An Investigation of the Effect of Chewing on Rhythmic Motor Tasks

Brittany S. Samulski
Old Dominion University, bespear@gmail.com

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AN INVESTIGATION OF THE EFFECT OF CHEWING ON RHYTHMIC MOTOR TASKS

by

Brittany S. Samulski
B.A. May 2004, University of Virginia
D.P.T. May 2011, Old Dominion University

A Dissertation Submitted to the Faculty of Old Dominion University in Partial Fulfillment of the Requirements for the Degree of

DOCTOR OF PHILOSOPHY

KINESIOLOGY AND REHABILITATION

OLD DOMINION UNIVERSITY
MAY 2020

Approved by:

Steven Morrison, Ph.D. (Director)
Daniel Russell, Ph.D. (Member)
Tara Newcomb, RDH, MS (Member)
ABSTRACT

AN INVESTIGATION OF THE EFFECT OF CHEWING ON RHYTHMIC MOTOR TASKS

Brittany S. Samulski
Old Dominion University, 2020
Director: Dr. Steven Morrison

Chewing gum and walking has traditionally been cited as the quintessentially difficult dual task, but little is known regarding chewing effects on motor control. The aims of this dissertation include describing chewing patterns across adulthood, describing chewing’s influence on secondary motor tasks, and investigate entrainment patterns of chewing and gait per established patterns of coupled oscillators. Three experiments were conducted to describe chewing patterns and to examine the effect chewing has on other motor tasks, particularly walking, in young and old adults. The first experiment used a metronome to manipulate chewing rates and measured associated gait parameters. This experiment established that chewing affects gait. As chewing speed increases or decreases, step rate also changes accordingly. Tasks such as walking, finger tapping, and simple reaction time all slow with advancing age. This experiment established chewing as a task resistant to neuromotor slowing with age. The second experiment examined the effect of chewing on a variety of secondary motor tasks. This experiment confirmed that chewing interferes with performance of a discrete secondary task, such as reaction time, whereas chewing entrains with cyclic movements, like finger tapping and gait. The final experiment varied the timing of when chewing was initiated to highlight the inherent organization of task influence. This experiment confirmed that chewing consistently impacts gait, but not vice versa. A top-down hierarchy where chewing drives changes in gait was
The physiological basis for the observed behavior is discussed in terms of coupled neural oscillators, such as the central pattern generators in the hindbrain and spinal cord. The findings from the series of experiments highlights oral sensory information as a potentially novel method of influencing movement patterns throughout adulthood. The functional implications of chewing are paramount to survival, but the connection between the mouth and the legs has not been well documented. Understanding the mechanisms associated with this inimitable relationship whereby the mouth is driving leg motion during gait could lead to innovative rehabilitative techniques for gait training.
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This thesis is dedicated to anyone who feels like “doing research” is boring, unfulfilling, or impossible. Growth happens in the periods of discomfort, but that does not mean those times cannot be exciting.

“Exploration is what you do when you don’t know what you are doing.”

Neil deGrasse Tyson
ACKNOWLEDGEMENTS

“There is no such thing as a self-made man. You will reach your goals only with the help of others.”
– George Shinn

This dissertation is the apogee of over 4 years of post-professional graduate work. I have experienced unprecedented personal and professional growth over those years which is in large part due to the efforts of several special individuals.

I would first like to thank God who has been my unwavering support as I traveled this road. From my days in high school when I first learned about rehabilitation to a clinician of nearly 10 years, He has guided me on this path to fulfill my calling as a healer and educator.

I would also like to offer my sincerest appreciation to my committee members Dr. Steven Morrison, Dr. Daniel Russell, and Ms. Tara Newcomb. I thank each of you for your guidance during this journey toward becoming a better researcher and academic. Your patience and caring throughout the process has been much appreciated. I often joke that “I came back to school to teach but stayed for the research.” This change of heart was in no small part due to this excellent group of people.

Steve Morrison, I appreciate you encouraging me to pursue the crazy idea of investigating chewing gum and walking. Embarking on that journey has brought me some of my closest friends, taught me some of my most pivotal lessons (like there is always time for coffee), and helped me reidentify myself as a clinician researcher. You helped me begin to see a wider perspective of the world and to never forget to check my fonts. Thank you for taking time to mentor me through the process. It changed my life.

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give me thoughtful, honest feedback. I appreciate your time spent mentoring me through the first steps in this next chapter of my life.

Jessica Prebor and Cortney Armitano-Lago, I would not have finished this dissertation without you both. You helped me survive personal tragedy and a worldwide pandemic while writing this. The words in this book are born out of the friendship that grew while writing them. You two showed me that work can feel like a party when your lab mates are your best friends. Thank you for learning with me, for challenging me, and for laughing with me. “Truly great friends are hard to find, difficult to leave, and impossible to forget.” – G. Randolf

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I would also like to express my deep gratitude to all the wonderful people who donated their time to assist me during data collection and to be participants in my research studies. You have been fundamental to this personal achievement. I also want to show my gratitude to the School of Rehabilitation Sciences, as well as the College of Health Sciences at Old Dominion University for the unwavering support throughout writing this dissertation. I have truly grown to feel like a member of the ODU family.
### NOMENCLATURE

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<tbody>
<tr>
<td>$\phi$</td>
<td>Relative phase</td>
</tr>
<tr>
<td>$\Delta \omega$</td>
<td>Asymmetry term</td>
</tr>
<tr>
<td>$\sqrt{q_{x_t}}$</td>
<td>Noise term</td>
</tr>
<tr>
<td>$a$ or $b$</td>
<td>Coefficients to indicate periodicity</td>
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<tr>
<td>ANOVA</td>
<td>Analysis of variance</td>
</tr>
<tr>
<td>BG</td>
<td>Basal ganglia</td>
</tr>
<tr>
<td>CN</td>
<td>Cranial nerve</td>
</tr>
<tr>
<td>CN V</td>
<td>Fifth cranial nerve, trigeminal nerve</td>
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<tr>
<td>CN VII</td>
<td>Seventh cranial nerve, facial nerve</td>
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<tr>
<td>CNS</td>
<td>Central nervous system</td>
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<tr>
<td>CPG</td>
<td>Central pattern generator</td>
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<tr>
<td>DST</td>
<td>Dynamic systems theory</td>
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<tr>
<td>DTI</td>
<td>Dual task interference</td>
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<tr>
<td>EMG</td>
<td>Electromyography</td>
</tr>
<tr>
<td>GLM</td>
<td>Generalized linear model</td>
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<tr>
<td>GTO</td>
<td>Golgi tendon organ</td>
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<tr>
<td>HKB model</td>
<td>Haken-Kelso-Bunz model</td>
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<tr>
<td>H-reflex</td>
<td>Hoffman reflex</td>
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<tr>
<td>IIV</td>
<td>Intra-individual variability</td>
</tr>
<tr>
<td>IRB</td>
<td>Institutional review board</td>
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<tr>
<td>ISD</td>
<td>Individual standard deviation</td>
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<tr>
<td>MLR</td>
<td>Mesencephalic locomotor region</td>
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<td>MU</td>
<td>Motor unit</td>
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<td>Abbreviation</td>
<td>Definition</td>
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<tr>
<td>PPN</td>
<td>Pedunculopontine nucleus</td>
</tr>
<tr>
<td>RT</td>
<td>Reaction time</td>
</tr>
<tr>
<td>SD</td>
<td>Standard deviation</td>
</tr>
<tr>
<td>TMJ</td>
<td>Temporomandibular joint</td>
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<tr>
<td>V</td>
<td>Potential function</td>
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<tr>
<td>VPM nucleus</td>
<td>Ventral posteromedial nucleus</td>
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CHAPTER 1
GENERAL INTRODUCTION

1.1 Introduction

Waves ebb and flow, fireflies blink in unison, and the heart beats. There is a nested cyclicity that self-organizes and underlies most natural phenomena. The interplay between human physiology and movement is a prime example of embedded natural rhythms creating behavior. The endocrine glands release hormones, the lungs expand and contract to supply oxygen to the body, and the brain pulses commands to control movement. The human anatomy is an intricate network of rhythmic events. These events begin to interact to create a variety of complex behaviors. The behaviors take on a similar cyclic structure which echoes the elaborate coordination dynamics across multiple micro and macro levels of biological organization.

Dynamic Systems Theory (DST) is exemplified by self-organization of multiple systems within the human body (i.e., cardiovascular system, neuromuscular system, endocrine system) which interact with one another, the environment, and the constraints of the goal task to dictate coordinated patterns of human movement (Newell, 1989). Chaos theory attempts to explain the complex dynamics at play, including why certain coordination patterns self-organize given a specific combination of factors (Newell & Slifkin, 1998). Actions that appear to be increasingly complex or chaotic can often give way to a mixture of synchronized, though not necessarily periodic movements (Strogatz, 2012). Per Dynamic Systems Theory, there is not a single governing entity responsible for the organization of the coordinated movement patterns. Rather, each system is self-organized in either a vertically nested hierarchy or horizontal domains of interaction. The central nervous system (CNS) is an example of a system that operates within multiple self-organized arrangements. It exhibits characteristics of a vertically nested system (i.e., biochemical components of neuronal cell structure give rise to neuron cells which give rise
to organs, such as the brain and spinal cord, and the organs form the nervous system which remains subject to physical and mathematical laws from the environment), as well as a horizontally interactive system that influences other bodily systems (i.e., the cardiopulmonary system) (Kandel, Schwartz, Jessell, Siegelbaum, & Hudspeth, 2000).

Human movement exhibits many instances of rhythmic behavior including walking, finger wagging, tapping, and chewing. During these oscillatory movements, the same actions are repeated over-and-over in succession. Coordination dynamics attempt to describe how gross movements are coordinated across multiple subsystems. Changes in gross movements can be measured as either alterations in movement quantity (i.e., rates or speed) or variability (i.e., consistency).

Experiments in this study will investigate the interplay of rhythmic motor behaviors, specifically chewing on other motor tasks, throughout adulthood. Understanding which behaviors emerge naturally given systematic changes to a factor in the dynamical system aids in understanding the overall mechanisms at play during coordinated movement. Interventions created with a mechanistic understanding of motor control improves our approach to rehabilitation. A number of previous studies have identified dual tasking as a task constraint that can impair overall performance of both activities, especially when executing a motor and cognitive task simultaneously (Patel, Lamar, & Bhatt, 2014; Schaefer & Schumacher, 2011). Typically, when two tasks are performed concurrently there is a degradation of performance either in speed or accuracy (Fitts, 1954). However, the influence of performing two motor tasks simultaneously has not been well studied and tend to focus on how cognitive processing is affected (Rémy, Weneroth, Lipkens, & Swinnen, 2010).
Motor slowing and aging

The process of aging is, for a wide range of movements, typically associated with slowing of movement behaviors. There are a number of potential reasons for this slowing. Slowing has been viewed as reflective of the fast time scales which refer to neural processes and movements with a relatively high frequency (Morrison & Newell, 2015; Newell, Liu, & Mayer-Kress, 2001; Newell, Mayer-Kress, & Liu, 2009). There are a variety of physiological mechanisms associated with overall slowing of the aging central nervous system (Spirduso, Francis, Eakin, & Stanford, 2005). A number of structural and functional changes in the CNS have been noted with aging (Morrison & Newell, 2015). For example, structural changes include loss of white and grey matter, decreased number of dopamine receptors, and deterioration of the cerebellum and proprioceptive system (Seeman et al., 1987; Seidler et al., 2010; Wang & Young, 2014). Many of these structural changes may contribute to slowed neural conduction velocities, and consequently, slowed reactions, especially after the age of 60 (Dorfman & Bosley, 1979). In addition to changes in the physical anatomy, functional changes, such as cortical activation patterns have also been noted whereby older adults demonstrate increased activation patterns over a wider cortical area compared to younger adults performing the same task. This increase in activation seems to preferentially involves regions within the prefrontal cortex and basal ganglia (Seidler et al., 2010). Ironically, the areas where there is increased neural activity are the same areas where neuronal loss is greatest for the elderly (Raz et al., 1997; Soares, Marques, Magalhães, Santos, & Sousa, 2014). This mismatch between neural activation and patterns of tissue degradation, especially in areas closely related to motor control, may be why changes in time scales and variability occur with aging.
Peripheral structures also undergo structural and functional changes with aging which may contribute to altered motor activation patterns. Muscle atrophy via loss of cross-sectional area and reduction in overall muscle mass are structural changes to the motor unit also noted with aging. (Jubrias, Odderson, Esselman, & Conley, 1997). Additionally, there is a remodeling of fast-twitch muscle fibers to slow twitch muscle fibers and a general loss of the overall number of alpha motor neurons which contributes the variability of motor unit firing (Power, Dalton, & Rice, 2013). There are also functional changes in the way the motor units operate. There is decreased force output by muscles, declines in average motor unit firing rates, and an overall shift in recruitment threshold toward lower firing rates (Erim, Beg, Burke, & de Luca, 1999; Jubrias et al., 1997). The muscular changes in aging adults mirror that of fatigued younger adults, but the effects are more permanent.

Slowed or inaccurate movements have long been associated with aging, as well as dual tasking (Lamoth et al., 2011). Neuromotor declines with age has been established in a variety of tasks including reaction time, movement time, physiological tremor, isometric force production, gait, and finger tapping (Morrison & Newell, 2015; Newell et al., 2001; Newell et al., 2009). The most common findings are an overall slowing of movement across all systems, as well as an overall change in the variations of performance from instance-to-instance, which is commonly referred to as intra-individual variability (IIV) of movements. Increased IIV has also been associated with dual tasking, especially during performance of gait with another motor or cognitive task (Springer et al., 2006; Yoge-Seligmann et al., 2010).
Variability measures and aging

The concept of variation from a typical aging pattern is a much newer concept in gerontology. One way to examine variability is to calculate the overall mean and standard deviation (SD) of several individuals in a study. This measure gives an overall idea about movement, but many of the details about how a single person’s movement varies from trial to trial is lost (i.e., a low-resolution examination of the variability). Intra-individual variability (IIV) is a measure of change between each performance of a behavior within a single person. The IIV is calculated by taking the mean SD of all trials for each subject (aka individual standard deviation or ISD), then finding the mean of the ISD values for each participant. The mean ISD values per participant are then used to calculate a group mean of the ISDs for all participants in that group, which is considered the IIV. The significance of this variability measure has evolved over time and is still debated today but is usually associated with aging and disease. Lipsitz and Goldberger (1992) proposed a theory suggesting a loss of complexity as indicated by decreases in physiologic and behavioral variability is typical of aging. They also suggested that loss of complexity manifests as difficulty to adapt to stressors for some individuals.

Vaillancourt and Newell (2002) proposed that aging is associated with bidirectional changes in variability. The direction of change is dependent on the interaction of many aspects of the movement task, characteristics of the individual, and constraints on that interaction (perhaps situational). Researchers argued that changes in variability may reflect a pattern of aging that is more associated with a chaotic attractor, resulting in the need for a more complex understanding of the system before speculating as to the benefit or harm of directional changes in variability. Buzzi and colleagues (2003) attempted to simplify the explanation of variability by advocating for an intermediate state between the two ends of the variability spectrum: complete regularity or
complete randomness. Anyone in an intermediate range was considered to have a “healthy” neurological system. Decreases in variability were associated with a rigid, less adaptable system and increases indicated a noisy, unstable system. This latter speculation attempted to join theories about neural noise with complexity theories to explain changes with aging. Newell and colleagues (2006) were able to connect two underlying changes noted with aging: loss of the fast/short time scales and changes in complexity. They asserted that the shorter the timescale of a motor task being studied, the more sensitive that particular task would be for determining the onset and early influence of aging or disease. Though no unifying theory of aging has been defined, there does appear to be a healthy level of complexity and variability, and deviations from this yet-to-be-defined pattern may offer a way to measure aging, injury, or disease effects on the nervous system.

