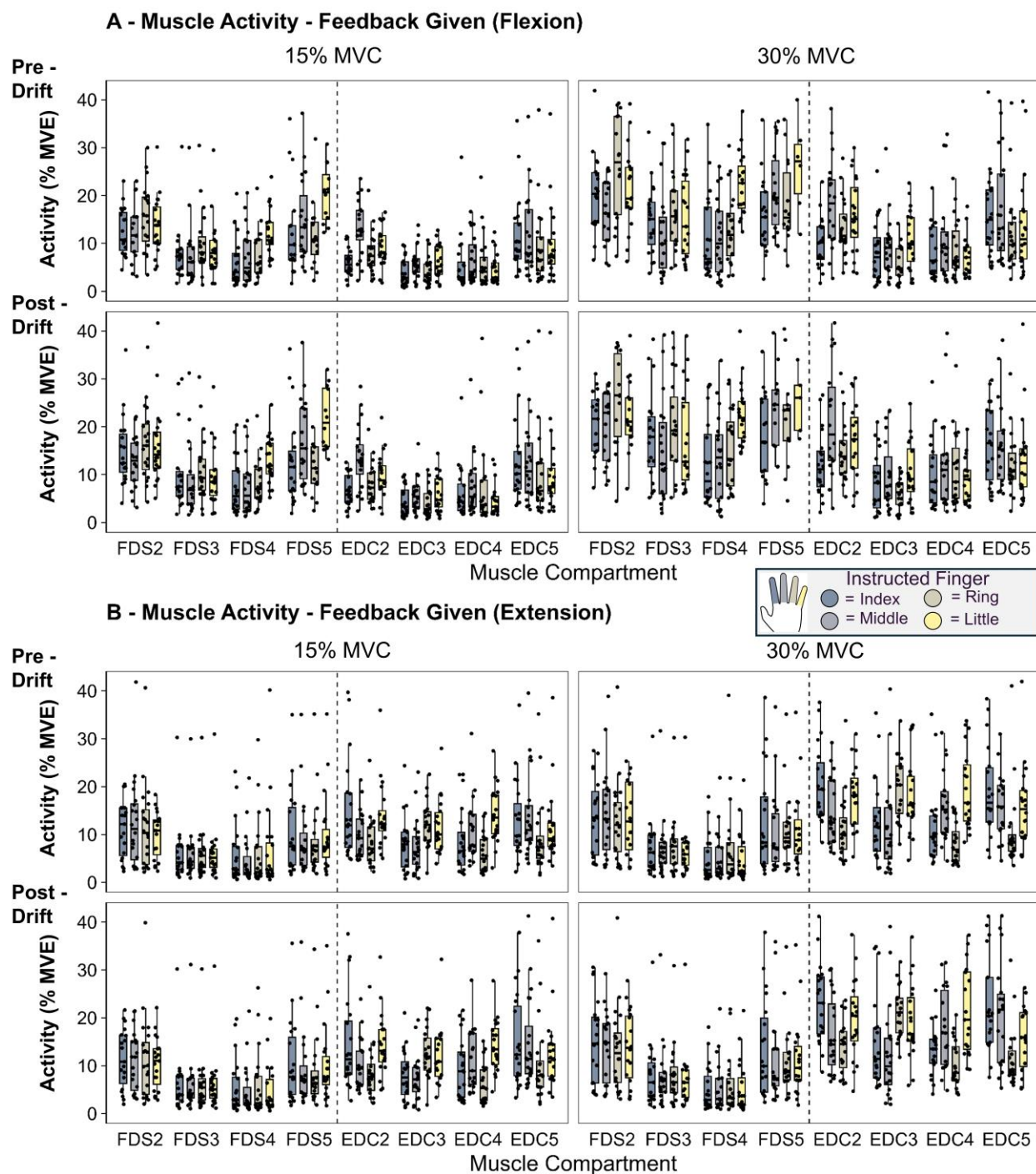


Figure 3.6: Mean muscle activity (% MVE) produced by each finger in the **feedback given condition** for (A) flexion and (B) extension. Each set of four plots presents the average muscle activity recorded in compartment (FDS 2-5, EDC 2-5) from 5-10 seconds (top plots) and 25-30 seconds (bottom plots) force targets of 15% MVC (left plots) and 30% MVC (right plots). Box plots are coloured according to the instructed finger. The three lines on each box show the 25th percentile, median and 75th percentile with error bars representing the minimum and maximum activations excluding outliers.

Table 3.4: EMG ANOVAs run on the **feedback given condition**. Estimated effects of muscle (FDS2, FDS3, FDS4, FDS5, EDC2, EDC3, EDC4, EDC5), and feedback (pre-drift, post-drift) on muscle activity (%MVE). Estimates F[DFn, DFd], effect sizes (η^2), and p-values were derived from a separate muscle (8) \times Time (2) repeated measures ANOVA run for each finger and direction (8 total models). Pre-drift and post-drift muscle activations were calculated as the average muscle activity recorded the second before feedback was removed (5-10 s) and in the final second (25-30 s) of each trial.