Control of chewing

The majority of dual tasking research that examines the effects of chewing focus on how it affects sustained attention, mood, and alertness (Allen & Smith, 2011; Scholey et al., 2009). Chewing negatively impacts sustained attention during the initial five minutes of a task, but later appears to enhance sustained attention up to 30 minutes of task performance (Hirano & Onozuka, 2015; Tucha & Simpson, 2011; Tucha, Mecklinger, Maier, Hammerl, & Lange, 2004). This time-sensitive effect is attributed to chewing-related arousal (Onyper, Carr, Farrar, & Floyd, 2011), although less is known about the ways chewing may influence and modulate motor control of simultaneously performed tasks.

Chewing gum has been shown to interfere with recalling musical rhythms and can enhance thought suppression of rhythms that interfere with concurrent task performance (Allen
Interestingly, gum chewing also interferes with signal propagation of stress-related information in the brain stress network after an external auditory stressor (i.e. a loud noise) (Yu, Chen, Liu, & Zhou, 2013). Typically during dual tasking, there is a notable interference effect of the primary task (designated as the task receiving increased attentional resources) on the performance of the secondary task (Ebersbach, Dimitrijevic, & Poewe, 1995; Pashler, 1994). In contrast to other motor tasks, chewing increases arousal and alertness, as well as can improve motor performance of tasks during a dual tasking situation (Hirano et al., 2013). Gum chewing also creates internal and external rhythmic sensory cues. The stretch receptors of the masseter, as well as the mechanoreceptors in the periodontal ligament transmit sensory information to the ventral posteromedial nucleus (VPM) of the thalamus via the trigeminothalamic tract (Kandel et al., 2000). The anterior trigeminothalamic tract transmits sensory information about crude touch, pain and temperature, whereas the posterior trigeminothalamic tract conveys discriminative touch and proprioception from the oral cavity. The trigeminothalamic tracts project from the trigeminal ganglion to the pons, synapses with the spinal trigeminal nucleus, then crosses midline and travels to the VPM in the contralateral thalamus. The information is then conveyed to the sensory cortex, specifically the regions for the face near the post-central gyrus (Kandel et al., 2000). The chewing central pattern generators (CPGs) are located in the reticular formation within the pons (Kandel et al., 2000; Lund & Kolta, 2006). When the oral sensory information activates the CPGs, a rhythmic chewing pattern is established. Additional auditory information from the sound of the gum is transmitted to the ears, as well as through the mandible to the auditory sensory system.

The phase-dependent reflex, a reflex response which differs despite the activation by a similar stimulus, may connect chewing and walking. Lund and Rossignol (1981) noted phase-
dependent reflex reversal in oral movements. During chewing, stimulation of the jaw-open reflex varies with mouth position. If the reflex is stimulated during the mouth opening phase of chewing, the reflex is weaker than when stimulated during the mouth closing phase. One functional reason for this is protection of the teeth. If the mouth is closing and the reflex is particularly excitable, it prevents the teeth from clattering together which could result in injury.

Forssberg, Grillner and Rossignol (1975) noted a unique limb flexion response when the foot was advancing in swing phase, yet an opposite extension response in the limb when the foot contacted the ground in stance—a phase-dependent reflex similar to the one seen in the oral cavity. Due to similarities in the underlying reflex physiology of the mouth and the limbs, the bilateral innervation of perioral musculature, and the multidimensional sensory information created during chewing, it’s possible that chewing may function as a more salient sensory input for setting internal rhythms, especially for influencing gait rhythms.

**Reaction time**

Traditionally reaction time (RT) has been considered a way to directly measure the speed of processing within the nervous system. Two methods to assess reaction time include measuring simple RT and choice RT (Snodgrass, Luce, & Galanter, 1967). A simple RT task presents the individual with a single stimulus and measures the amount of time from stimulus presentation (i.e., turning on a light) until completion of the single target task (i.e., clicking a button). A choice RT task is similar, however, the participant is presented with more than one stimulus which may have one or more desired behavioral responses associated with it (Welford, 1977; Welford, 1988). Reaction time can be measured from the presentation of the stimulus to the start of the motor time as marked by initiation of visible movement. Premotor response time is
measured from the onset of the stimulus to the activation of motor units—this occurs when motor unit recruitment is noted on electromyography (EMG), but visible movement has not yet occurred. Motor response time is the amount of time between the onset of motor unit activity and the peripheral movement component of the response. The movement time is the latency of the entire desired response (i.e. button press) from first visible movement to termination of the movement. Simple reaction time measure consists of the premotor response time and the motor response time (Botwinick & Thompson, 1966). Choice reaction time consists of the premotor response time, the motor response time, and the central processing time. Central processing time is additional time required when selecting between more than one type of response (Morrison & Newell, 2015). The central processing time can be calculated using a subtraction method (Gottsdanker & Shragg, 1985). Figure 2.1 depicts the various components of each reaction time measure.

Reaction time tends to be negatively affected by increasing age and increased latency is first noted in the mid-20s (Morrison & Newell, 2015; Welford, 1988). Slower reactions occur with tasks of increasing complexity (Stuss, Binns, Murphy, & Alexander, 2002). Potential reasons for the slowing of reactions with increasing age can be linked to both behavioral and physiological factors. There is evidence to suggest that older adults tend to selectively choose more cautious movement strategies prioritizing accuracy over speed of movement compared to younger adults (Spirduso, Francis, & MacRae, 1995). Speed and accuracy during a task are at odds with one another during movement. Examining how this tradeoff is negotiated by individuals begins to reveal differences in motor control strategies. This behavioral strategy was described as a speed-accuracy relationship by Fitts (1954) and the principles he outlined to explain this behavior became widely known as Fitts’s law (Fitts, 1954; Salthouse & Somberg, 1982; Teichner, 1954). A preference for
accuracy over speed is not simply a self-selected functional adaptation, but also has structural influences. There is a decline in white matter along connections between the supplementary motor area and the basal ganglia, as well as between the prefrontal areas to the caudate and putamen which is associated with disinhibition of the cortex (Forstmann et al., 2011; Haber 2016). Physiological changes in the dopaminergic system also contribute to slowing of reaction time in older adults. There is a decline in dopamine receptor density and number with age, especially in the frontal cortex (Kaasinen et al., 2000; Seeman et al., 1987). As age-related decreases in dopamine receptors have been associated with longer reaction time latencies and an increased difficulty during speedy initiation of movements (MacRae, Spirduso, & Wilcox, 1988). Waning dopaminergic function in the basal ganglia, in particular, has been associated with slower simple reaction time in older adults (van Dyck et al., 2008).

These structural changes to neural connectivity, neurotransmitter systems, and peripheral anatomy, as well as functional changes to neural activation patterns and selection of movement strategies create differences between how older and younger adults move. Additionally, older adults demonstrate more inter-trial variability in their reaction time than younger adults, though the meaning of this measure has yet to be clearly defined (Morrison & Newell, 2015).
Figure 2.1

Schematic Illustration of Two Types of Reaction Time.

Note. The illustration above denotes the relative timing of simple reaction time (top) and choice reaction time (bottom) components for a visual stimulus. Abbreviations: RT: response or reaction time, EMG: electromyography, MU: motor unit.
Neural control of gait

One of the consequences of increasing age is that individuals tend to walk slower. Interestingly, the process of slowing is not driven by changes in gait cadence, but rather by shorter step lengths, increased time in double limb support, and wider stance (Maki, 1997; Samson et al., 2001; Winter, Patla, Frank, & Walt, 1990). These gait changes are consistent with older adults choosing an alternative movement strategy that appears more conservative, similar to the way older adults choose accuracy over speed in movement time tasks. It is thought that slowing processes reflect a strategy adopted by older adults in order to improve their stability and/or decrease their risk of falling (Maki, 1997). Like other motor tasks, gait patterns are also associated with a change in variability as individuals increase in age. Stride-to-stride variability increases with age, and more variability is associated with an increased fall risk (Maki, 1997; Springer et al., 2006). Interestingly, dual tasking during walking does not appear to increase gait pattern variability for most individuals. The only exception to this is for elderly adults aged 65 to 85 years who are at an increased risk of falling, thus making it a useful tool for differentiating healthy elderly gait patterns from more maladaptive patterns associated with falls (Springer et al., 2006).

Slowed gait speed in the elderly appears to be related to changes in step length over cadence (Winter et al., 1990). Older adults take shorter steps, but exhibit similar stepping cadence to their younger counterparts (Samulski, Prebor, Armitano, & Morrison, 2019). Gait velocity slows with age as a function of shortening step length (Maki, 1997; Samson et al., 2001; Winter et al., 1990). The step cadence appears relatively stable during adulthood (Elble, Thomas, Higgins, & Colliver, 1991). The changes observed in geriatric gait indicate modifications favoring a more conservative movement strategy which increases postural stability to decrease falls (Maki, 1997). The focus of these modifications appear to be in widening the base of support and shortening step length to
improve postural stability during gait (Krebs, Goldvasser, Lockert, Portney, & Gill-Body, 2002). Greater variability of gait has been observed in older adults compared to their younger counterparts, and the difference in step variability is due to declines in lower extremity strength and range of motion, rather than slowed speed (Kang & Dingwell, 2008). Interestingly, dual tasking during walking does not increase gait pattern variability except in elderly adults who are at an increased risk of falling (Springer et al. 2006). Dual tasking requires increased use of executive function resources, and the pre-frontal cortex has been found to be particularly active during gait (Sheridan & Hausdorff, 2007; Yogev-Seligmann, Hausdorff, & Giladi, 2008). The prefrontal cortex also exhibits thinning associated with deficits in executive function with increasing age (Salat et al., 2004). Both functional and structural changes to the CNS and peripheral structures contribute to the slowing of movement with age.

**Finger tapping**

Finger tapping is a common motor task used to assess the fastest possible neuromotor response, and subsequently reveals systemic slowing with age (Aoki & Fukuoka, 2010; Cousins, Corrow, Finn, & Salamone, 1998; Morrison & Newell, 2015). Changes in tapping speed demonstrate the decline of the neuromuscular system during typical aging or age-related disease. The overall process of aging is reflected by an overall slowing of maximal tapping speed, as evidenced by longer inter-tap intervals (Aoki & Fukuoka, 2010). The reason for the slowing of finger tapping is not clear. Slowed tapping speed does not appear to be associated with decreases in peripheral sensation or declines in maximum pinch strength (Aoki & Fukuoka, 2010). Finger tapping has been shown to successfully differentiate out individuals with CNS-related motor dysfunction and is a sensitive measure for assessing fall risk in the elderly.
Finger tapping variability (i.e. the time between taps) also tends to increase with increasing age, especially when the tapping tasks are performed at maximal speeds (Shammi, Bosman, & Stuss, 1998; Sternad, Dean, & Newell, 2000).

**Dual tasking**

In addition to aging, slowed performance of a task can occur when dual task interference occurs. A dual task is performance of two separate tasks simultaneously. A baseline measure of each component task must first be measured, then the dual task performance can be measured. A comparison of performance between the baseline single task conditions and the dual task condition is known as a dual task paradigm methodology (Della Sala, Baddeley, Papagno, & Spinnler, 1995). Dual task studies are central to understanding how the brain optimizes movement while balancing cognitive resources. Harold Pashler (1994) once said:

> Overloading a system is often one of the best ways to figure out what the parts of the system are and how these parts function together. For this reason, studying dual task interference provides an important window on basic questions about the functional architecture of the brain. (p.220)

Dual task interference is the most common outcome noted during dual tasking experiments (Hartley & Little, 1999; Luck, 1998; Pashler, 1994).

Much of the dual tasking research focuses on the interaction of cognitive and motor tasks (Huang & Mercer, 2001; Verhaeghen, Steitz, Sliwinski, & Cerella, 2003). Dual task interference is thought to result from either shared cognitive resources, a central bottleneck of neural processes, or a hybrid of parallel and serial processing systems (Marti, King, & Dehaene, 2015; Shimoyama, Ninchoji, & Uemura, 1990).
Pashler, 1994). Dual tasking, namely a cognitive task added to a walking task, appears to be associated with an increase in gait variability (Hollman, Kovash, Kubik, & Linbo, 2007; Springer et al., 2006; Yogev-Seligmann et al., 2010).

The effects of performing two motor tasks at the same time is less frequently researched. Studies investigating the coordination dynamics of bimanual finger tapping suggest that performing two motor tasks may not always result in an interference phenomenon. The rhythmic movements of the two fingers are controlled by coupled neural oscillators that despite perturbations to tap timing seem to consistently return to one of two stable rhythms (Yamanishi, Kawato, & Suzuki, 1980). The timing of two motor tasks is key to eliciting a coupling effect, without task interference (Klapp, 1979).

1.2 Statement of the problem

Chewing is a task performed daily and is central to basic survival, yet little is known about the motor control of chewing. Current knowledge of the physiological components involved in chewing mechanisms have been derived from animal models, and often not replicated in humans due to a variety of ethical and methodological barriers. It is known that there is no single ideal chewing pattern for best performance, rather we see changes to the chewing behavior based on task or organism-related constraints (Po et al., 2011; Yamashita, Hatch, & Rugh, 1999). Behavioral studies often focus on understanding chewing in young adults, but not older adults (Ferrario et al., 2006; Plesh, Bishop, & McCall, 1987).

Neural control of chewing bares similarities to that of walking. Chewing and walking both exhibit aspects of conscious control during initiation, and throughout the task to allow for on-line modifications (Kandel et al., 2000). They both also have reflex mechanisms and central pattern
generators identified and associated with each movement (i.e. jaw opening and jaw closing, leg flexion or extension-based stepping reflexes). They both also exhibit phase-dependent reflex reactions associated with protective functions (Forssberg et al., 1975). During chewing, stimulation of the jaw-open reflex varies with mouth position. If the reflex is stimulated during the mouth opening phase of chewing, the reflex is weaker than when stimulated during the mouth closing phase. One functional reason for this is protection of the teeth. If the mouth is closing and the reflex is particularly excitable, it prevents the teeth from occluding together which could result in injury. Similarly, during gait the lower limb exhibits a more sensitive flexion reflex when advancing in swing phase, yet an opposite extension response in the limb when the foot contacts the ground in stance. It’s possible that coupling of the two phase-dependent reflex reversals in gait and chewing may be a mechanism underlying a larger coordination pattern (i.e., jaw closing appears to be closely associated with stance phase of each limb) observed in recent studies (Samulski et al., 2019).

Many studies investigating dual tasking tend to focus on cognitive-motor interactions. An interference effect is prominently noted in most studies on dual tasking, which generally translates to poorer performance of one or both tasks. The theories of shared cognitive resources where information is processed in parallel, as well as the theory of a central neural processing bottleneck where information is processed serially are most cited as the mechanisms resulting in dual task interference (Marti et al., 2015; Pashler, 1994). Interestingly, dual task interference has not been consistently replicated in dual motor task studies. There appears to be a mixed effect when performing two motor tasks simultaneously and the phenomenon is not well understood. Most studies investigating the effects of performing two motor tasks simultaneously use gait as the benchmark task, however, secondary tasks are highly varied in complexity and character. The
current study proposes that chewing may function as a highly salient, age-resistant cue that can influence gait patterns in healthy adults, and chewing motion may enhance, rather than interfere with, stepping control via an inherent neural coupling.

**1.3 General purpose of the study**

The general purpose of this study is to examine chewing patterns throughout adulthood and determine how chewing and stepping influence one another. The most prominent changes to gait throughout the aging process is a general slowing of movement (Prince, Corriveau, Hebert, & Winter, 1997). This same slowing process has not been clearly demonstrated in chewing patterns. An understanding of how chewing dynamics change with age would help establish how chewing may interact with other motor tasks, such as gait, when the two tasks are performed simultaneously. Measures of motor task performance changes during chewing and at rest, as well as investigating factors such as timing of task introduction on the performance of each task will improve our understanding of this possible unexpected coordination pattern. Understanding the coordination mechanism linking gait and chewing would allow researchers to develop innovative rehabilitation techniques to cue gait patterns.