Term			Muscle			Time			Muscle x Time		
Magnitude	Direction	Finger	F [7, 133]	η^2	p	F [1, 19]	η^2	p	F [7, 133]	η^2	p
15% MVC	Flexion	Index	7.44	0.14	< 0.001	17.93	0.46	< 0.001	1.75	0.04	0.102
		Middle	7.97	0.26	< 0.001	10.22	0.32	0.005	1.31	0.02	0.249
		Ring	10.03	0.31	< 0.001	8.05	0.26	0.011	1.77	0.04	0.099
		Little	5.39	0.18	< 0.001	15.06	0.41	< 0.001	1.24	0.01	0.283
	Extension	Index	5.30	0.18	< 0.001	1.71	0.03	0.206	2.37	0.06	0.026
		Middle	3.30	0.10	0.003	1.62	0.03	0.219	2.52	0.07	0.018
		Ring	3.52	0.11	0.002	8.09	0.26	0.010	2.44	0.07	0.022
		Little	5.39	0.18	< 0.001	1.69	0.03	0.209	0.96	0.00	0.462
30% MVC	Flexion	Index	6.81	0.23	< 0.001	8.43	0.27	0.009	0.65	0.00	0.712
		Middle	9.05	0.29	< 0.001	17.65	0.45	< 0.001	0.59	0.00	0.765
		Ring	9.58	0.30	< 0.001	1.86	0.04	0.188	0.56	0.00	0.784
		Little	6.51	0.22	< 0.001	1.81	0.04	0.195	1.59	0.03	0.143
	Extension	Index	9.98	0.31	< 0.001	5.71	0.19	0.027	0.94	0.00	0.482
		Middle	8.25	0.27	< 0.001	5.64	0.19	0.028	2.88	0.09	0.008
		Ring	13.09	0.38	< 0.001	0.16	0.00	0.698	1.11	< 0.01	0.361
		Little	7.83	0.25	< 0.001	2.69	0.08	0.118	0.57	0.00	0.783

In the feedback removed condition, we also observed substantial muscle coactivation regardless of the task conditions (Figure 3.7). Reassuringly, the distribution of muscle activity measured pre-drift in the feedback removed condition is visually similar to the feedback given condition, indicating participants performed the two sets of tasks using consistent baseline (pre-drift) muscle activity patterns. For an example of this similarity, compare the feedback given and feedback removed pre-drift 30% MVC flexion plots (i.e., upper right panel of Figure 3.6 A vs, Figure 3.7 A). Significant Muscle \times Time interactions were found for the index finger ($F[7, 133] = 2.3, p = 0.028$) at 15% MVC flexion, the middle ($F[7, 133] = 3.7, p < 0.001$) and ring ($F[7, 133] = 3.3, p = 0.003$) fingers at 30% MVC flexion, and the middle finger at 30% MVC extension ($F[7, 133] = 2.9, p = 0.007$) (Table 3.5). Once again, follow-up pairwise comparisons found no significant changes in muscle activity within compartments in any of our models. See Table S2 for an example of pairwise comparisons of the effect of time (i.e., pre-drift – post-drift) on each muscle compartment in the 30% MVC feedback removed condition. Significant main effects of time on muscle activity were found when the little finger flexed at 15% MVC ($F[1, 19] = 8.9, p = 0.008$) and the index, middle, and little fingers flexed at 30% MVC (index: $F[1, 19] = 4.7, p = 0.044$, middle: $F[1, 19] = 7.6, p = 0.013$, little: $F[1, 19] = 10.0, p = 0.005$) (Table 3.5). Contrasting with the feedback given condition, the significant main effects of time in our feedback removed models were always associated with decreased muscle activity. In these conditions, gross muscle activity across all eight compartments decreased by between 0.7% and 2.3% MVE in the 20 seconds following the removal of visual feedback.

Table 3.5: EMG ANOVAs run on the **feedback removed condition**. Estimated effects of muscle (FDS2, FDS3, FDS4, FDS5, EDC2, EDC3, EDC4, EDC5), and feedback (pre-drift, post-drift) on muscle activity (%MVE). Estimates F[DFn, DFd], effect sizes (η^2), and p-values were derived from a separate muscle (8) \times Time (2) repeated measures ANOVA run for each finger and direction (8 total models). Pre-drift and post-drift muscle activations were calculated as the average muscle activity recorded the second before feedback was removed (9-10 s) and in the final second (29-30 s) of each trial in the **feedback removed condition**.

Term			Muscle			Time			Muscle x Time		
Magnitude	Direction	Finger	F [7, 133]	η^2	p	F [1, 19]	η^2	p	F [7, 133]	η^2	p
15% MVC	Flexion	Index	6.80	0.22	< 0.001	0.62	0.00	0.440	2.34	0.06	0.028
		Middle	10.24	0.32	< 0.001	0.55	0.00	0.467	0.89	0.00	0.520
		Ring	7.74	0.25	< 0.001	0.99	0.00	0.333	0.78	0.00	0.606
		Little	5.67	0.19	< 0.001	8.89	0.28	0.008	1.43	0.02	0.198
	Extension	Index	4.06	0.13	< 0.001	0.01	0.00	0.942	1.65	0.03	0.128
		Middle	3.97	0.13	< 0.001	3.04	0.09	0.097	1.74	0.04	0.105
		Ring	4.22	0.14	< 0.001	2.84	0.08	0.108	1.69	0.03	0.117
		Little	5.21	0.17	< 0.001	2.49	0.07	0.131	2.32	0.06	0.029
30% MVC	Flexion	Index	7.89	0.26	< 0.001	4.67	0.15	0.044	1.02	< 0.01	0.422
		Middle	11.19	0.34	< 0.001	7.56	0.12	0.013	3.74	0.12	0.001
		Ring	8.10	0.26	< 0.001	3.20	0.10	0.089	3.29	0.10	0.003
		Little	4.78	0.16	< 0.001	10.02	0.31	0.005	1.19	< 0.01	0.314
	Extension	Index	8.26	0.27	< 0.001	0.35	0.00	0.563	1.39	0.02	0.215
		Middle	8.12	0.26	< 0.001	0.01	0.00	0.923	2.93	0.09	0.007
		Ring	10.29	0.32	< 0.001	0.25	0.00	0.625	0.74	0.00	0.642
		Little	8.69	0.28	< 0.001	1.63	0.03	0.217	0.29	0.00	0.958

3.5. Discussion

This study explored short term changes in finger independence during static finger force production, also known as unintentional force drifts. Our novel use of EMG and inclusion of finger extension tasks provides a robust analysis of this phenomenon under a wide variety of task conditions. When visual feedback is removed in the flexion conditions, the force produced by the instructed fingers drifted downwards by an average of 28% of the initial target magnitude over a period of 20 seconds (i.e., 8.4% MVC at 30% MVC target) (Figure 3.4). Significant downward drifts were identified in all four instructed fingers at 30% MVC extension, but not at 15% MVC extension where significant upward instructed finger force drifts were measured in the ring and little fingers. Downward instructed finger force drifts were associated with decreased muscle activity over time, suggesting the neural drive to the finger muscles decreased involuntarily over time (Figure 3.7). When the instructed fingers were held at fixed magnitudes in the feedback given condition, the uninstructed fingers drifted towards greater force magnitudes. These drifts were generally very small (~3-4% MVC summed across the three uninstructed fingers) and were observed alongside increased muscle activity in several task conditions. Removing visual feedback on the instructed fingers reduced the uninstructed force drifts to +/- 1% MVC across the three fingers, essentially eliminating them (Figure 3.6).

Downward instructed finger force drifts are often interpreted under a feed forward model of force production, where an internal efferent representation of the desired state of the fingers (i.e., position, velocity) is compared to afferent sensory feedback representing the actual state of the fingers (i.e., tactile, visual, proprioceptive) (Feldman, 2015; Scott, 2004). Sensory afferents are subject to systemic sources of error (i.e., noise) and produce an imperfect internal representation of the fingers' task performance (Faisal et al., 2008). However, a noisy sensory

system alone does explain why the instructed fingers consistently drifted towards lower force production. A similar phenomenon, termed ‘slacking,’ is observed in studies of repetitive reaching, where muscle activity consistently decreases when movement errors are small (Reinkensmeyer et al., 2009). These phenomena are potentially related, reflecting the tendency of the central nervous system to minimize the energy cost of motor actions (Scott, 2004). Isometric pressing may be considered energetically wasteful by the central nervous system, and gradually decreased if task performance is otherwise maintained.

Force drifts are not consciously perceived by individuals, as indicated by their inability to correct drifts in real time. It follows that a necessary component of downward force drifts is the distortion of sensory feedback perception. In our study, we observed significant downward force drifts in the 30% MVC extension condition, but not the 15% MVC extension condition. Drifts in flexion force have been observed at force targets as low as 7% MVC in the literature (Hirose et al., 2020). This discrepancy highlights the potential significance of tactile feedback in modulating force drifts. The glabrous skin on the palmar surface of the hand is innervated by a far greater number of tactile afferents than the hairy skin on the dorsum of the hand (Corniani & Saal, 2020). Perhaps, downward instructed force drifts result from a slow increase in the signal gain of tactile afferents in the fingers. However, our results may also indicate that the absolute magnitudes of the normalized force targets used for the 15% MVC extension condition were too small to elicit consistent force drifts. Finger extension strengths measured in the MVC trials (index = 10.0 ± 3.4 N, middle = 7.6 ± 2.5 N, ring = 6.2 ± 2.4 N, little = 6.6 ± 2.2 N) were much smaller than flexion strengths (index = 40.6 ± 14.7 N, middle = 30.5 ± 9.5 N, ring = 19.8 ± 8.1 N, little = 20.5 ± 10.6 N). As a result, 15% MVC extension targets were usually less than 2 N, and which were possibly too small to be subject to any consistent drifting behaviour.

Our results did not support our a priori hypothesis that removing visual feedback on the instructed finger would increase the magnitude of uninstructed finger drifts. Instead, removing visual feedback nearly eliminated the uninstructed finger force drifts in the flexion conditions. Thus, in the feedback removed condition the uninstructed fingers may be subject to two competing sets of drifts: (1) drifts towards greater force production affecting only the uninstructed fingers, and (2) drifts towards less force production affecting both the instructed and uninstructed fingers. When mechanical connections are considered, this finding seems intuitive as any decrease in agonist force at the instructed finger should cascade through these connections and decrease uninstructed finger forces as well. However, new results suggest intertendinous force transmission between FDP and FDS is limited to $< 14\%$ and $< 2\%$ of the task magnitude (Maas et al., 2024). Additionally, intertendinous connections between the fingers behave differently during force unloading compared to loading. Decreasing the tension in the flexor tendons of the instructed fingers will not necessarily unload tension transferred to adjacent tendons (Keen & Fuglevand, 2003). Thus, it is unlikely the uninstructed finger force drifts in the feedback removed condition were attenuated purely through reduced mechanical force transfer from the instructed finger.

Instead, we suggest that downward instructed finger force drifts occur at the task level (i.e., whole hand) resulting in reduced neural drive to the uninstructed fingers as well. When visual feedback is used to hold the instructed finger at a constant force, a slow spread of excitatory potentials to neighbouring neurons in M1 is suggested to occur, resulting in increased force production by the uninstructed fingers. When visual feedback is absent, this spread of cortical excitation may still occur but we suggest this effect is attenuated by a general decrease in the excitatory state of the M1 hand area. This effect has not previously been observed because

Hirose et al. (2020) used visual feedback gain manipulation to fix the uninstructed finger forces when observing the instructed finger force drifts.