**1.4 Specific aims and hypotheses**

*Experiment one*

The aim of this study is to examine the impact chewing at different frequencies have on walking performance for healthy young and older adults.

Specifically, it is hypothesized that:
1. An individual’s stepping rate (and consequently gait speed) will increase or decrease to match the individual’s chewing rate.

2. Chewing rates do not demonstrate age-related changes as noted in gait.

Experiment two

The aim of this study is to examine the effect of aging and chewing on a variety of motor tasks. Specifically, it is hypothesized that:

1. An individual’s preferred rate of movement decreases with age for a variety of motor tasks.

2. Chewing while performing another motor task has a differential effect on the performance of the second task.

Experiment three

The aim of this study is to examine whether chewing continues to influence stepping rates depending on when the chewing is begun relative to walking tasks.

Specifically, it is hypothesized that:

1. Chewing will drive the walking rates when two motor tasks are performed simultaneously. Stepping rates will match chewing rates regardless of when chewing is initiated.

2. Chewing does not need to occur prior to initiation of the secondary (i.e. walking) task to influence the movement rate of the task.
CHAPTER 2

REVIEW OF THE LITERATURE

2.1 Overview of Chewing

Anatomy of the temporomandibular joint

The temporomandibular joint (TMJ) is a key anatomical structure of mastication. The cranial surfaces of the TMJ consists of the squamous portion of the temporal bone (upper) along with the glenoid fossa and condyle of the mandible (lower). The TMJ has a unique and complicated mechanism as the articular surfaces of the bones do not contact (in health), and are separated by a synovial disc. Both joints are considered bicondylar or ellipsoid due to the oval shape of the mandibular condyles and the similar concavity of the mandibular fossa. (Piette, 1993).

An articular disc covers the condyle and interposes below the glenoid fossa has a biconcave or oral shape—this cartilaginous disc has an anterior and posterior portion. The anterior portion of the disc consist of an upper layer of fibroelastic fascia and a inferior fibrous layer. The disc divides each joint into an upper and lower compartment. The upper compartment is called the discotemporal joint space and the lower compartment is called the discomandibular joint space. The anterior portion of the of the articular disc is in contact with the joint capsule, articular eminence, condyle and the lateral pterygoid muscle. The posterior portion of the disc is associated with bilateral retro-disc tissue behind the condyle, the glenoid fossa, the condyle and the temporal bone. The medial and lateral aspects of the disc attach to the mandibular condyle. All of which is fully innervated with nerve and blood supply. (Piette, 1993). The entire TMJ complex is surrounded by a joint capsule, as well as several supporting ligaments. Laterally, there are the temporomandibular ligaments in which the base of
the ligament attaches at the zygomatic process of the temporal bone and the apex at the lateral side of the neck of the condyle. This joint prevents excessive retraction or posterior movement of the jaw (Dutton, 2020). Medially, there are the sphenomandibular and stylomandibular ligaments. The sphenomandibular ligament runs from the angular spine of the sphenoid bone to the lingula—it’s primary function is to protect the TMJ from an excessive translation of the condyle. The stylomandibular ligament runs from the styloid process of the temporal bone to the angle of the mandible—it serves to limit excessive protrusion of the mandible.

There are 5 muscles of mastication which include the masseter, medial and lateral pterygoids, temporalis, and digastric muscles. Each set of muscles are found bilaterally on the head and due to the fixed nature of the mandible, must work together to move each side of the jaw in a coordinated manner (Sessle, Avivi-Arber, & Murray, 2012). The masseter is located on the lateral aspect of the mandible. The masseter has a superficial head which originates on the zygomatic bone and deep head which originates on the zygomatic arch (Standring, 2015). The two heads fuse inferiorly and attach on the mandibular angle and mandibular ramus. The masseter assists with closure of the mouth by elevating the mandible. The pterygoids are located medially to the mandible. The medial pterygoid has deep and superficial head. The deep head originates on the medial aspect of the lateral pterygoid plate of the sphenoid bone, whereas the superficial head attaches on the maxilla and palatine bones (Standring, 2015). The two heads fuse and insert on the ramus of the mandible. Simultaneous activation of the medial pterygoid muscles results in closing of the jaw, as well as assist in jaw protrusion. The lateral pterygoid muscles have a superior and inferior head. The superior head originates on the superior temporal fossa and the lateral pterygoid plate, which is where the inferior head also originates. Both lateral pterygoids fuse posteriorly and insert on the condylar process of the mandible. Activation of the
lateral pterygoids together results in protrusion of the jaw, whereas unilateral activation of the lateral pterygoid results in jaw movement to the side contralateral side. The temporalis muscle originates from the temporal fossa and insert on the coronoid process of the mandible. Activation of the temporalis muscle results in closing of the jaw (vertical anterior fibers) and retraction of the jaw (posterior horizontal fibers) (Standring, 2015). The digastric muscles have an anterior head which originates on the digastric fossa of the mandible and a posterior head which arises from the mastoid notch in the temporal bone. Both heads of the digastric muscles attach to the body of the hyoid bone via a tendinous loop. All of the muscles of mastication are innervated by the mandibular portion of the trigeminal nerve (cranial nerve (CN) V) except for the digastric muscle which is innervated by the inferior alveolar branch of the trigeminal nerve (CN V) anteriorly, and the facial nerve (CN VII) posteriorly. All structures associated with the TMJ are supplied blood by the external carotid artery, typically the superficial temporal branch, as well as the deep auricular artery, maxillary artery, ascending pharyngeal artery, and anterior tympanic artery to a lesser extent (Dutton, 2020; Standring, 2015).

**Neural control of chewing**

Walking and chewing tasks are performed daily with a variable amount of automaticity. If an individual is chewing something of predictable substance, the biting pattern is regular and automatic. However, if the consistency of the substance is more variable, then the biting pattern will change, and chews will continue under more conscious control.

Like walking, Sherrington (1917) also found that chewing was a result of reflex-chaining by which the masseter and temporalis (jaw-closing muscles) and digastrics and infrahyoid (jaw-opening muscles) were subject to reciprocal inhibition similar to the lower extremity flexor and
extensor musculature. Sherrington (1917) described a jaw opening and jaw closing reflex which alternated to result in rhythmical chewing patterns. As food was placed in the opened mouth, the closure muscle spindles would be stretched and cause a contraction which would initiate mouth closing. The mouth closing would, in turn, stimulate sensory receptors for tooth pressure, thus resulting in mouth opening. This alternating opening and closing of the mouth is considered to be the chewing motor program. Bazett and Penfield (1922) used pre-collicular, meaning the midbrain was transected between the superior and inferior colliculi, cat models for their research. The decerebrate cats were able to perform rhythmic chewing patterns when food was placed between the molars, which they attributed to the jaw opening and closing reflexes. However, Dellow and Lund (1971) were able to dispel the concept of reflex-driven chewing by instead suggesting the presence of an oral pattern generator in the brainstem which drives rhythmic chewing patterns. Sumi (1969) found that electrical stimulation of the motor cortex in rabbits resulted in rhythmic chewing patterns, which was later replicated in humans by Lund (1991). Lennartsson (1979) found that the digastric muscles are nearly void of muscle spindles. Nakamura and colleagues (2013) confirmed the masseter and temporalis muscles do not demonstrate reciprocal inhibition with any associated antagonist muscle group. This information appears to support a similar neurophysiological basis for chewing as with walking; the central pattern generators (CPGs) can be activated by descending control from the cerebrum or by sensory stimuli.

When chewing CPGs are activated by sensory information, such as placing food in the mouth. The mechanoreceptors in the periodontal ligament transmit sensory information to the ventral posteromedial nucleus (VPM) of the thalamus via the trigeminothalamic tract (Kandel et al., 2000). The anterior trigeminothalamic tract transmits sensory information about crude touch,
pain and temperature, whereas the posterior trigeminothalamic tract conveys discriminative touch and proprioception from the oral cavity. The trigeminothalamic tracts project from the trigeminal ganglion to the pons, synapses with the spinal trigeminal nucleus, then crosses midline and travels to the VPM in the contralateral thalamus. The information is then conveyed to the sensory cortex, specifically the regions for the face near the post-central gyrus (Kandel et al., 2000). The chewing CPGs are located in the reticular formation within the pons (Kandel et al., 2000; Lund & Kolta, 2006). When the oral sensory information activates the CPGs, a rhythmic chewing pattern is established. Lund and Rossignol (1981) noted phase-dependent reflex reversal in oral movements, much like in walking. During chewing, stimulation of the jaw-open reflex varies with mouth position. If the reflex is stimulated during the mouth opening phase of chewing, the reflex is weaker than when stimulated during the mouth closing phase. One functional reason for this is protection of the teeth. If the mouth is closing and the reflex is particularly excitable, it prevents the teeth from clattering together which could result in injury. It’s possible that coupling of the two phase-dependent reflex reversals in gait and chewing may be a mechanism for the 1:1 coordination pattern (jaw closing appears to occur simultaneously with stance phase of each limb) observed in recent studies.

The conscious decision to begin chewing can also initiate chewing patterns via descending control from the motor cortex with further influence on coordination of chewing patterns from the cerebellum, basal ganglia, and brainstem. The corticobulbar tract carries motor information from the motor cortex to brainstem where it is relayed to the trigeminal motor neurons for activation of the muscles of mastication. The cerebellum is involved in coordinating chewing with tongue movements, adjusting the fine coordination of jaw movements, as well as modulating the CPG frequency in response to sensory stimuli (Bryant, Boughter, Gong, LeDoux,
& Heck, 2010). The basal ganglia are involved in timing of initiation of chews and amplitude of the chews as is evidenced by chewing dysfunction in patients with Parkinson’s disease (Bakke, Larsen, Lautrup, & Karlsborg, 2011). More research is needed to understanding chewing patterns and the mechanisms that contribute to the motor control of chewing.

*Mechanical Factors of Chewing*

Jaw movements are surprisingly complex. Because the TMJ is a ginglymoarthroidial joint, the articulation allows for both sliding and hinging motions (Alomar et al., 2007). There are three degrees of freedom of movement at the TMJ. The movements associated with the sliding component of movement are protrusion (anterior movement of the mandible) and retrusion (posterior movement of the mandible). Depression is a lowering of the jaw, whereas elevation is raising of the jaw. Both depression and elevation are associated with the hinge component of jaw movement. Mouth opening and closing consists of combination movements, though the hinge component is most prominent. Mouth opening is associated with depression and protrusion of the jaw, whereas closing of the mouth is associated with elevation and retrusion of the jaw. Mandibular rotation and translation are the two primary arthrokinematic movements associated with the TMJ (Dutton, 2020).

During initial opening of the mouth, the mandibular condyle rotates anteriorly on the disc while also gliding inferiorly and laterally. This initial motion refers to the discotemporal (upper compartment) portion of the movement. During this phase of movement, the disc undergoes a posterior glide and the superior lateral pterygoid begins to contract to facilitate the rotation (Tucha & Simpson, 2011). As the mouth opens wider, the discomandibular (lower compartment) motion begins when the disc and mandibular condyle undergo anterior translation on the articular eminence of the temporal bone (Shaffer, Brismée, Sizer, & Courtney, 2014). This
Table 2.1.

*Movements of the Temporomandibular Joint and Associated Muscles*

<table>
<thead>
<tr>
<th>Movement</th>
<th>Definition of movement</th>
<th>Primary muscles used</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mouth opening</td>
<td>Inferior movement of the mandible away from</td>
<td>Bilateral activation of inferior head of lateral pterygoids and digastric muscles</td>
</tr>
<tr>
<td>(mandibular depression)</td>
<td>temporal bone</td>
<td></td>
</tr>
<tr>
<td>Mouth closing</td>
<td>Superior movement of the mandible toward the</td>
<td>Bilateral activation of the temporalis, masseter, and</td>
</tr>
<tr>
<td>(mandibular elevation)</td>
<td>temporal bone.</td>
<td>medial pterygoid muscles</td>
</tr>
<tr>
<td>Protrusion</td>
<td>Anterior movement of the mandible</td>
<td>Bilateral activation of lateral pterygoids, medial pterygoids, and vertical fibers of anterior temporalis muscles</td>
</tr>
<tr>
<td>(also, protraction)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Retrusion</td>
<td>Posterior movement of the mandible</td>
<td>Bilateral activation of horizontal fibers of posterior temporalis muscles and the digastric muscles</td>
</tr>
<tr>
<td>(also, retraction)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lateral deviation</td>
<td>Lateral movement of the mandible to both the</td>
<td>Activation of the ipsilateral masseter and contralateral pterygoid muscles (both medial and lateral)</td>
</tr>
<tr>
<td>(also, lateral excursion)</td>
<td>right and left</td>
<td></td>
</tr>
</tbody>
</table>
anterior translation of both the disc and condyle occur when the lateral pterygoid contracts to pull the structures forward. Discomandibular motion cannot occur without the discotemporal movements first being fully executed. As the mouth closes, the mandibular condyles and disc begin to slide posteriorly and superiorly along to temporal bone due to activation of the masseter, medial pterygoid, and temporalis muscles. Table 2.1 highlights the muscles primarily responsible for each of the movements of the TMJ.

Chewing requires repeated opening and closing of the mouth. Occlusion is the position when the mouth is fully closed and there is contact between some of the teeth. Chewing effort is typically focused on a single side at a time, either right or left. The tongue will be used to position a bolus of food or gum between the molars. The side of the mandible that is actively performing the chewing motion rotates laterally during mouth opening and is referred to as the working or rotating side (Schubert, Pröschel, Schwarz, Wichmann, & Morneburg, 2012). The contralateral side is considered the orbiting or balancing side. During repetitive chewing, the working side performs rotations in the horizontal and vertical plane while the balancing side performs translation. This coupled movement of the joints on either side of the mandible results in movement of the mandible in a circular pattern.

Chewing is a movement that is primarily controlled by the CPGs located in the brainstem. However, when the task or environment (i.e. bolus consistency, bolus size, etc.) changes, control of the movement can be modulated by descending input from the cerebral cortex to allow for conscious, voluntary alterations to chewing patterns. Additionally, there are jaw reflexes that occasionally drive jaw movement. These reflexes are initiated when afferent sensory information triggers a jaw-opening reflex (Lund et al., 1983). These reflexive
movements are considered protective to avoid dentition fracture given a very hard bolus, like a nut or seed.

*Differences between chewing and biting*

The primary difference between chewing and biting motions are rooted in function. Biting is used for cutting or tearing off a small piece of food from a larger piece of food, whereas the goal of chewing is to grind food and prepare it to be swallowed as part of digestion (Liu, Wang, Chen, & Van der Glas, 2018). Biting tasks have a discrete beginning and end that can involve sustained activation of the mouth closing musculature. Alternatively, chewing is a repetitive task with a defined cycle.

There are three phases to chewing: 1. fast closing/closing, 2. slow closing/occlusion, and 3. opening (Morimoto, Inoue, Nakamura, & Kawamura, 1984; Yamada & Yamamura, 1996). The fast closing phase occurs from the jaw being in the fully open position to the point where the teeth contact the food bolus (Meenakshi & Paul, 2017). The function of this phase is positioning of the bolus in preparation for chewing, but there is little to no breakdown of food in this phase. The slow closing phase is associated with food breakdown. Masseter and temporalis muscle activation is higher during this phase than during the fast closing phase, especially with foods that offer more mechanical resistance (Pröschel, Jamal, & Morneburg, 2008; Trulsson, 2006). The periodontal mechanoreceptors in the periodontal ligament are central to catching and positioning food in the teeth during the fast closing phase, as well as preventing damage to dentition during the slow closing phase by transmitting pressure sensation to the brain (Trulsson, 2006). This sensory feedback from the periodontal mechanoreceptors help guide oral fine motor control during chewing, especially the amount and direction of force (Trulsson & Gunne, 1998).
The last phase of chewing is the opening phase, which is characterized by a slow movement of the mandible away from the maxilla, followed by a faster movement into full opening (Meenakshi & Paul, 2017).