Downward drifts at the task level of control (i.e., affecting multiple fingers) are more congruent with the functional organization of the M1 than single-finger force drifts. Voluntary finger movements are produced through the activation of cortical neurons in the hand area of M1, which relies on sensory information encoded by the neighbouring primary somatosensory cortex (S1) (Yousry et al., 1997). In S1, spatially distinct groups of cortical neurons are active in processing sensory information from individual fingers (Schieber and Hibbard, 2001). These groups of neurons are functionally organized, with the likelihood of two sensory receptors being active simultaneously determining the proximity of their representations in S1. In contrast, representations of the individual fingers in M1 are distributed and invariant within individuals, possibly reflecting the higher dimensional structure of motor commands encoded at the task level (Ejaz et al., 2015). Therefore, unintentional force drifts probably result from a distributed decrease in the excitatory state of the M1 hand area, rather than one localized to a single finger.

Drifts in muscle activity differed between the feedback given, and feedback removed conditions, as illustrated by the main effect of time in our models (Table 3.4, 3.5). When feedback was provided, upward uninstructed finger force drifts were measured alongside drifts towards greater muscle activity. Although increased muscle activity has not been previously identified in studies explicitly addressing unintentional force drifts, May & Keir (2018) found the descending phase of isometric ramp contractions to be associated with greater muscle activity and greater uninstructed finger forces. Our study expands on this finding by identifying drifts towards less extrinsic finger muscle activity when visual feedback is removed. In the feedback removed condition, downward instructed finger force drifts were associated with decreased

muscle activity. However, muscle activity drifts were not universal and much smaller in magnitude than the instructed finger force drifts. Significant main effects of time were only observed in 4/16 conditions. All of these tasks were at 30% MVC flexion, which also had the greatest instructed finger force drifts.

This study was subject to two primary limitations. First, the thumb was not captured by our experimental setup. We decided to exclude the thumb because it acts in opposition to digits 2-5 when flexed, confounding the forces measured in the non-thumb fingers. Instead, the thumb was left unconstrained and participants were instructed not to engage their thumb during force production tasks. It is possible that involuntary activation of the thumb muscles contributed to rotational forces about the wrist, but these forces were minimized by our custom brace which immobilized the forearm. Second, the forearms of several participants were quite narrow, which may have resulted in activity from muscle compartments being picked up by neighbouring electrodes. However, we were able to reliably locate the four compartments of EDC and FDS through manual palpation. Palpation was performed with the arm in the same mid prone position (i.e., thumb pointing up) it was braced in to limit the movement of muscles underneath the skin.

3.6. Conclusions

Neural interdependencies between the fingers arise from complex strategies used to simultaneously coordinate the many joints and muscles of the human hand. We explored drifts in these interdependencies with visual feedback given on the instructed finger force, and with no feedback given on the instructed or uninstructed fingers. Measuring drifts in each finger performing both flexion and extension coupled with the novel use of EMG for quantifying force drifts enabled us to perform a robust analysis of this phenomenon. With respect to force drifts by the instructed fingers, this study reiterates the finding that in the absence of visual feedback, the

instructed finger slowly drifts towards less flexion force over a period of roughly 30 seconds. However, these drifts did not solely affect the instructed finger. When visual feedback was removed, the upward uninstructed finger force drifts observed in the feedback given condition were abolished and muscle activity decreased. We hypothesize these “instructed finger” force drifts may be occurring at the task level, affecting all the fingers rather than just the instructed finger.

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3.8 Supplementary Tables

Table S1: Pairwise comparisons (Tukey’s method) of the uninstructed finger force drifts (%MVC) for each instructed finger between the feedback given and feedback removed conditions (left). Beside the comparison of each instructed finger, the estimated marginal mean [95% confidence interval] uninstructed finger force drift in the feedback given (center) and feedback removed (right) conditions are presented.

Pairwise comparisons [Instructed × Feedback]	Pairwise comparisons [Instructed × Feedback]				Feedback Given			Feedback Removed	
	estimate	SE	t	p	Instructed	mean [95% CI]	SE	mean [95% CI]	SE
Flexion									
Index [Feedback given] - Index [Feedback removed]	0.72	0.31	2.33	0.330	Index	1.22 [0.74, 1.71]	0.23	0.51 [-0.10, 1.11]	0.29
Middle [Feedback given] - Middle [Feedback removed]	1.94	0.53	3.68	0.028	Middle	2.08 [0.85, 3.32]	0.59	0.14 [-0.99, 1.27]	0.54
Ring [Feedback given] - Ring [Feedback removed]	2.30	0.61	3.76	0.024	Ring	2.59 [1.16, 4.02]	0.68	0.29 [-0.49, 1.07]	0.37
Little [Feedback given] - Little [Feedback removed]	4.35	1.16	3.76	0.023	Little	3.84 [1.37, 6.30]	1.18	-0.51 [-2.08, 1.05]	0.75
Extension									
Index [Feedback given] - Index [Feedback removed]	1.32	0.79	1.68	0.699	Index	1.70 [0.20, 3.20]	0.72	0.38 [-0.39, 1.14]	0.37
Middle [Feedback given] - Middle [Feedback removed]	1.77	0.91	1.93	0.546	Middle	2.21 [0.12, 4.30]	1.00	0.45 [-1.04, 1.94]	0.71
Ring [Feedback given] - Ring [Feedback removed]	1.36	1.60	0.85	0.988	Ring	3.75 [0.82, 6.67]	1.40	2.39 [-0.30, 5.07]	1.28
Little [Feedback given] - Little [Feedback removed]	-0.99	0.74	-1.33	0.874	Little	0.56 [-0.83, 1.96]	0.67	1.55 [0.31, 2.80]	0.60

Table S2: Pairwise comparisons (Tukey’s method) of the main effect of time in separate muscle (8) × time (2) repeated measures ANOVA run for each finger and direction (8 total models). Comparisons show the mean muscle compartment activity pre-drift (5-10 s) and post-drift (25-30 s) [95% CI]. Estimated mean differences (% MVE) for each instructed finger, direction, and magnitude are also presented for the feedback given condition (left) and the feedback removed condition (right).

Magnitude	Direction	Finger	Feedback Given					Feedback Removed				
			Pre-drift [95% CI]	Post-drift [95% CI]	Drift	t	p	Pre-drift [95% CI]	Post-drift [95% CI]	Drift	t	p
15% MVC	Flexion	Index	8.4 [6.8, 10.0]	9.6 [8.1, 11.1]	1.2	4.2	0.001	8.8 [7.4, 10.2]	9.1 [7.3, 10.9]	0.3	0.8	0.440
		Middle	9.4 [7.5, 11.3]	10.1 [8.1, 12.2]	0.7	3.2	0.005	9.1 [7.2, 11.0]	9.5 [7.9, 11.2]	0.4	0.7	0.467
		Ring	10.3 [8.8, 11.7]	10.8 [9.4, 12.2]	0.6	2.8	0.011	10.4 [9.0, 11.8]	10.1 [8.6, 11.6]	-0.3	-1.0	0.333
		Little	10.3 [8.4, 12.2]	11.3 [9.4, 13.3]	1.0	3.9	0.001	10.5 [8.8, 12.2]	9.8 [8.2, 11.5]	-0.7	-3.0	0.008
	Extension	Index	10.2 [8.0, 12.4]	10.5 [8.5, 12.6]	0.3	1.3	0.207	9.5 [7.2, 11.8]	9.6 [7.7, 11.5]	0.0	0.1	0.942
		Middle	8.6 [6.9, 10.3]	8.8 [7.1, 10.5]	0.2	1.3	0.219	8.2 [6.3, 10.0]	8.6 [6.8, 10.4]	0.4	1.7	0.097
		Ring	10.7 [9.0, 12.5]	11.2 [9.5, 12.8]	0.5	2.8	0.010	10.5 [8.6, 12.5]	11.2 [9.3, 13.0]	0.6	1.7	0.108
		Little	9.4 [7.4, 11.4]	9.6 [7.7, 11.6]	0.3	1.3	0.209	9.2 [7.1, 11.3]	10.0 [8.0, 12.0]	0.8	1.6	0.131
30% MVC	Flexion	Index	13.0 [11.1, 15.0]	14.5 [12.6, 16.4]	1.5	2.9	0.009	14.2 [12.1, 16.3]	13.2 [11.2, 15.2]	-1.0	-2.2	0.044
		Middle	14.1 [12.2, 16.0]	15.7 [13.7, 17.7]	1.6	4.2	0.001	15.3 [13.1, 17.4]	13.9 [11.8, 16.1]	-1.4	-2.7	0.128
		Ring	15.9 [13.9, 18.0]	16.8 [14.9, 18.6]	0.8	1.4	0.188	16.6 [14.4, 18.8]	15.3 [13.3, 17.2]	-1.3	-1.8	0.089
		Little	15.5 [13.0, 18.1]	16.8 [14.8, 18.9]	1.3	1.3	0.195	15.9 [13.5, 18.4]	13.7 [12.1, 15.3]	-2.3	-3.2	0.005
	Extension	Index	13.1 [10.9, 15.2]	14.2 [12.2, 16.2]	1.2	2.4	0.027	12.7 [10.7, 14.7]	12.3 [10.3, 14.3]	-0.4	-0.6	0.563
		Middle	11.2 [9.5, 12.9]	12.3 [10.6, 13.9]	1.1	2.4	0.028	11.0 [9.2, 12.8]	11.0 [9.1, 13.0]	0.0	0.1	0.923
		Ring	14.0 [12.2, 15.9]	14.2 [12.7, 15.8]	0.2	0.4	0.698	13.6 [11.8, 15.5]	13.4 [11.8, 14.9]	-0.3	-0.5	0.625
		Little	12.4 [10.0, 14.7]	13.0 [10.9, 15.1]	0.7	1.7	0.118	11.9 [9.6, 14.3]	12.9 [10.2, 15.5]	0.9	1.3	0.217

Table S3: Pairwise comparisons (Tukey’s method) of the activity measured in each muscle compartment (%MVE) pre-drift (9-10 s) and post-drift (29-30 s) in the feedback removed condition. Estimated mean differences (%MVE) within each muscle compartment are presented for each instructed finger (left to right) in both flexion (top) and extension (bottom). Differences are based on separate muscle (8) × Time (2) repeated measures ANOVA run for each finger and direction (8 total models).