Jaw muscle activation patterns also vary between biting and chewing based on the amount of mouth gape (Pröschel et al., 2008). More gape (openness) in the mouth is associated with activation patterns that differ from chewing, whereas the muscle activation patterns of chewing and biting become more similar as the mouth gape gets smaller. The muscle activation patterns are important as there has been evidence that static biting can modulate activity in the soleus muscles of the legs (Hellmann et al., 2015; Takada, Miyahara, Tanaka, Ohyama, & Nakamura, 2000), and jaw clenching is a behavior used to improve motor activation and, in some cases, performance (Ringhof, Stein, Potthast, Schindler, & Hellmann, 2015).

2.2 Overview of Gait

*Neural control of gait*

Walking is an everyday task that many individuals perform focused mostly on the destination, but with little attention paid to the mechanics involved. Watching the very young or the very old walk, it becomes apparent that control of gait wavers between automaticity and conscious awareness of each step. It begs the question: How do we walk?

Initially, Sherrington (1910) suggested that gait, in animals, resulted from the chaining of lower limb reflexes. As he stimulated afferent sensory fibers in the skin, he noted that the muscles necessary for flexion of the limb would contract and the muscles associated with extension of the limb would relax. He argued that as the foot contacted the ground, this provided the necessary sensory stimulus to initiate the flexion reflex of the limb. The sensory information
would activate the flexor agonists of the lower limb, the limb would flex, the muscle spindles in the antagonist muscles would be stretched, and subsequently initiate contraction of the antagonist (extensor) musculature. This reciprocating lower limb flexion-extension reflex was considered to be a gait-based motor program.

Brown (1914) and Grillner & Zangger (1975) identified areas in the spinal cord of deafferented cats that, when electrically stimulated, would result in the appearance of rhythmic flexion and extension of the lower limbs. These areas in the spinal cord appeared to be directly related to initiating rhythmic aspects of gait and were subsequently referred to called central pattern generators (CPGs). These areas were originally believed to contain the motor program involved in walking. Following on from this line of research, both Brown and Grillner conducted research using cats where the spinal cord was transected, specifically to cut the dorsal sensory pathways. Despite the loss of sensory input, the cats were able to perform stepping patterns. Two important concepts arose from Brown’s and Grillner’s works: First, descending sensory input was not necessary to begin or sustain the rhythmic limb movements for gait. Second, the neural circuits for the stepping reflex are contained in the spinal cord. Restricting movement of a single limb did not interfere with the movement of the other three limbs, indicating that each limb functions independently and has the ability to coordinate with the other limbs. Additionally, Grillner and colleagues (1975) also emphasized that the reciprocal activation of flexors and extensors may be controlled differently than the precise coordination of multiple muscles during gait. The deafferented cats were walking on flat treadmills with only speed being varied. This set-up is a far cry from a human walking over ground which must take into consideration obstacles or terrain changes. Forssberg, Grillner and Rossignol (1975) noted phase-dependent reflex reversal, a differential response to a similar stimulus. He noted a unique limb flexion
response when the cat’s foot was advancing in swing phase, yet an opposite extension response in the limb when the cat’s foot contacted the ground in stance. Functionally, this allows for modification of gait, even by the CPGs in the spinal cord, to accommodate for fixed obstacles. More elaborate neural control is required for more complex obstacles.

A coordinated gait rhythm is established by the CPGs in the spinal cord, but descending input can modulate the motor output which results in increasingly gradual conscious control of gait. CPGs are less developed in humans, as compared to animals, which means the descending neural control of gait may play a more important role in motor control of human gait. There are many neural components that contribute supraspinal input to gait including the brain stem, basal ganglia, cerebellum, and motor cortex.

One area crucial to regulation of neural control of gait is the mesencephalic locomotor region (MLR) which is located in the midbrain. Stimulation of the MLR in animals has been directly linked to locomotor patterns (Shik, 1966). It was found that increasingly faster stimulation of this area results in a related increase in the animal’s walking speed. Animal models have also revealed that gradually stronger stimulation to these areas will result in a behavioral phase transitions (i.e., walking to trotting to running/ galloping). It has also been shown that the MLR directly interacts with vestibular/postural control inputs during gait (Sherman et al., 2015). There are two nuclei within the MLR, the pedunculopontine (PPN) and cuneiform nuclei. The PPN plays a central role in integrating sensory information, specifically vision, which allows for modulation of descending neural control of gait (Lau et al., 2015). There are direct inputs from the cortex to the MLR and the outputs run to the basal ganglia, thalamus, and the medullary region of the reticular formation. From the reticular formation, the lateral (medullary) reticulospinal tract is activated which inhibits extensor activity in the trunk muscles
to allow for limb movement, whereas the medial (pontine) reticulospinal tract activates trunk extension which is key to postural control. The two parts of this pathway work together to maintain balance during voluntary, dynamic activities, such as walking. The reticulospinal tract projects to the spinal cord and is thought to influence the CPGs, but no specific pathway has been identified. The vestibulospinal pathway also contributes to balance during gait, though the medial tract is for head control and the lateral tract is for postural control from the neck down. The basal ganglia (BG) also play an important role in modulating gait. At rest, the BG stimulates the thalamus to inhibit movement. The disinhibition of the BG results in the initiation and stopping of coordinated movements. Without the control provided from the BG, timing of movements, initiation of movement, and postural control during dynamic activities becomes difficult and awkward.

When walking in challenging situations, such as on uneven surfaces or in crowds, there must be mechanisms in place to allow for voluntary modification of gait. The corticospinal and rubrospinal pathways are the primary ways fine adjustments are made to gait. The corticospinal tract integrates information from the primary somatosensory and premotor areas to plan out more complex gait patterns. The information from the cortex allows for motor planning, decision-making and processing of sensory information which allows for coordination of more complex tasks, such as stepping over a rolling ball. The corticospinal tract consists of an anterior and a lateral portion. The lateral portion crosses the midline in the spinal cord and contributes the majority (about 90%) of descending control to the contralateral limb, whereas the anterior portion stays on the same side of spinal cord and contributes the remaining 10% of control to the ipsilateral limb, as well as trunk musculature (Kandel et al., 2000). The rubrospinal tract is an additional efferent tract that conveys upper limb motor information, as well as postural control.
during gait. The cerebellum provides additional feedback to the motor system as a manner of providing on-line feedback during walking. Information about the limb position, as well as muscle length and force are conveyed from the limbs to cerebellum via the spinocerebellar pathways. Visual and auditory information is relayed to the cerebellum through the reticular formation. Additional sensory information from the vestibular system is integrated into the gait motor signal in the cerebellum and transmitted to the spinal cord via the vestibulospinal and rubrospinal tracts (Kandel et al., 2000).

**Mechanical factors of gait**

A person’s gait pattern can be a type of unique signature. Gait is inherently complex because it involves the three major joints of the lower limb, the pelvis, and over 15 major muscles. The three major joints include the hip, the knee, and the ankle. All three joints are synovial joints. The hip is a ball-and-socket joint meaning that the ball of the femoral head articulates on the socket of the acetabulum. This type of joint allows for more movement than any other type of joint. The knee joint is a hinge joint comprised of the femoral condyles articulating on the tibial plateau. The knee primarily has one degree of freedom, though some rotary movement also occurs at this joint. The ankle is comprised of three joints. The talocrural joint is a mortise and tenon joint where the tibia, fibula and talus articulate, the subtalar joint is a plane joint where the talus and the calcaneus articulate, and the tibiofibular syndesmosis is a fibrous connection between the tibia and fibula.

Though walking is a repetitive task, there is a defined cycle of movement for each limb. The entire gait cycle is described per limb and the coordination of the two limbs is reciprocal—each limb moving anti-phase with the other. That is, while the right limb is moving from relative
hip flexion to hip extension, the left limb is moving from hip extension to a position of hip flexion. One limb functions as the stance limb, providing support to the body, while the other limb advances forward and prepares to accept weight as the body moves forward. Walking is essentially a series of controlled falls from one limb to the next. Initial contact is the point where the reference limb first touches the ground and it initiates the stance phase of the limb where muscle extensors are primarily active to provide stability to the limb. The two phases of stance are weight acceptance and single-limb support. Weight acceptance occurs as the stance limb begins to support the body weight, and the single-limb support phase begins when the contralateral limb is no longer in contact with the ground. As the body weight travels forward, the reference limb must advance forward to catch and support the body weight to prevent a fall. The reference limb begins swing phase, which is broken into three different phases (initial swing, mid-swing, and terminal swing) describing the act of the foot leaving the ground, the flexors of the limb becoming more active to clear the extremity as it is moved forward a full step length. This transfer of the body weight forward in a zig-zag pattern between the two limbs constitutes gait.

The motion of the two limbs moving forward and backward has traditionally been modeled using an inverted pendulum-spring model (Kugler & Turvey, 1987). The limbs resonate in a predictable fashion based on the mechanical properties of the leg, and accuracy of these predictions about the limb movement during walking improves when the activity of the muscles is accounted for via the addition of a spring to the model. The center of mass roughly moves in a figure-eight or butterfly pattern that becomes narrower with increased gait speed (Tesio & Rota, 2019). This pattern of pelvic movement ensures balance and a base for postural stability during walking. A similar pattern of circular movement in three planes is noted with
chewing (Pröschel et al., 2008), as well as different coordinated movements on each side of the jaw. Akin to the stance and swing limbs, the working or rotating side of the jaw is differentiated from the contralateral orbiting or balancing side of the jaw based on the rotation of the mandibular condyles (Yashiro, Yamauchi, Fujii, & Takada, 1999).

Gait can be described by kinematic movements, kinetic forces, or spatiotemporal parameters. Kinematic movements focus on the angles between body segments. Kinetic analysis describes gait by the forces acting on the limbs to cause them to move. Spatiotemporal parameters of gait describe the pattern of stepping that results from a particular walk. The spatial parameters are measurements of distance between steps, whereas the temporal parameters measure the amount of time associated with stepping. Derived measures include cadence and gait velocity. Table 2.2 has a list of spatiotemporal measures and a brief description of each measure.

2.3 Overview of Physiological Motor Reflexes

Reflexes and their significance in motor control have been an area of investigation for at least the last century. Sherrington (1910) performed some of the first experiments on spinalized animals to define a reflex. He described a spinal reflex as a muscle contraction resulting from a sensory stimulus. The concept of a motor program, a centralized control mechanism that organizes the coordination and performance of a motor task, fit well with reflex-chaining theories that were prevalent. Reflex-chaining was the concept that several reflexes could occur in succession. The effects of one reflex providing the necessary sensory stimulus to initiate the next reflex. The result is a coordinated movement or motor program (James, 1890). For this reason, it was believed that an understanding of reflexes would result in an understanding of motor control mechanisms.
### Table 2.2.

**A List of Spatiotemporal Measures and a Brief Description of Each Measure**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Type</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stride length</td>
<td>Spatial</td>
<td>Distance from the heel of the right step to the heel of the next right step.</td>
</tr>
<tr>
<td>Step length</td>
<td>Spatial</td>
<td>Distance from the heel of the right step to the heel of the left step.</td>
</tr>
<tr>
<td>Step width/base of support</td>
<td>Spatial</td>
<td>Distance between the right and left steps.</td>
</tr>
<tr>
<td>Stride time</td>
<td>Temporal</td>
<td>Amount of time to complete a full gait cycle (stance and swing phase).</td>
</tr>
<tr>
<td>Step time</td>
<td>Temporal</td>
<td>Amount of time to complete half of a gait cycle (stance).</td>
</tr>
<tr>
<td>Double limb support time</td>
<td>Temporal</td>
<td>Amount of time the person is supported by both limbs during gait.</td>
</tr>
<tr>
<td>Single limb support time</td>
<td>Temporal</td>
<td>Amount of time the person is supported by only one limb during gait.</td>
</tr>
<tr>
<td>Velocity</td>
<td>Derived</td>
<td>Walking speed (Total distance walked/ total amount of time to walk that distance)</td>
</tr>
<tr>
<td>Cadence</td>
<td>Derived</td>
<td>Stepping frequency (Number of steps/ unit of time)</td>
</tr>
</tbody>
</table>
All reflexes have a reflex arc which consists of a way to take sensory information and convert it to an action potential that allows for muscle movement and interaction of the individual with the environment. Sensory information is translated into an action potential at the sensory receptor. The resulting action potential moves along the afferent nerve to the central processing unit where another action potential is then sent to the muscles via an efferent nerve (Latash, 2008). These connections between the afferent and efferent portions of the reflex can be relatively simple, as is the case for the monosynaptic reflex which, as its name implies, only involves a single synapse. Reflexes can, however, be infinitely complex as there are oligosynaptic reflexes which involve two or three synapses, as well as polysynaptic reflexes which utilize greater than three synapses. Monosynaptic reflexes are the ones best understood and are typically the ones used for clinical evaluation and empirical study of the nervous system.

Often these reflexes are termed spinal reflexes as their central processing unit resides in the spinal cord. For these spinal reflexes, there are two main sensory receptors: the muscle spindle and the Golgi tendon organ (GTO). The muscle spindle is located inside the muscle and oriented parallel to the muscle fibers. The muscle spindle is sensitive to changes in the length of the muscle and the rate at which the length of the muscle is changing. The GTO is in the tendons of the muscles in series with the muscle fibers and is sensitive to the tension on a muscle. The muscle spindle communicates information in the form of action potentials along type Ia sensory fibers to the spinal cord, whereas GTOs use type Ib fibers (Latash, 2008). The afferent sensory fibers enter the dorsal horn of the spinal cord where they synapse with efferent motor fibers, also known as alpha or gamma motor neurons, which exit the spinal cord via the anterior horn. The alpha motor neurons innervate the extrafusal muscle fibers and the gamma motor neurons innervate the intrafusal muscle fibers. The combination of the alpha motor neuron and extrafusal
muscle fibers is the motor unit. The location where the efferent nerve meets the muscle fibers is called the neuromuscular junction. The action potential from the alpha motor neuron causes the release of the neurotransmitter, acetylcholine, which causes calcium channels to open resulting in a contraction of the muscle (Latash, 2008). These spinal stretch reflexes can be assessed either mechanically or with electrical stimulation. Mechanical stimulation can be measured by tapping the tendon which stimulates the muscle spindles, thus causing a visible muscle contraction.

Electrical stimulation of the afferent or efferent nerves requires use of electromyography on the muscles of interest to measure output from the electrical stimulation input. The amplitude of the electrical signal and the thickness of the nerve fiber influence how a signal is transmitted. The thickest fibers, the Ia afferent fibers, are most easily stimulated followed by the slightly smaller alpha motor neurons. When a nerve is electrically stimulated, the resulting reflex is named an H-reflex or Hoffman reflex (Latash, 2008). The latency and the amplitude of the H-reflex can be measured in many muscles in the body. A typical H-wave latency is 28-35ms after stimulation depending on whether the upper or lower extremity is being tested (Frijns, Laman, Van Duijn, & Van Duijn, 1997; Jabre, 1981). Longer afferent and efferent nerves or an increased number of synapses results in longer latency periods. At low amplitudes of electrical stimulation, only the H-reflex is noted on EMG tracings because only the thick Ia afferent fibers are being activated. As the amplitude of the electrical stimulation increases, more and more alpha motor neuron fibers are recruited, and an M-wave response appears on the tracing. The M-wave indicates the direct stimulation of the alpha motor neuron and the latency is much shorter around 3-6ms (Scaglioni, Narici, Maffiuletti, Pensini, & Martin, 2003). If the alpha motor neuron is stimulated along the axon, there is a response that travels out from the epicenter of stimulation both toward the muscle and toward the spinal cord, called orthodromic and antidromic conduction,
respectively (Latash, 2008). The size of the M-wave increases with the amplitude of the stimulation wave. Alternatively, the M-wave can also stay the same size but be stimulated at a gradually higher frequency. Eventually, the stimulus amplitude becomes so high or so frequent that it only stimulates efferent fibers and extinguishes that H-reflex completely (Latash, 2008).