Finger	Index				Middle				Ring				Little			
	est	SE	t	p	est	SE	t	p	est	SE	t	p	est	SE	t	p
Flexion																
FDS2 [pre - post]	1.67	1.19	1.40	0.982	5.53	1.60	3.45	0.120	3.10	1.48	2.10	0.748	2.03	1.94	1.05	0.999
FDS3 [pre - post]	2.92	1.99	1.46	0.975	0.98	1.03	0.95	1.000	0.37	1.98	0.19	1.000	0.74	0.92	0.81	1.000
FDS4 [pre - post]	0.59	0.81	0.72	1.000	0.74	1.00	0.74	1.000	5.93	1.53	3.87	0.053	-0.01	0.67	-0.01	1.000
FDS5 [pre - post]	-1.88	1.66	-1.13	0.998	0.55	0.80	0.69	1.000	-4.58	3.26	-1.40	0.982	2.47	1.61	1.54	0.962
EDC2 [pre - post]	0.65	0.42	1.57	0.956	0.89	0.63	1.41	0.981	2.87	1.11	2.58	0.459	2.50	1.23	2.03	0.782
EDC3 [pre - post]	0.58	0.37	1.59	0.951	1.28	0.76	1.69	0.925	1.07	1.65	0.65	1.000	4.27	1.99	2.14	0.721
EDC4 [pre - post]	1.35	0.86	1.56	0.958	0.21	1.03	0.20	1.000	0.54	0.35	1.52	0.966	2.17	1.29	1.68	0.929
EDC5 [pre - post]	-0.85	3.75	-0.23	1.000	-6.25	3.12	-2.01	0.796	-9.49	4.10	-2.32	0.618	0.99	3.54	0.28	1.000
Extension																
FDS2 [pre - post]	0.68	0.50	1.38	0.984	-0.39	0.32	-1.25	0.993	-0.37	0.41	-0.91	1.000	-2.11	2.20	-0.96	1.000
FDS3 [pre - post]	0.27	0.21	1.28	0.992	-0.31	0.25	-1.25	0.994	-0.09	0.12	-0.76	1.000	-0.31	0.31	-1.00	0.999
FDS4 [pre - post]	-1.96	2.00	-0.98	0.999	0.04	0.08	0.46	1.000	-0.16	0.12	-1.29	0.991	-0.61	0.32	-1.90	0.846
FDS5 [pre - post]	0.32	0.53	0.60	1.000	0.37	0.28	1.31	0.990	-0.21	0.22	-0.99	0.999	-0.71	0.25	-2.82	0.334
EDC2 [pre - post]	1.39	2.87	0.49	1.000	-0.23	1.41	-0.17	1.000	-0.89	1.16	-0.77	1.000	-0.83	0.90	-0.93	1.000
EDC3 [pre - post]	-2.58	1.80	-1.43	0.979	3.06	1.85	1.65	0.937	1.20	0.95	1.26	0.993	-0.78	1.21	-0.65	1.000
EDC4 [pre - post]	1.54	1.52	1.01	0.999	-1.60	0.56	-2.87	0.311	2.01	1.97	1.02	0.999	-0.61	1.40	-0.44	1.000
EDC5 [pre - post]	8.35	3.31	2.53	0.492	-0.04	2.11	-0.02	1.000	5.65	2.54	2.23	0.671	8.04	2.15	3.73	0.070

Chapter 4: Thesis Discussion

4.1 Contributions

Our study successfully replicated the finding that in the absence of visual feedback, the instructed finger force gradually decreases over time. Apart from the original force drift study by Vaillancourt & Russell (2002), studies of unintentional force drifts are highly concentrated within a single research group. Given the substantial role force drifts appear to play in shaping finger interdependencies during prolonged pressing, it is crucial for researchers to be able to independently replicate these drifts. A distinct strength of this work is our novel inclusion of static extension tasks. At 30% MVC extension, but not 15% MVC extension, we measured similar downward instructed finger force drifts to those in flexion tasks. A greater normalized force threshold for eliciting force drifts in extension than flexion may indicate tactile feedback plays a crucial role in modulating force drifts.

Instructed and uninstructed finger force drifts are identified as two distinct phenomena in the literature, both reflecting distinct drifting behaviour at the level of the individual finger. However, the feedback structure of our study allowed us to draw potential connections between these two sets of drifts. When feedback was removed, the downward instructed finger force drifts nearly eliminated the uninstructed finger force drifts observed in the feedback given condition. This interaction suggests the downward instructed force drifts may affect all the fingers rather than just the instructed finger.

4.2 Rationale for Methods

The aim of this thesis was to investigate the short-term changes in finger independence associated with the phenomenon of unintentional finger force drifts. Prior to this work, unintentional force drifts had been extensively studied by a single research group at The

Pennsylvania State University (Ambike et al., 2015; Cuadra et al., 2018; Hirose et al., 2020). A few studies from this research group (See section 2.3.1 for review) address the effects of unintentional force drifts on finger independence. However, their methodologies and conclusions are shaped heavily by the theory of spatial referent control, making them difficult to interpret in the broader landscape of finger independence research (Abolins & Latash, 2021). Therefore, in addition to testing our specific hypotheses, the methodology of this thesis aimed to produce a high-quality descriptive account of the changes in finger independence associated with unintentional force drifts. With this goal in mind, simple task parameters (i.e., single finger pressing) and a wide variety of task conditions (i.e., instructed fingers, force magnitudes, force direction) were used. Of note is our inclusion of extension tasks, which had not previously been assessed in studies of force drifts. This thesis also sought to strengthen our understanding of unintentional force drifts by linking them with drifts in muscle activity measured via surface EMG. Despite being understood as a neural phenomenon, unintentional force drifts have exclusively been studied through changes in the force production of the fingers. Despite high variability, (Table S3, SE values) our use of EMG was fruitful, as our study linked downward instructed finger force drifts with decreased muscle activity, which may describe underlying neural strategies for coordinating movement.