In research, the ratio of maximal amplitude of the H-wave to the M-wave is used as a way to measure reflex excitability (Schieppati, 1987). H-waves and M-waves demonstrate an overall decrease in amplitude with age, the H:M-wave ratio appears to be a way to differentiate out healthy and pathologic reflex function (Scaglioni et al., 2003). F-waves are also recorded on EMG during electrical stimulation studies. The F-wave is an antidromic stimulation of the efferent fiber which causes the alpha motor neuron to fire an orthodromic action potential to the muscle (Latash, 2008). The F-wave is about 0.5ms faster than the H-wave on the EMG tracing as it does not involve a synapse—it only utilizes the efferent nerve fiber.

Reflex Testing to Assess Neuromotor System Integrity

Reflex testing is a standard part of a clinical neurological examination. The tests focus on examining monosynaptic spinal reflexes and use mechanical stimulation of the tendon via a reflex hammer. The most common clinical tests are of the brachioradialis, biceps, and triceps for the upper extremity, as well as the knee jerk which uses the patellar tendon and the ankle jerk which uses the Achilles tendon for the lower extremity. These sites are chosen because they are easiest to elicit a response mechanically and visualize a corresponding muscle contraction. Diagnostic clinical EMG testing focuses on different muscle groups as they are more easily visualized with electric techniques. Burke (2016) differentiated out reflexes that are present at rest (soleus, quadriceps, flexor carpi radialis), those which require a voluntary contraction to
record (biceps brachii, extensor carpi radialis, abductor pollicis brevis, and tibialis anterior), and technically difficult reflexes that cannot always be measured well in healthy adults (abductor hallucis, abductor digiti minimi, brachioradialis, and triceps brachii). The H-reflex and tendon jerk are often considered to be assessment equivalents with the exception that the H-reflex bypasses the muscle spindle, but there are many important differences between the two (Burke, 2016). For example, electrical stimulation recruits Ia and Ib afferents equally, whereas mechanical stimulation excites Ia fibers more intensely. Also, voluntary contractions of muscles shorten the tendon jerk latency significantly, but not for the H-reflex. One reason we see this is due to the fact that mechanical stimulation allows more time for oligosynaptic inputs to modulate motor neuron recruitment. Clinically, percussion, or mechanical stimulation, allows the clinician to examine the integrity entire reflex system. Electrical stimulation helps to differentiate out the location of different pathologies. Latency can be compared between individuals and normative values for the soleus and flexor carpi radialis H-reflexes have been established (Schimsheimer, de Visser, Kemp, & Bour, 1987). Amplitude is too variable for between-subject comparisons, but are useful for interlimb comparisons using the reflex excitability ratio (H:M wave ratio) (Burke, 2016). For example, the latencies of the M-, H-, and F-waves can indicate pathology in the efferent nerve by demonstrating increased F-wave latencies, whereas normal F-wave latencies in combination with extended H-wave latencies may indicate a synapse issue. Performing the testing in combination with voluntary contraction of either the muscle being tested (electrically) or of other remote muscles via the Jendrassik maneuver (manually) can be a method of identifying low central excitability when compared to findings at rest. It is known for the last century that the Jendrassik maneuver is an effective way to facilitate motor output during spinal reflex testing, but the mechanisms behind why it works are still being debated (Gregory, Wood,
There are two main theories: the first theory suggests that the voluntary contraction of remote muscles can cause the muscle spindles to become more sensitive to stretch sensations (Ribot-Ciscar, Rossi-Durand, & Roll, 2000), whereas the second theory focuses on a reduction of presynaptic inhibition of the alpha motor neurons by the Ia afferents (Hultborn, Meunier, Pierrot-Deseilligny, & Shindo, 1987). The idea that the Jendrassik maneuver directly facilitates the alpha motor neuron pool was not found to be a viable mechanism (Dowman & Wolpaw, 1988). Mental imagery was found to have no effect on the modulation of the alpha motor neurons, only activation of remote muscles including jaw muscles via teeth clenching appeared to work via subcortical mechanisms (Boroojerdi, Battaglia, Muellbacher, & Cohen, 2000; Passmore & Bruno, 2012). Remote muscle contractions, including clenching of the teeth activates the corticospinal pathways to the upper and lower limbs (Boroojerdi et al., 2000). Increased trunk stiffness has been noted during static, submaximal biting tasks, suggesting that postural neural tracts may also be similarly affected by modulatory mechanisms during the Jendrassik maneuver and isometric biting tasks (Ringhof et al., 2015).

**Reflexes Associated with Chewing and Walking**

Based on research investigating the effects of static biting on H-reflex modulation, there have also been studies that look as the oscillatory task of chewing. Studies that have investigated postural stability during static biting and chewing tasks have all demonstrated increased trunk stiffness and decreased center of pressure excursion, as well as velocity (Alghadir, Zafar, Whitney, & Iqbal, 2015; Kushiro & Goto, 2011; Ringhof et al., 2015). No formal studies have been conducted to specifically examine the effects of chewing on H-reflex modulation, but voluntary static teeth clenching has been found to facilitate H-reflexes in the soleus and pretibial
musculature in a force-dependent manner (Miyahara, Hagiya, Ohyama, & Nakamura, 1996; Takada et al., 2000). A major difference between chewing and static biting is the amount of bite force that occurs during each. Chewing cannot be considered repetitive biting. Chewing forces are more of a precision motor task to avoid dental damage as the teeth repetitively approximate, whereas holding an isometric bite force involves much higher sustained pressures through the dental structures. Chewing must be investigated as its mechanisms for H-reflex modulation appear to differ from static biting. Early research on jaw reflexes revealed that they exhibit phase-dependent properties similar to reflexes of the lower extremities (Lund, Drew, & Rossignol, 1984; Sherrington, 1917). The jaw opening reflex has similarities to the flexion withdrawal reflex of the lower limb and serves a similar protective mechanism (Lund et al., 1984). There are two main jaw reflexes examined clinically and empirically: the jaw jerk or masseter reflex and the masseter inhibitory reflex. The masseter reflex is initiated from percussion to the chin which causes the jaw to open quickly and stimulate the muscle spindles in the bilateral masseter muscles. The afferent fibers send information to the trigeminal mesencephalic nucleus which has collateral projections the mid-pons to activate ipsilateral motor neurons associated with jaw closing musculature (Aramideh & Ongerboer de Visser, 2002). A typical jaw jerk reflex latency is 5-10ms and a difference of greater than 0.8ms between the right and left sides of the jaw is considered pathological (Aramideh & Ongerboer de Visser, 2002). The masseter inhibitory reflex causes reflex inhibition of the jaw-closing musculature and is elicited by sensory stimulation, either mechanical or electric, to the inside of the mucosa of the mouth or skin on the lower half of the face (Aramideh & Ongerboer de Visser, 2002). There are two “silent periods,” one early and one late, during which voluntary closing of the jaw is inhibited. The first silent period occurs 10-15ms after stimulation and the later silent period
occurs 40-50ms after stimulation (Aramideh & Ongerboer de Visser, 2002). The initial silent period occurs after the sensory information is communicated via the mandibular or maxillary branches of the trigeminal nerve to an inhibitory interneuron near the trigeminal motor nucleus in the mid-pons. The interneuron projects bilaterally to the motor neurons which stimulate jaw-closing musculature. The second silent period takes longer to occur as the afferent fibers project to the spinal trigeminal tract where the signals are modulated by a polysynaptic chain of excitatory interneurons in the reticular formation at the pontomedullary junction. Both ipsilateral and contralateral collaterals sprout from the reticular formation and ascend to both right and left spinal trigeminal nuclei to inhibit the trigeminal motor neurons (Aramideh & Ongerboer de Visser, 2002). The jaw jerk reflex is a monosynaptic reflex that can be tested clinically with a reflex hammer, but the visible motor output is difficult to interpret. The master inhibitory reflex is rarely used clinically and requires the use of EMG for meaningful interpretation. Often cranial nerve tests are performed clinically which focus on either the afferent or efferent components of the reflex, but only testing the actual reflex gives the clinician or researcher insight into the functioning of the system as a whole.

There is much more investigation to be done on the likenesses and motor connections between the craniomandibular system, the upper limbs, and the lower limbs. These techniques, such as the Jendrassik and teeth clenching, have long been exploited during clinical examination of the neurological system without having a complete understanding of the underlying mechanisms. An understanding of the intrinsic connections and neural mechanisms may help guide future intervention for individuals who have suffered injury or age-related degeneration of these systems.
2.4 Dual Task Paradigm

Humans rarely perform tasks independently of one another. More often daily life involves multi-tasking, but task performance can suffer when attention is split. Traditionally, measurement of simultaneous task performance has occurred using the dual task paradigm. The dual task paradigm measures baseline performance of each task individually, then combines the task and quantifies the decrement to performance (Plummer & Eskes, 2015). Most commonly, cognitive and motor tasks have been studied in combination to reveal the phenomenon of task interference. Task interference occurs when performance of one or both tasks suffers when they are performed concurrently. The most common changes to performance include either slowed or erroneous responses and movements.

The two leading theories to account for the dual task interference effect is either a serial bottleneck model or a capacity sharing model. The serial bottleneck model was described by Pashler (1984, 1994) who stated that the altered performance results from the system being limited to fully processing a singular task at a time. Alternatively, the capacity sharing model asserts that the system can process multiple actions in parallel, but the processing capacity is limited and the more complex the task, the more apparent changes to performance become (Tombu & Jolicœur, 2003, 2005).

Dual task interference (DTI) is expressed as a percentage of isolated task performance. Task speed (i.e., gait speed or reaction time) and task accuracy (i.e., number of errors) are measured based on the associated parameters of the task. DTI is calculated for each task per 2.1.

\[
\text{DTI (\%)} = \left( \frac{\text{dual task performance} - \text{isolated task performance}}{\text{isolated task performance}} \right) \times 100\% 
\]  

(2.1)
Tasks in which a higher number indicates better performance are calculated using equation 1. The difference in the dual and single task performance measure is multiplied by negative one for tasks where higher values indicate worse performance (Plummer & Eskes, 2015). Plummer et al. (2015) developed a novel model for characterizing the interaction of motor and cognitive tasks. The model is depicted in figure 2.2. She showed that tasks can have one of five outcomes: 1. Prioritization of the motor task, 2. Prioritization of the cognitive task, 3. Mutual interference, 4. Mutual facilitation, or 5. No interference. The effect of performing two motor tasks has not been studied as thoroughly as concurrent performance of cognitive and motor tasks. The findings from dual task studies that pair two motor tasks are inconclusive (McIsaac, Lamberg, & Muratori, 2015). Studies found that performing various manipulation tasks were as detrimental to walking performance as performing a concurrent cognitive task, but others found that spatiotemporal gait parameters were differentially effected depending on the task (Bock, 2008; Laessoe, Hoeck, Simonsen, & Voigt, 2008). The relationship between performing two motor tasks concurrently has not yet been fully described and further investigation in this area is warranted.
Figure 2.2.

*Illustration of Theoretical Model for Describing Cognitive-Motor Dual Task Outcomes.*

*Note.* This graphic shows that dual task outcomes exist on a spectrum between facilitation and interference for each task. Outcomes are classified into four potential categories: 1. Mutual facilitation, 2. Mutual interference, 3. Gait—priority trade off, or 4. Cognitive-priority trade off. Facilitation refers to improved performance, whereas interference refers to worse performance. Graphic is adapted from Plummer et al. (2015)
2.5 Models of Coupled Rhythmic Motor Oscillators

Human movement exhibits many instances of rhythmic behavior including walking, finger wagging, and chewing. During these oscillatory movements, the same gross movements are repeated in succession. A single body part moving independently may move differently than multiple body segments moving simultaneously. Coordination dynamics attempt to describe how gross movements are coordinated within and between limbs accounting for these preferred oscillatory rates.

Bernstein (1967) first described the degrees of freedom problem which highlights that people can use a variety of movement strategies to achieve a similar outcome. Additionally, the problem highlights the importance of coordination across multiple levels of body structures. Bernstein suggested that the body develops synergies, neural and muscle activation patterns that follow a gross organization but are mutable in the presence of sensory feedback. The synergies were considered to be primitives, or motor programs, stored within the central nervous system (CNS). By this theory, synergies can describe how basic chewing patterns (i.e., opening/closing of the mouth) and stepping patterns (i.e., swing and stance phases) are coordinated, but lacks many details inherent to the tasks. For example, jaw motion during chewing involves more than just jaw opening and closing, and mastication involves coordination of the tongue and lips manipulating the food bolus (Gillings, Graham, & Duckmanton, 1973; Lund & Kolta, 2006). Turvey and Carello (1996) described the presence of rhythmic movements as being fundamental to all living things. It is a way that organisms coordinate behaviors with high levels of precision and repeatability. They also stated that rhythmic movements appear to follow basic guidelines that, when added together, form the basis for more complex behaviors. This reductionist approach, a belief that understanding the parts of a phenomena will reveal how the greater
system functions, has been one of the main approaches used by researchers over the last century to understand rhythmic movements.

Though the concept of physiological synergies appears to vaguely describe how coordination of movement occurs, it fails to address specific mechanisms of coordination or ways to predict coordination. Turvey and Carello (1996) highlighted five challenges to Bernstein’s concept of synergies including how certain muscles are activated to create a particular movement, how the amount and timing of muscle activation occurs with precision, how to separate out aspects of a movement, how to correct degrees of freedom so that a movement is optimized to a variable relevant for the movement goal, and how to synchronize different body segments that naturally move at different frequencies. Examining chewing and walking frequencies attempts to address this latter challenge.

An oscillator can describe any movement that demonstrates periodic behaviors (Strogatz & Stewart, 1993). Von Holst (1937) completed some of the first studies examining the movement frequencies of appendages in the lamprey fish. He established that different fins, dorsal and pectoral, on the fish oscillate rhythmically at different frequencies. He transected the spinal cord of the lamprey fish and would place it back in water to test for motor control without descending input from the brain. He termed the preferred rate of oscillation as the maintenance tendency (Von Holst, 1937). His experiments examining the natural movements of fins revealed three basic properties regarding formation of a synergy: (1) parts of a synergy can compete, which results in the maintenance tendency being most prevalent, (2) parts of a synergy can combine resulting in superimposition during which two frequencies join in an additive manner to create a frequency with larger amplitude compared to the maintenance tendencies, or (3) parts of a synergy can couple and form a novel hybrid frequency intermediate to the coupled
maintenance tendencies. Kugler and Turvey (1987) were able to confirm the presence of the magnet effect using pendulum swinging of the upper extremities in human subjects. The frequency of each arm swinging the pendulum individually varied greatly from the frequency of both arms swinging the pendulums in-phase or anti-phase. Coupled oscillators can become phase-locked, meaning that they are performing the same rhythmic behavior but not necessarily at the same time (Strogatz & Stewart, 1993). Gait can be an example of understanding how the movement of individual legs at their preferred frequencies (individual eigenfrequencies) can couple and a 1:1 coordination between right and left legs emerges per the pendulum-spring model (Kugler & Turvey, 1987). Von Holst (1937) also noted that when fins are moving in a coupled manner, stabilizing one fin (appendage) causes the other fin to move away from the magnet frequency and return to the individual fin’s maintenance tendency. These findings seem to give a general explanation of the mechanisms behind coordination of amplitude and timing of two limbs.