Our experiment utilized a custom 3D printed hand and arm brace mounted on aluminum rails made of 80/20 aluminum tubing (Figure 3.1) (80/20, inc. Colombia City, Indiana, USA). Studies of finger interdependencies often leave the fingers unrestrained, either resting on top of platforms resembling piano keys or held in flexible loops suspended from force transducers positioned above (Ambike et al., 2015, Martin et al., 2011, Zatsiorsky et al., 2000). These apparatuses are not capable of measuring extension forces and may overestimate flexion force

due to gravity acting downwards on the fingers. Instead, we chose to brace the forearm in 90° pronation (i.e., thumb pointed up) with the fingers held at 0° MCP flexion using plastic cuffs. This setup effectively measured flexion and extension forces without a bias from gravity. However, several subjects described our arm/hand brace to be uncomfortable or awkward, particularly in our extension conditions. We initially considered that 0° MCP flexion may be too close to the end range of motion to effectively produce extension forces, but pilot testing at 30° MCP flexion did not improve comfort or increase extension strength.

Separate statistical approaches were used to analyze the drifts in the instructed and uninstructed fingers. For the instructed fingers, mixed effects models were favoured, as they enabled us to make direct comparisons between the slopes (% MVC / s) of the instructed fingers while accounting for interparticipant variability via the random slope terms. The structure of the Finger × Time interaction terms (i.e., slopes) where each finger is compared to the index finger, are easily interpreted because the index finger most consistently exhibited strong downward force drifts. Repeated measures ANOVAs were used to analyze the uninstructed finger force drifts instead of mixed effects models because the multiplicative effect of adding interaction terms created more slope comparisons than our study was adequately powered for.

4.3 Future Directions

So far, unintentional force drifts have been studied extensively at the level of the fingers, with changes in force production used to make inferences about changes occurring in the nervous system. This study continues to work backwards along this continuum by identifying opposing drifts in gross finger muscle activity depending on whether visual feedback is present. Therefore, the next logical step is to explore this phenomenon at the level of the motor unit. Common neural inputs to groups of motor units in separate finger muscles are speculated to

contribute to limiting finger independence. Studies estimate the strength of these common inputs by measuring the frequency of synchronized firing between two motor units (McIsaac & Fuglevand, 2007). It follows that drifts towards greater force sharing between the fingers may reflect increased usage of these common inputs. Indwelling electrodes should be used in cooperation with motor unit decomposition techniques to determine changes in the degree of synchrony across compartments during prolonged pressing. The recent development of a high-definition indwelling electrode array may be valuable in detecting changes in common input strength associated with force drift, as these devices capture a larger population of motor units than traditional needle microelectrodes (Chung et al., 2023).

Researchers should also attempt to unify unintentional finger force drifts with the concept of ‘slacking’ observed in studies of repetitive reaching (Reinkensmeyer et al., 2009). Drifts in muscle activity should be measured during cyclical finger movement tasks and compared to the drifts in muscle activity observed in our study. The decrease in muscle activity we observed in the absence of visual feedback is congruent with the hypothesis that unintentional force drifts reflect a preference for minimizing the energy cost of motor actions. Consistent, involuntary drifts towards less muscle activity observed in both cyclical finger movements and static pressing tasks would further support this hypothesis. The observation of ‘slacking’ muscle activity during finger movement tasks would be significant, as it would indicate the presence of drifts in muscle activity across tasks relying on different sensory modalities (i.e., force sense vs. position sense).

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Appendix A – Letter of Informed Consent



LETTER OF INFORMATION / CONSENT

Investigating extrinsic muscle activation and interdependencies in finger pressing tasks

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Purpose of the Study:

When humans are asked to move or apply forces with a single finger, movement and/or force is produced by the other fingers as well. Finger independence is limited by mechanical (e.g., tissues holding muscles together) and neural (e.g., our brain cannot activate one muscle alone) factors. The contribution of mechanical versus neural factors remains unclear. The purpose of this research is to clarify the mechanisms limiting independent finger control. A better understanding of the mechanisms that limit finger independence can help us develop strategies to improve finger control.

Procedures involved in the Research:

You will be asked to not perform heavy arm exertions the day prior to your lab visits.

In these studies, we will measure forces, muscle activity, and finger movement. To measure muscle activity, we use surface electrodes to measure the forearm muscles. These electrodes only monitor the electrical activity of the muscle of interest and do not send any electrical signals to the body. Surface electrodes are small circular self-adhesive pads with a conductive gel in the middle. The skin over each muscle of interest may be optionally shaved. The skin will be cleansed with alcohol and two surface electrodes will be affixed like stickers on the skin. For this study, nine electrodes will be placed on the forearm.

You will be asked to perform a series of finger movements and maximal and submaximal (i.e., less than maximal such as pressing with 20% of your maximal finger force) contractions. The finger movements involve finger flexion and extension. During these finger movements, a video recording (and photos) of your arms will be required to be taken for our analysis to measure finger joint angles. Your face will not be recorded. The maximal and submaximal contractions will involve measuring your finger forces. You will be seated with your arm placed within an apparatus on the table. There will be padding on the table for your elbow and wrist. Your fingers will be inserted into 4 adjustable padded rings. The rings will not move while you perform the tasks. For the maximal contractions, you will flex or extend as strongly as possible with each individual finger over 10 seconds. You will be given 60 seconds of rest between each maximal contraction. For the submaximal contractions, you will perform trials of finger flexion or extension with each individual finger over 5-30 seconds at a contraction level up to 40% of your maximum finger strength. Your task is to exert a force with your finger to hold the target force level (less than maximum force).