What then happens when two asymmetrical appendages need to couple for successful completion of a motor task? Kugler and Turvey (1987) argued that coordination patterns emerge from the interplay of physical characteristics of the limbs, aspects of the environment, and dynamics of neural control. Basic coordination patterns between limbs are grossly assembled and sensory information from the organism (intrinsic feedback) and from the environment (extrinsic feedback) appear to modify these coordinations into more specific patterns (Kugler & Turvey, 1987). The influence of sensory information and asymmetry has been confirmed in studies in the upper and lower extremities (Hatsopoulos & Warren, 1996; Russell, Kalbach, Massimini, & Martinez-Garza, 2010; Schmidt & Turvey, 1994). When examining coordination of movement between the arms and legs during slow gait, a 2:1 coordination is noted due to the asymmetries in
the arm length compared to the leg length, consistent with the pendulum-spring model (Kugler & Turvey, 1987). Individuals are able to perform unique coordination patterns by exploiting the physical and environmental affordances using sensory information to modify basic inherent coordination patterns.

Kelso and Schöner’s (1988) finger wagging experiments contributed to the description of preferred movement patterns at varying frequencies. Kelso had participants wag their fingers side to side at slow and increasingly faster speeds, as well as from different starting positions. At low frequencies, individuals were able to perform in-phase (fingers moving together) and anti-phase (fingers moving opposite of one another) coordination without difficulty. As finger wagging speed increased, the participants consistently reverted to an in-phase pattern regardless of starting position (in-phase or anti-phase). Synergetics examines the influencing factors of system behavior and synergetics of motor control attempts to understand why certain coordination patterns predictably emerge given a certain task, situation and constraints (Turvey & Carello, 1996). Bernstein referred to this self-organization as “slaving” and explained that it is a way degrees of freedom can be decreased to improve successful completion of task (Bernstein, 1967). The shift to an in-phase coordination during finger wagging was described as an attractor state, the emergence of a stable, preferred behavior during that particular movement. The more stable an attractor state, the less time it takes for the system to return to that state after a perturbation (Kelso & Schöner, 1988). The shift from one pattern of coordination to another is known as a phase transition and is akin to the way quadrupeds shift between walking, trotting and galloping based on their locomotion speed. In both the finger wagging and quadruped locomotion cases, movement frequency is the control parameter. As the control parameter
changes, there are stepwise order parameters which indicate changes in the coordination patterns toward each relevant attractor state.

**Haken-Kelso-Bunz (HKB) Model**

Rhythmic behaviors can be measured as either a time series or a phase plot, both of which examine position and velocity in different ways (Strogatz & Stewart, 1993). A time series plots position over time and velocity is the slope of the position function. The relative phase can be calculated on a time series by using the point estimate technique, which is a comparison of where corresponding points (i.e., minima or maxima) occur on the time series (Kelso, 1984). In a phase plot, position is described relative to velocity and gives the whole range of movement in the state space. Another technique is to compare the angle of corresponding points on these phase plots which is known as continuous relative phase (Kelso & Scholz, 1985). Kelso and Schöner (1988) and Von Holst (1937) measured coordination using relative phase, which are ways to measure the frequency of two tasks relative to one another based on the size of the appendages and the strength of the coordination between the two appendages. This relationship evolved into a potential function which dictates the number of stable attractor states. The stability of these attractor states is measured by the standard deviation of the relative phase. An energy landscape can be visually depicted by graphing $V$ (a potential function) against relative phase and the ratio of $b/a$, which are coefficients describing the coupling motion (Kelso & Schöner, 1988). The deeper the wells in this energy landscape graph, the more stable a particular attractor state. The relationship of all these variables is the Haken-Kelso-Bunz (HKB) model (Haken, Kelso, & Bunz, 1985) which describes the coordination and stability of self-organizing nonlinear coupled dynamic systems. The HKB potential function is listed in 2.2 where $V$ is the
potential function, $a$ and $b$ are coefficients to indicate the periodicity of each of the oscillatory movements, and $\phi$ is the relative phase. This equation describes coordination between symmetrical oscillators that have attractors at 0- and 180-degrees relative phase. To describe asymmetrical oscillators, the first derivative of the potential function is used with the addition of delta omega ($\Delta \omega$) to describe the asymmetry and a noise term ($\sqrt{Q_\xi_t}$) (Kelso, Del Colle, & Schöner, 1990). The HKB first derivative of the potential function is listed in 2.3.

$$\dot{\phi} = \Delta \omega - a \sin \phi - 2b \sin2\phi + \sqrt{Q_\xi_t}$$

The attractors for asymmetrical coupled oscillators vary from 0 and 180 degrees of relative phase. Deviation from the natural attractor states is associated with a reduction in stability (Jeka, Kelso, & Kiemel, 1993; Russell et al., 2010; Sternad, Turvey, & Schmidt, 1992).

**Limitations of the HKB Model**

Jirsa, Friedrich, Haken, and Kelso (1994) revised their model to account for multistability of the brain and attempted to describe the connection between internal neural dynamics and external movement dynamics. This described how the brain can go from a resting state to performing a pattern based on the presence of meaningful sensory stimuli, in this case pressing a button between tones to create a syncopated rhythm. Beek and colleagues (2002) went on to identify two shortcomings of the original HKB model. The first was to describe polyrhythmic,
oscillatory movements that did not have a 1:1 coordination. The second was to describe the relationship between phase transitions and critical frequencies, the frequency at which a phase transition occurs with regard to amplitude of oscillation. The updated function includes four coupled oscillators—two neural and two effectors. This is an attempt to describe the interaction of neural and limb dynamics.

As you can see, there has been much investigation into coupled oscillators and the multitude of variables measured in an attempt to accurately predict their motion. There appears to be coupling between the act of chewing and stepping during gait. Bernstein might describe this relationship as a synergy—merely a way to decrease degrees of freedom and simplify movement as a response to the increased cognitive and physical load of performing two tasks simultaneously. Based on our measures, chewing and stepping appear to couple in a 1:1 fashion and should theoretically follow a form of the HKB model. Some considerations for using the HKB model to describe the coupling between chewing and walking would be the asymmetry of the two actions. Unlike when Kelso and colleagues measured finger wagging, chewing and walking have very different physical properties associated with them. Gait has been extensively described using the pendulum-spring model, there has been very little similar modeling of jaw mechanics (Kugler & Turvey, 1987). During chewing and walking, there are two legs moving anti-phase (for gait) relative to a singular jaw moving up and down. The concept of increasing the number of coupled oscillators that become phase-locked has been studied, but this work was done on coupled symmetrical oscillators (Golubitsky & Stewart, 1985). The physiological asymmetries and added complexity of multiple phase-locked oscillators must be considered.

Based on current findings from the most recent chewing and walking study, it appears chewing rate sets the coupling pattern for stepping (Samulski et al., 2019). A typical preferred
chewing rate for healthy adults is about 1.2-1.3 Hz, whereas a typical self-selected stepping frequency is about 1.8 Hz (Bellisle, Guy-Grand, & Le Magnen, 2000; Shumway-Cook & Woollacott, 2017). The chewing rate and the stepping frequencies are nearly identical and consistently match the set chewing rate despite stepping rates being completely self-selected. It seems that the maintenance tendency of the chewing was superior to the walking and drove the overall coupled frequency. The presence of a magnet effect between the two frequencies would result in a hybrid frequency between 1.2 and 1.8 Hz to emerge during the preferred chewing and preferred walking condition. Instead, the individuals tended to walk at about 1.2Hz which is consistent with the preferred chewing frequency.

There are a number of avenues to examine chewing and walking for future research. One study could examine the effects of increasing and decreasing the chewing speed to extremes to see what happens to the walking pattern over a larger range of frequencies. This would confirm areas of stable coupling and where the coupling completely breaks down. Another study could use the idea of stability and examine the amount of time it takes for the chewing and walking coupling to re-emerge after perturbing the system (Kelso & Schöner, 1988). If the system returned quickly to the coupled state, this would indicate a stable attractor. This stability could also be examined across a number of chewing and stepping frequencies. It may also be worthwhile to examine the bi-directionality of coupling between chewing and walking by setting the step cadence and having participants begin chewing mid-gait. Again, we would want to see if a particular maintenance tendency remains prevalent or if a magnet effect emerges. This would also confirm whether the chewing maintenance tendency is the lead frequency or if the frequency performed first temporally sets the coupling pattern. Finally, measuring relative phase of jaw motion relative to bilateral leg motion would also reveal the unique interaction of two coupled
oscillatory tasks with three components (right leg, left leg, and jaw). This may validate or make an argument for modification of current HKB models.

2.6 Typical Patterns of Age-Related Motor Function Decline

A general slowing of movement has long been associated with aging. English poet Percy Bysshe Shelley once stated, “The mind of man, his brain, and nerves, are a truer index of his age than the calendar…” (Trelawny, 1887). Typical patterns of neuromotor decline have been examined in discrete tasks, such as reaction time and movement time, as well as in continuous tasks such as physiological tremor, isometric force production, gait, and finger tapping. The most common findings are an overall slowing of movement across all systems, as well as an overall change in the variations of performance from instance to instance, which is known as the intra-individual variability (IIV) of movements.

Reaction Time

Reaction time (RT) has, for years, been considered a way to directly measure the function of the nervous system. There are two main ways to assess reaction time: simple RT and choice RT. A simple RT task presents the individual with a single stimulus and measures the amount of time from stimulus presentation (i.e., turning on a light) until completion of the single target task (i.e., clicking a button). A choice RT task is similar, but the participant is presented with more than one stimulus which may have one or more desired behavioral responses associated with it. The whole response time can be measured from the presentation of the stimulus to the completion of the response behavior. Alternatively, central processing time, or the premotor response time, is measured relative to the onset of the motor, or peripheral, response from the
onset of the stimulus. There is a clear increase in the amount of reaction time for a task as we age, which is exacerbated by tasks of increasing complexity. Movement time, which is the amount of time the motor component of the response to a stimulus, is also slower as age increases. The speed-accuracy relationship described by Fitts’s law still applies to older adults, but their overall movement speeds are slower compared to young adults (Fitts, 1954; Salthouse & Somberg, 1982). There is also some evidence to suggest that they choose alternative, more cautious movement strategies to younger adults which may alter their movement time (Spirduso et al., 1995). Additionally, older adults demonstrate more inter-trial variability in their reaction time than do younger adults (Morrison & Newell, 2015).

**Strength**

An isometric contraction describes the activation of a muscle when that muscle is held at a set length. Isometric force production is important for a number of tasks, like holding a foam cup. Overproduction of force would crush the cup, whereas underproduction of force would result in the cup being dropped. Managing the amount of fluctuation while creating these isometric forces is important, the steadier the better. Older adults were found to exhibit increased variability of isometric force control, specifically due to larger variation in the amplitude of the forces. This change in variability is associated with losses in motor control during a task, rather than losses in strength. Additionally, older adults were found to exhibit more variability of force production during discrete contractions as compared to continuous contractions (Vaillancourt & Newell, 2003).
Gait

As people age, overall gait speed slows. Interestingly, the slowing does not arise from a change in gait cadence, rather from shorter step lengths, increased time in double limb support, and wider stance (Maki, 1997; Samson et al., 2001; Winter et al., 1990). Similar to the way older adults choose accuracy over speed in movement time tasks, these gait changes are consistent with older adults choosing an alternative movement strategy that appears more conservative. Specifically, it seems that the older adults are attempting to improve stability to decrease falls. Maki (1997) confirmed this association between the previously noted gait changes and adults who are at increased risk of experiencing a fall. Similar to the other motor tasks, gait patterns are also associated with a change in variability as individuals age. The stride-to-stride variability increases with age, and more variability is associated with an increased fall risk (Maki, 1997; Springer et al., 2006). Interestingly, dual tasking during walking does not appear to increase gait pattern variability except in elderly adults who are at an increased risk of falling, thus making it a useful tool for differentiating healthy elderly gait patterns from more maladaptive patterns associated with falls (Springer et al., 2006).

Finger Tapping

Measurement of finger tapping reveals an overall slowing of tapping speed which is related to longer inter-tap intervals. Changes in tapping speed are considered a glimpse at the decline of the neuromuscular system typical aging more so than a result of changes to peripheral sensation or pinch strength (Aoki & Fukuoka, 2010). Finger tapping has been shown to successfully differentiate out individuals with motor dysfunction associated with CNS origin.
and may indicate that finger tapping a sensitive measure for assessing fall risk in the elderly (Shimoyama et al., 1990).

**Slowing of Movement with Increasing Age**

Overall we see a loss of the fast and short time scales which refer to neural processes and movements with a relatively high frequency (Morrison & Newell, 2015; Newell et al., 2001; Newell et al., 2009). There are a variety of physiological mechanisms associated with the overall slowing of the aging nervous system (Spirduso et al., 2005). A number of structural changes in the CNS have been noted, including loss of white and grey matter, slowed conduction velocity, and breakdown in neural communication via neurotransmitters (Seidler et al., 2010). In addition to changes in the physical anatomy, cortex activation patterns have also been noted in older adults. The brains of older adults demonstrate greater activation patterns over more area, specifically in prefrontal cortex and basal ganglia (Seidler et al., 2010). Ironically, the areas where there is increased neural activity are the same areas where neuronal loss is greatest for the elderly. This mismatch between neural activation and patterns of tissue degradation, especially in areas closely related to motor control, may be why changes in time scales and variability occur with aging. Peripheral structures also undergo changes with aging which may contribute to altered motor patterns. As we age, muscle atrophy via loss of cross-sectional area, reduction in overall muscle mass, and decreased force output by muscles are all noted (Jubrias et al., 1997). Additionally, there is a loss of fast-twitch muscle fibers and a loss of the overall number of alpha motor neurons which contributes the variability of motor unit firing (Power et al., 2013). The muscular changes in aging adults mirror that of fatigued younger adults, but the effects are more permanent.
In the 1950’s, the neural noise hypothesis emerged stating that age-related declines in cognition and motor function were due to an increase in neural noise (Crossman & Szafran, 1956; Welford, 1981). The neural noise arose due to weakened neural communication from cortical cell loss or weak inhibition of background noise (Salthouse & Lichty, 1985). But Sosnoff and Newell (2011) measured the amount of neural noise present during five motor tasks (postural tremor, isometric finger strength, two and three finger grip strength, and standing still) and found that the overall levels of neural noise did not differ across age groups for any of the tasks. Instead they found increased variability in completion of the tasks by the older adults compared to the young healthy adults. This solidly shifted focus to understanding the mechanisms that drive variability and how measures of variability can offer insight into the process of aging.

Changes in Movement Pattern Variability with Age

The concept of variation from a typical aging pattern is a much newer concept in gerontology. One way to examine variability is to calculate the overall mean and standard deviation (SD) of several individuals in a study. This measure gives an overall idea about movement, but many of the details about how a single person’s movement varies from trial to trial is lost (i.e., a low-resolution examination of the variability). Intra-individual variability (IIV) is a measure of the change between each performance of a behavior within a single person. It is considered a measure of movement consistency. The IIV is the within-task variability across trials for an individual. The significance of this variability measure has evolved over time and is still debated today but is usually associated with aging and disease. Lipsitz and Goldberger (1992) proposed a theory that suggested a loss of complexity as indicated by decreases in physiologic and behavioral variability is typical of aging. They also suggested that this loss of
complexity manifests as difficulty by the individual to adapt to stressors. The focus of Lipsitz and Goldberger’s research was on heart rate variability. Recall from earlier that variability of physiologic tremor can be variable-dependent. That is, frequency variability decreases, but amplitude variability increases with aging. Vaillancourt and Newell (2002) argued that a bidirectional change in variability is noted with aging. The direction of change is dependent on the interaction of many aspects of the movement task, characteristics of the individual, and constraints on that interaction (perhaps situational). They were arguing that the changes in variability may reflect a pattern of aging that is more associated with a chaotic attractor, which would result in the need for a more complex understanding of the system before speculating as to the benefit or harm of directional changes in variability. Buzzi and colleagues (2003) attempted to simplify the explanation of variability by advocating for an intermediate state between the two ends of the variability spectrum: complete regularity or complete randomness. Anyone in this intermediate range was considered to have a “healthy” neurological system. Decreases in variability were associated with a rigid, less adaptable system and increases indicated a noisy, unstable system. This latter speculation attempted to join theories about neural noise with complexity theories in an attempt to explain changes with aging. Newell and colleagues (2006) were able to connect two underlying changes noted with aging: loss of the fast/short time scales and changes in complexity. He and his colleagues asserted that the shorter the timescale of a motor task being studied, the more sensitive that particular task would be for determining the onset and early influence of aging or disease. Though no unifying theory of aging has been defined, there does appear to be a healthy level of complexity and variability, and deviations from this yet-to-be-defined pattern may offer a way to measure aging or disease effects on the nervous system.
CHAPTER 3

EXPERIMENT ONE: COUPLING OF MOTOR OSCILLATORS – WHAT REALLY HAPPENS WHEN YOU CHEW GUM AND WALK?