There will be three visits. In the first visit, we will ask you to perform 16 maximal and 48 submaximal contractions. During some submaximal contractions, visual feedback of your force will be removed. In the second and third visits, we will ask you to perform movement and force trials before and after a fatiguing protocol. The protocol will fatigue either your finger flexor or extensor muscles. This will be randomized across the second and third visits. During the fatiguing task, you will perform a submaximal contraction until you are no longer able to maintain the target force. Prior to the fatiguing protocol, you will perform 8 movement trials, 16 maximal contractions, and 16 submaximal contractions. Following the fatiguing protocol, you will perform 8 movement trials, 16 maximal contractions, and 8 submaximal contractions.

Each visit will be separated by at least 7 days and take approximately 2 hours long. In total, your time commitment will involve around 6 hours spread across the three visits. Each of the visits will take place in the McMaster Occupational Biomechanics Laboratory in the Ivor Wynne Centre.

Potential Harms, Risks or Discomforts:

There is minimal risk with participation in this study. You may experience some muscle soreness. We try to minimize this with rest breaks. Any soreness should not prevent you from your normal daily activities and should dissipate within 72 hours. The electrodes have a hypoallergenic adhesive. Although rare, you may experience a temporary reaction to the adhesive from the electrodes. You may experience mild discomfort or skin irritation from potentially being shaved and cleansed in preparation for electrode placement. This is usually very mild and clears within 24 hours. Should you experience serious

discomfort following the study, please contact the Faculty Supervisor, Dr. Peter Keir. You will be excluded from participation if you have a known allergy to adhesives. If you have experienced an injury to your upper extremity in the past year that currently causes pain or a chronic effect on your limb function, you will be excluded from the study.

Potential Benefits:

You will receive no direct benefits from participating in this study. However, your willingness to serve as a participant for this experiment will help develop an understanding of finger independence and control. This may benefit individuals in the future.

Incentive/Payment or Reimbursement:

You will be provided for \$20 for each visit of the study you complete. As the study has three total sessions, participants can receive a maximum total of \$60. The compensation will be given through an e-money transfer. Due to processing the incentives, the Kinesiology Graduate Administrator will know that you will have participated in the study.

Confidentiality:

Your identity will be kept confidential, and the data collected will be used for teaching and research purposes only. As described above, photos and videos will be taken as mandatory for our analysis. In addition, you will be optionally asked if you would be willing to have these photos and videos of you taken for use in publications and presentations. Photo and video data will only be used for dissemination purposes with your consent. No facial features will be captured. The information directly pertaining to you will be kept in a password protected computer and external hard drive in a lab for a maximum of 10 years. Hard copy data will be stored in a locked cabinet within our secured laboratory (locked doors with keycard hallway access). Digital data will be stored in MacDrive of McMaster University and/or encrypted server in Dr. Peter Keir's office for a maximum of 10 years. Only the research team (Dr. Peter Keir, Paul Tilley, and Daanish Mulla) will have access to this information during that time. After this time, the data will be destroyed.

Participation and Withdrawal:

Your participation in this study is voluntary. If you are enrolled in a course instructed by anyone from the research team, your decision to participate or not will not influence your evaluation of your performance in the courses. If you decide to participate, you can decide to withdraw at any time, even after signing the consent form or part-way through the study. You will also be reminded during the testing process that you have the right to withdraw at anytime. If you withdraw from the study, data collected before withdrawal may still be used for analysis with your consent. If you would not like your data to be used for analysis, the withdrawal deadline is the end of our data collection and start of our data analysis (March 31, 2024). If you decide to withdraw, there will be no consequences to you and you will receive full compensation for the sessions attended.

Information about the Study Results:

You may obtain information about the results of the study by contacting the research team. An update will be emailed after completion of the study. If you would like an update, your email will be required. A summary of the results will be completed by approximately August 2024.

Questions about the Study:

If you have questions or need more information about the study itself, please contact the research team: Dr. Peter Keir (905-525-9140 ext. 23543), Paul Tilley (tilleyp@mcmaster.ca), or Daanish Mulla (mulladm@mcmaster.ca).

This study has been reviewed by the McMaster Research Ethics Board and received ethics clearance under project # 6840. If you have concerns or questions about your rights as a participant or about the way the study is conducted, please contact:

McMaster Research Ethics Office
Telephone: (905) 525-9140 ext. 23142
E-mail: mreb@mcmaster.ca

CONSENT

- I have read the information presented in the information letter about a study being conducted by Dr. Peter Keir, Paul Tilley, and Daanish Mulla of McMaster University.
- I have had the opportunity to ask questions about my involvement in this study and to receive additional details I requested.
- I understand that if I agree to participate in this study, I may withdraw from the study at any time.
- I have been given a copy of this form.
- I agree to participate in the study.

1. Would you like a copy of the study results?

Yes, I would like to receive a summary of the study's results with the following email:

_____ No, I do not want to receive a summary of the study's results.

2. I agree to allow photos and videos of my arm (no facial features will be captured and any other identifiable features will be pixelated) to be taken during the experimental tasks as **optional for our dissemination purposes**. Note that as part of the study, we will be required to take photos and videos as mandatory for our analysis. This question asks if you are willing to consent to making these photos and videos additionally available when we publish our work (conference presentations, published documents).

Photos	Videos
<input type="checkbox"/> Yes	<input type="checkbox"/> Yes
<input type="checkbox"/> No	<input type="checkbox"/> No

Signature: _____ Date: _____

Name of Participant (Printed) _____

In my opinion, the person who has signed above is agreeing to participate in this study voluntarily, and understands the nature of the study and the consequences of participating in it.

Signature: _____ Date: _____

Name of Researcher or Witness (Printed) _____