3.1 Introduction

The phrase “you cannot walk and chew gum” is commonly used in reference to the negative impact performing one task may have on the simultaneous performance of a second activity (Morquette & Kolta, 2014; Morquette et al., 2012). The basis for this view is that undertaking a challenging, usually more cognitively demanding task concurrently with the performance of a secondary motor tasks leads to decrements in the outcomes of the latter (Hiraga, Garry, Carson, & Summers, 2009; Patel et al., 2014). For example, walking at a slower speed or with increased variability have been reported under conditions where an individual has to perform a cognitive task such as counting backwards or spelling words (Patel et al., 2014). Although the inference has been widely reported that chewing would interfere with an individual’s gait, the impact of chewing on walking performance has never been explicitly examined.

Chewing and walking are primary neuromotor functions that individuals perform on an everyday basis. The neural mechanisms underlying both actions are believed to involve complex neuronal clusters (i.e., central pattern generators, CPG’s) within the spinal cord and/or brainstem with descending influences from higher regions moderating the resultant neuromotor outputs (McCrea & Rybak, 2008; Morquette et al., 2012; Westberg & Kolta, 2011). Although both actions can broadly be described as oscillatory, rhythmical motor tasks, they are, when undertaken independently, performed at different preferred frequencies involving different muscles/body segments with different overall goals.
Despite the aforementioned assumption that chewing would influence walking ability, there is little empirical evidence for any link between chewing and walking in humans. Previous research using animal models have reported that projections from the trigeminal system in the brainstem propagate to all levels of the spinal cord (Ruggiero, Ross, & Reis, 1981). Although similar axonal projections are not evident in humans, it has been reported that increasing the force of biting can lead to increases in neuromotor excitability (Boroojerdi, Battaglia, Muellbacher, & Cohen, 2000), enhancing reflex responses in muscles of both the upper and lower limbs (Miyahara, Hagiya, Ohyama, & Nakamura, 1996; Takada et al., 2000). Under these conditions, it is believed that the increased excitability of the α motor neuron pool observed during teeth clenching was generated through the corticospinal tract (Boroojerdi et al., 2000; Sugawara et al., 2005) with the added inference that these projections could influence postural actions (Hellmann et al., 2015; Kushiro & Goto, 2011). Although individuals do not typically chew with maximal force, it seems plausible that the same neural mechanisms and pathways underlying the increased excitability during teeth clenching would be evident when chewing. Consequently, there is some support to the idea that chewing may influence the pattern of lower limb muscle activity during purposeful actions such as walking.

Another factor to consider when assessing chewing function is the general effect of aging. Typically, increasing age is associated with a general slowing of motor function, as evident by declines in walking speed, reaction time, and finger tapping rates (Aoki & Fukuoka, 2010; Batterham, Bunce, Mackinnon, & Christensen, 2014; Dykiert, Der, Starr, & Deary, 2012; Gabell & Nayak, 1984; Morrison & Newell, 2017). However, there has been little direct assessment of whether the motor processes involved in chewing are similarly affected by aging. One suggestion is that, in comparison to other motor tasks such as walking, chewing rates in older
adults may be preserved given the increased neural input the masticatory muscles receive from both motor cortices (McCrea & Rybak, 2008; Morquette et al., 2012).

This study was designed to assess the impact chewing at different frequencies had on walking performance for healthy young and older adults. It was predicted that an individual’s stepping rate (and hence walking speed) would increase or decrease in line with the similar changes in chewing rates. It was also predicted that, while age-related differences would be seen in preferred walking speed, that no differences would be seen for chewing rates between the young and older individuals.

### 3.2 Methods

**Participants**

Fifteen healthy young adults (average age 23.2±4.2 years) and fifteen healthy older participants (average age 66.5±3.2 years) volunteered to participate in this study. Participants self-reported no orthopedic, neurological, cognitive, or arthritic conditions that would interfere with their ability to perform the tasks outlined in the study. Participants provided informed written consent prior to inclusion in the study and all procedures complied with the university IRB guidelines.

**Experimental Design**

Demographic data relating to age, height, weight, and preferred chewing side was collected from each participant prior to data collection. The following movement tasks were performed; 1) chewing only and, 2) chewing while walking. Details regarding the specific tasks and conditions are as follows:
**Chewing Only.** This task was performed to assess each person’s preferred chewing rate. Each person was required to perform this task under three chewing speed conditions: 1) preferred speed of chewing, 2) slow speed of chewing and, 3) fast speed of chewing. As the preferred speed of chewing has been reported to be around 1.1-1.2 Hz (Bellisle, Guy-Grand, & Le Magnen, 2000), the slow and fast speed conditions were set at 1 Hz and 2 Hz respectively (Paphangkorakit, Leelayuwat, Boonyawat, Parniangtong, & Sripratoom, 2014). Individuals performed three 30 sec trials for each chewing condition. Subjects were seated for these tasks. For condition 1 (i.e. preferred chewing), subjects self-selected their preferred chewing speed. For conditions 2 and 3 (i.e. slow and fast chewing), individuals initially practiced chewing at these specified rates while a metronome (set at either 1 Hz or 2 Hz) was played. After this practice period, the metronome was turned off. Participants then performed the specified conditions with relevant chewing data being recorded.

**Gait and Chewing.** For the gait-chewing task, four chewing conditions were performed. All walking was performed at the individual’s preferred speed. Individuals performed three walking trials for each condition. All walking trials were performed in a straight line over a distance of 25 ft. The conditions were: 1) walking at a persons preferred speed without chewing, 2) walking while the individual chewed at their preferred rate, 3) walking while chewing at a slow rate (1 Hz), 4) walking while chewing at a faster rate (2 Hz). For conditions 1 and 2, individuals self-selected their preferred walking speeds and (for condition 2 only), their preferred chewing rates. For the fast and slow chewing conditions, individuals initially practiced chewing at these specified rates while a metronome (set at either 1 Hz or 2 Hz) was played. After this practice period, the metronome was turned off. Participants then performed the specified conditions with relevant chewing and gait data being recorded.
For all chewing conditions, participants were provided with one piece of Trident® spearmint gum and were given up to one minute to chew and soften the gum, as well as establish a comfortable chewing pattern before data collection commenced. Individuals were asked about the preferred side for chewing and asked to chew on that side for the duration of the study (Wintergerst, Throckmorton, & Buschang, 2008). Participants were able to exchange the gum bolus between each trial; however, bolus size was kept consistent across all trials. Individuals removed the gum during the no-chewing conditions.

**Data Collection and Processing**

All data processing and analyses were performed using custom software developed in MATLAB (MathWorks R14). EMG activity was recorded from the masseter muscle the Delsys Trigno system (Delsys, Boston, MA) at a sample rate of 2000 Hz. Prior to data analysis, EMG data were down sampled to 1000 Hz, rectified, then filtered using a second-order low-pass Butterworth filter (cut-off frequency 400 Hz). In addition, a linear envelope of the EMG signal was attained using a low pass filter set at 20 Hz.

Assessment of each person’s gait was collected using three Delsys triaxial accelerometers. These sensors were positioned on the head, lower back (L3 spinous process), and lower leg (distal Achilles tendon) during the walking trials as per our previous research (Armitano, Morrison, & Russell, 2017; Morrison, Russell, Kelleran, & Walker, 2015). Gait-related acceleration data was collected at 148 Hz using the Delsys Trigno system (Delsys, Boston, MA), down sampled to 100 Hz and filtered using a second-order low-pass Butterworth filter with a cutoff frequency of 40 Hz. The following analyses were subsequently performed on the EMG and acceleration data:
**Chewing.** For all conditions, an indication of each individual’s chewing rates was derived from a surface EMG sensor placed over the belly of the masseter muscle on the individual’s preferred chewing side. A measure of the overall chewing frequency (rate) for each chewing condition was attained by determining the number of contractions (based upon the EMG signal) for the masseter muscle over the period for each trial. Selection of a muscle contraction was based upon a peak picking algorithm which identified the maximum peak within a pre-specified time window. The accuracy of the peak-picking algorithm was verified by visual inspection of 25% of the trials in each condition. The average (mean) responses and the intra-individual variability (IIV) were calculated for the chewing rates.

**Gait.** Consistent with the chewing measures, measures of the number of steps (step rate) were attained for each trial within each condition from the accelerometer data. Selection of each step were based upon a peak picking algorithm which identified the maximum peak within a pre-specified time window. The accuracy of the peak-picking algorithm was verified by visual inspection of 25% of the trials in each condition. Average and IIV values were calculated for step rates for comparison.

In addition, a 20-foot Zeno pressure sensitive walkway (Protokinetics, Havertown, PA, sample rate: 120Hz) was used to provide additional spatio-temporal gait measures. Average (mean) and IIV measures were calculated for the following spatio-temporal gait variables: step length (cm), step time (sec), and gait velocity (cm/sec). All gait-related IIV calculations were based upon the between-trial standard deviation (SD) for each individual. This data was processed using the Protokinetics PKMAS software (ProtoKinetics LLC).

**Statistics**
For all tasks, a repeated-measures, mixed generalized linear model (GLM) was used to assess differences between the two age groups and as a function of the specific conditions. Significant interaction effects were explored using planned contrasts (one-way ANOVA’s) within the mixed model design. All tests were performed using SAS statistical software (SAS Institute Inc., Cary, NC) with a significance level of $p<0.05$.

3.3 Results

**Chewing Only Conditions**

Overall, participants were able to accurately follow instructions regarding the different frequency of chewing when seated. The average rate ($F_{2,56}=3680; p<0.001$) and intra-individual variability (IIV) measures ($F_{2,56}=1316.79; p<0.001$) consistently differed among the slow, preferred, and fast chewing conditions within both young and older adult groups. For both analyses, planned contrasts revealed differences between all three conditions (all $p$’s<0.001). A significant age group effect was also observed for the IIV of the chewing rates ($F_{1,28}=5.40; p=0.032$) with the older adults exhibiting greater variability compared to the young adults. No interaction effects were found. Figure 3.1 illustrates the pattern of activity for the masseter muscle during the slow, preferred and fast chewing conditions for a single older adult. In addition, differences in the chewing rates (both mean and intra-individual variability, IIV) as a function of age and across the three conditions are also shown.
Figure 3.1.

Representative EMG Signals (top) Illustrating Rate of Chewing for the Slow, Preferred and Fast Chewing Conditions.

Note. EMG traces are shown for a single older individual. In addition, graphs (bottom) depicting changes in average and intra-individual variability of the chewing rates are also represented for the two age groups as a function of the three chewing conditions. For all graphs, error bars represent one SE of the mean.
**Chewing: Walking and Seated Comparisons**

Inferential analysis was performed to assess whether the average chewing rates were different between the seated (chewing only) and walking/chewing conditions. Comparisons were made between similar conditions only (i.e. slow-slow, fast-fast, or preferred-preferred). The results revealed no significant differences between similar chewing conditions (all p’s>0.50).

**Walking and Chewing**

**Chewing Rates.** An example of the EMG and acceleration signals for both chewing and walking during each of the three chewing-walking conditions (i.e., slow, preferred and fast) are shown in figure 3.2. For chewing rates, a significant condition effect was found for both the average (F_{2,56}=860.27; p<0.001) and IIV (F_{2,56}=4.25; p=0.007) measures. Planned contrasts revealed significant differences between all conditions (p’s<0.001) with the mean and IIV values being lower during the slow chewing condition and increasing across the preferred and fast chewing conditions respectively. No differences were found for the chewing rates between the two age groups.

**Walking (Stepping) Rates.** For the gait-acceleration data, the overall number of steps and the timing between individual steps (i.e. inter-step intervals) were determined for further analysis. A significant condition effect was found for average (F_{3,81}=241.6; p<0.001) and variability (F_{3,81}=3.17; p=0.023) of the step rate measures. For the average measures, planned contrasts revealed the differences were between all conditions (all p’s<0.001) except the preferred gait/no chewing and the fast chewing conditions. For the IIV of step rate, differences
Figure 3.2.  
Representative EMG (right) and Acceleration (left) Signals Illustrating Rate of Chewing (EMG) and Walking (acceleration) Patterns for the Slow, Preferred and Fast Chewing Conditions.

Note. EMG and acceleration traces are shown for a single older individual.
were seen between the slow chew/walking and both the fast chew/walking and preferred walking/no chew conditions (all \( p \)'s <0.001). No interaction effects or differences between the two age groups were observed for these measures. Figure 3.3 illustrates the pattern of change in the chewing and gait responses (both mean and IIV) for the young and older groups across the experimental conditions.

**Walkway Assessment of Gait**

In addition to the gait analysis performed above, further gait assessments were attained from the pressure sensitive walkway. The summarized changes in step time, step length and gait velocity between the two groups and across conditions are shown in figure 3.4. These results revealed significant age by condition interaction effects for gait velocity (\( F_{3,84} = 9.93; p < 0.001 \)), step time (\( F_{3,84} = 21.62; p < 0.001 \)), and step length (\( F_{3,84} = 38.23; p < 0.001 \)). For the velocity measures, planned contrasts revealed differences between the slow chewing and all other conditions (\( p \)'s <0.05). Generally, the older adults walked at a slower velocity compared to the young adults. Similarly, for the step time and step length measures, differences were observed between the same chewing conditions (\( p \)'s <0.01) with the exception of the fast chewing/walking and the no-chewing/preferred conditions. Step lengths were greatest during the fast chewing/walking conditions and decreased during the slow chewing/walking condition. Similarly, step times were longer during the slow chewing/walking conditions and shorter during the fast chewing/walking condition (\( p \)'s <0.01). Across all conditions, the older adults exhibited significantly decreased step lengths and increased step times compared to the young adults (\( p \)'s <0.01).
Figure 3.3.

Graphs Depicting Changes in Average and IIV of Chewing Rates and Step Intervals for the Two Age Groups as a Function of the Different Conditions.

Note. For all graphs, error bars represent one SE of the mean.
Figure 3.4.

Graphs Depicting Changes in Gait Velocity (bottom), Step Time (middle) and Step Length (top) for the Two Age Groups as a Function of the Different Conditions.

Note. For all graphs, error bars represent one SE of the mean.
3.4 Discussion

The aim of this study was to examine the effect chewing at various rates has on walking performance for healthy young and older adults. The results revealed that step rates (and hence walking speed) was strongly influenced by chewing rate, with both the young and older adults walking either faster or slower depending on the specified chewing rates. Interestingly, while the older adults tended to walk slower (i.e. slower velocity) compared to the younger adults, there were no differences in the average chewing rates as a function of age. This finding suggests that despite the widespread slowing of motor function seen with aging, mastication itself does not appear as affected by aging.

Impact of Chewing on Gait

A prominent finding from the study was that changes in the rate of mastication had a significant impact on stepping rates (and, consequently, gait velocity) for both the young and older adults. When individuals chewed at a faster or slower pace, their step rate changed in a similar, systematic fashion. As highlighted in figure 3.3, an individual’s step rate during walking was tightly linked to the rate at which they were chewing. While there would seem to be no doubt that the rhythmical action of chewing had a strong driving influence on an individual’s gait, the question of importance lies in the physiological basis for chewing driving a person’s gait. One possible explanation is that the greater neural input related to mastication (in comparison to the neural drive for muscles involved in walking) may effectively lead to coupling of step rate with chewing rates. Previous research has demonstrated that mastication is a complex motor process, arising from the combination of neuro-oscillatory output from central
pattern generators (CPG) within the pons and medulla (Kolta, Morquette, Lavoie, Arsenault, & Verdier, 2010), modifying inputs from higher motor centers of the CNS and sensory feedback from receptors within the face and mouth (Lund & Kolta, 2006; Westberg & Kolta, 2011). Furthermore, the masseter muscles (i.e. those involved in chewing) receive bilateral neural signals from both motor cortices (Nordstrom, 2007; Nordstrom et al., 1999), while the lower limb muscles central to walking only receive input from a single, contralateral hemisphere. Entrainment between these two motor processes would likely require some neural connections between the respective CPG’s. Previous research using animal models have reported projections from the spinal trigeminal nucleus to the cervical, thoracic, and lumbosacral levels of the spinal cord (Ruggiero et al., 1981) although it should be pointed out that similar projections have not been reported for humans. For humans, a more likely pathway could be the corticospinal tract as it has been reported that forceful (voluntary) clenching of the teeth can lead to increased excitability of the α motor neuron pool for muscles of both the upper and lower limbs (Boroojerdi et al., 2000; Sugawara et al., 2005). This increased excitability observed during teeth clenching, which was propagated through the corticospinal tract, was also reflected by enhanced reflex responses within the soleus (lower limb) and first dorsal interosseous (upper limb) muscles. Consequently, it may be that there is increased neural drive related to chewing in comparison to that seen for gait, thus leading to a coupling of a person’s step rate to chewing rates when the two tasks are performed simultaneously. The inference from this is that the descending drive for mastication may not only lead to excitation of the α motor neuron pool for muscles of both the upper and lower limbs but may actually entrain the muscle activity of the legs during walking. Irrespective of the underlying physiological mechanism, the results show
that changes in chewing speed tends to drive stepping rates (and hence gait speed) in both young and older adults.

**Age-Related Impact on Chewing**

Under the chewing only conditions, there were no differences in the average chewing rates for the young and older adults. The lack of any age-related differences in chewing rates is of interest given the general pattern of movement slowing commonly reported for other voluntary actions (S. Morrison & Newell, 2012; Morrison & Newell, 2017; Welford, 1984). For example, increasing age has been linked with declines in gait speed, slower rate of finger tapping, and increased reaction time (Cousins, Corrow, Finn, & Salamone, 1998; Himann, Cunningham, Rechnitzer, & Paterson, 1988; Welford, 1988; Williams, Hultsch, Strauss, Hunter, & Tannock, 2005). Indeed, in the current study, the older adults exhibited significantly slower walking speeds during both the chewing and non-chewing conditions, affirming the general view that gait speed declines with increasing age. The lack of any age-related differences in chewing rates across the various speed conditions may indicate that the control mechanisms underlying chewing are less affected by normal aging compared to the neuromotor processes responsible for lower limb movements.

Interestingly, the preservation of similar rates of chewing for the young and older adults did not extend to the pattern of intra-individual variability during chewing. For these measures, the chewing responses of the older adults were characterized by increased within-subject variability compared to the young participants. This increased variability provides evidence to support the view that changes in IIV measures may be a more sensitive biomarker of age-related decline
compared to average values (Lovden, Li, Shing, & Lindenberger, 2007; Newell, Incledon, Bodfish, & Sprague, 1999; Sosnoff & Newell, 2006).

3.5 Conclusion

The main findings of this study were that the rate at which a person chewed had a strong driving influence on the stepping rate (and hence walking speed) for both young and older healthy adults. One suggestion for this coupling is that, when performed simultaneously, the neural drive related to chewing entrains the muscles involved in the basic gait action of stepping. The coupling of stepping with chewing rates for both the young and older adults was observed despite overall age-related differences in walking speed. On this point, while the older adults tended to walk slower compared to the young adults, there were no differences in the average chewing rates as a function of age. This finding suggests that despite the widespread slowing of motor function seen with aging, mastication itself does not appear to be similarly affected by increasing age.
CHAPTER 4

EXPERIMENT TWO: AGE-RELATED CHANGES IN NEUROMOTOR FUNCTION
WHEN PERFORMING A CONCURRENT MOTOR TASK

4.1 Introduction

The normal process of aging is typically associated with a decline in the function of various physiological and behavioral processes. The consequences of this decline are widespread, affecting features such as attention, memory, strength, physical activity, and movement capability. Within the context of movement, these declines tend to impact the speed at which many movements are performed, with slower walking speed, reaction times, and tapping responses all being observed with increases in chronological age (Morrison & Newell, 2015; Newell et al., 2001; Newell et al., 2009). These age-related changes are most pronounced when movements are performed at a faster rate but can be less noticeable when performed at a person’s preferred movement frequency (Newell et al., 2006). The observation of slowing being more pronounced at faster rates has been described in the context as a generalized loss of the faster time scales of movement function (Sosnoff & Newell, 2008).

There are numerous reasons why movements may slow with increasing age. Within the muscles, the loss of fast-twitch muscle fibers, remodeling of motor units (Power et al., 2013), loss of cross-sectional area, reduction in overall muscle mass, and decreased force output by muscles (Jubrias et al., 1997) have all been reported. Additionally, within the nervous system, the loss of white and grey matter, slowed conduction velocity, decreases in neurotransmitters (e.g., dopamine), and breakdown in neural communication (Seidler et al., 2010) could also impact the speed of voluntary movements. Further, increases in cortex activation patterns over wider areas (especially the prefrontal cortex and basal ganglia) have also been noted with aging.
Ironically, the areas where there is increased neural activity are the same areas where neuronal loss tends to be greatest for the elderly (Seidler et al., 2010). This mismatch between increased neural activation and the loss of neurons/synapses, especially in areas closely related to motor control, may contribute to the pattern of overall slowing of movement associated with aging.

The general slowing of movements in older adults is often magnified under dual task conditions, where two activities are performed at the same time. The differences in performance have been attributed to age-related changes in utilization of attentional resources within the brain, especially executive function (Huxhold, Li, Schmiedek, & Lindenberger, 2006; Springer et al., 2006). For the majority of studies, dual tasking has involved performing a motor task simultaneously with a cognitive one (Al-Yahya et al., 2011; Schaefer & Schumacher, 2011). Surprisingly, less is known about the impact of performing two different motor tasks simultaneously in older adults. Previous studies have reported that walking is affected when simultaneously clapping (Muzii, Warburg, & Gentile, 1984) or finger tapping (Ebersbach et al., 1995) in healthy adults. More recently, it has been shown that chewing gum at different rates affects an individual’s walking patterns, with velocity and cadence changing to match the persons chewing frequency (Samulski et al., 2019). Interestingly, these effects were found for both healthy young and older individuals. The authors speculated that the coupling between chewing and walking were driven by parallel oscillators within the CNS with the rates set by the chewing oscillator driving stepping rates during walking. However, it is unclear whether the same pattern of coupling between chewing and other voluntary motor tasks would emerge in both young and older adults.
The current study was designed to investigate the following questions: 1) how aging affects the performance of chewing, reaction time, finger tapping, and gait, and 2) whether performing a concurrent motor task (i.e. chewing) would affect the speed of reaction time, finger tapping, and walking tasks. For question one, it was predicted that the healthy older adults would exhibit slower rates of movement for all actions other than chewing compared than their younger counterparts. For the second question, it was predicted that the specified chewing rates (i.e. slow, preferred, fast) would significantly affect the selected motor tasks for both the young and older adults.

4.2 Methods

Participants

Fifteen healthy young adults (average age 23.2±4.2 years) and fifteen healthy older adults (average age 66.5±3.2 years) participated in this study. A summary of demographic information for the participants is listed in Table 4.1. Individuals with orthopedic, neurological, cognitive, and/or arthritic conditions that would interfere with their ability to perform the study tasks were excluded. Participants provided informed written consent prior to inclusion in the study and all procedures complied with the university IRB guidelines.
Table 4.1.

Participant demographics.

<table>
<thead>
<tr>
<th>Item</th>
<th>Young adults (n=15)</th>
<th>Old adults (n=15)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (mean±SD)</td>
<td>23.2±4.2 years</td>
<td>66.5±3.2 years</td>
</tr>
<tr>
<td>Gender</td>
<td>11 female/ 4 male</td>
<td>12 female/ 3 male</td>
</tr>
<tr>
<td>Preferred right chewing side</td>
<td>10</td>
<td>9</td>
</tr>
<tr>
<td>Dominant right hand</td>
<td>10</td>
<td>14</td>
</tr>
</tbody>
</table>

Experimental Design

Demographic data relating to age, height, and weight were collected from each participant prior to data collection. In addition, individuals were asked to specify their preferred chewing side.

Effect of Age on General Motor Function

To address the first question, individuals were instructed to perform a series of motor tasks including chewing, simple reaction time, finger tapping, and gait. None of the participants were asked to multitask during this part of the protocol. Participants of all ages performed each singular task to understand how aging affects motor performance. Details of these tasks are as follows:

Chewing

Chewing was initially performed a single task at three different speeds. The following three chewing conditions were performed: 1) self-selected/preferred chewing speed, 2) slow chewing
speed (1 Hz), and 3) fast chewing speed (2 Hz). Three trials were completed for each chewing condition. Individuals performed the chewing tasks while in a seated position. Participants were given a single piece of spearmint Trident gum during all chewing trials to standardize chewing consistency (Wintergerst, Throckmorton, & Buschang, 2008). A preferred chewing side was specified by individuals at the start of the study and participants were encouraged to chew on that side of the mouth for all recorded trials.

For the fast and slow chewing conditions, an auditory metronome was used to set the respective pace prior to recording. The fast and slow chewing rates were selected based on previous investigations (Bellisle, Guy-Grand, & Le Magnen, 2000; Samulski et al., 2019). Participants practiced chewing to the metronome beat for up to one minute. Once the individual demonstrated they could chew at the specified rate, the metronome was turned off and data collection commenced. All single task activities were recorded after the metronome had been stopped.

Surface electromyography (EMG) activity of the masseter muscle was used to determine chewing rates. All EMG activity was recorded using the Delsys Trigno system (Delsys, Boston, MA) at a sample rate of 2000 Hz. The EMG sensor was positioned over the belly of the masseter muscle on the dominant chewing side as determined by the participant at the start of the session. Processing of the EMG data was performed using custom software developed in MATLAB (MathWorks R14). EMG signals were down-sampled to 1000 Hz, rectified, and filtered using a second-order low-pass Butterworth filter with a 400 Hz cut-off frequency. The chewing frequency was determined by visualizing the peaks of the signal and using a custom MATLAB algorithm to count the peaks over the length of the specific trial.
**Reaction Time**

Participants completed a simple reaction time (RT) task where responses from the index finger were collected. All responses were performed with the individual’s preferred limb. Each person was told to press a button as quickly as possible after the visual stimulus was presented. After completing 5 practice trials, each person completed 20 recorded trials for each condition. Prior to analysis, RT data were trimmed by eliminating those trials which were completed in 150 ms or less (Bauermeister et al., 2017).

**Finger Tapping**

All participants completed a tapping task using the index finger of their preferred arm. Each person performed the task in a seated position with their forearms resting on a table. Individuals were asked to tap at a preferred and maximal speed. Participants tapped a Delsys triaxial accelerometer secured to the top of a table to collect tapping rates. Three 20-sec trials were performed for each condition. Tapping acceleration data was collected at 148 Hz using the Delsys Trigno system (Delsys, Boston, MA). Analysis of the acceleration (i.e. tapping) data was performed using MATLAB. The acceleration signals used to determine finger tapping rates were filtered using a second-order low-pass Butterworth filter with a cutoff frequency of 40 Hz. Determination of the tapping rates was attained using a custom written MATLAB algorithm. This algorithm calculated the number of peaks of the accelerometry signals with 50% of trials being visually inspected to verify the accuracy of the algorithm.
**Gait**

Individuals were instructed to walk at their preferred speed for four trials. Timing gates were positioned at the beginning and end of the walking path to record overall walking time. Four walking trials were collected. Spatiotemporal measures of gait were collected using a 20-foot Zeno pressure sensitive walkway (Protokinetics, Havertown, PA, sample rate: 120 Hz). The dependent measures collected included gait velocity, step length, and step cadence.

**Age-Related Effects of Chewing on RT, Gait, Balance and Tapping**

To address the second question, all persons performed the same reaction time, tapping, and walking tasks while chewing. Further, for this part of the experiment, persons were instructed to chew at different rates (i.e. preferred, faster, and slower speed). An auditory metronome was used to set the fast and slow chewing paces prior to recording. Participants were given up to one minute to practice chewing to the metronome rhythm before the metronome was turned off and the trial performance was recorded. All dual task activities were recorded after the metronome had been stopped.

The movement speed during the reaction time, tapping, and walking tasks while chewing was all self-selected. Comparisons were made between all chewing conditions, as well as the non-chewing (control) condition to investigate the effects of chewing on performance of various motor tasks. Specific details of the movements performed are as follows:

**Reaction Time**

Individuals performed the simple RT task as previously described while chewing at each of the three designated chewing speeds (i.e. self-selected/preferred, slow (1 Hz), and fast chewing
speed (2 Hz)). All responses were performed with the individual’s preferred limb and all chewing on the individual’s preferred chewing side. Each person completed 5 practice trials, followed by 20 recorded trials for each condition. As previously described, the RT data were trimmed by eliminating those trials which were 150 ms or less.

**Finger Tapping**

All participants completed a tapping task using the index finger of their preferred arm as previously described (i.e. preferred and fast tapping rates) while chewing and not chewing. All tapping was performed with the individual’s preferred limb and all chewing on the individual’s preferred chewing side. Three 20-sec trials were performed for each condition.

**Gait**

Individuals were instructed to walk at their preferred speed while chewing at each of the three designated chewing speed conditions as previously described. All chewing was performed on the individual’s preferred chewing side. All gait patterns were self-selected by the participant for each trial. Participants completed four walking trials for each of the chewing conditions.

**Statistical Analysis**

Statistical analyses were structured to address the previously outlined questions, namely: 1) how does aging affect the performance of chewing, reaction time, finger tapping, and gait, and; 2) does simultaneously chewing affect an individual’s reaction time, finger tapping, and walking performance. Descriptive statistics (mean ± standard deviation) were calculated for chewing, reaction time, finger tapping, and gait measures.
For question 1, a repeated-measures mixed generalized linear model (GLM) was used to assess for differences in the selected chewing, reaction time, finger tapping, and gait measures. Differences were assessed as a function of age (young, old).

For question 2, a repeated-measures mixed GLM was used to assess for differences in the reaction time, finger tapping, and gait measures as a function of chewing condition (i.e., preferred, slow, fast, no-chewing) and age (i.e., young and old). Significant interaction effects were investigated with planned contrasts using one-way mixed ANOVA. All tests were performed using SAS statistical software (SAS Institute Inc., Cary, NC) with a significance level of $p<0.05$.

4.3 Results

Effect of Age on General Motor Function

**Chewing Rates.** The rates for the preferred, slow, and fast conditions were $1.14 \pm 0.11$ Hz, $0.98 \pm 0.10$ Hz and $1.97 \pm 0.12$ Hz, respectively. For this data, there was a main effect for condition ($F_{2,56}=2656.47, p<0.0001$). Planned contrasts revealed that significant differences were found between all three chewing speeds. No main effects for age or condition by age interaction effects were observed ($p>0.30$). Figure 4.1 illustrates the differences in the average chewing rates, reaction times and tapping rates for the young and older adults. For chewing, mean rates are shown for the slow, preferred, and fast conditions.
**Reaction time.** For the mean group RT responses, there was a significant age effect ($F_{1,112}=19.78, p<.0001$) with older participants having significantly slower reaction times compared to the younger participants. The mean reaction time for the young and older adults were $228 \pm 64$ ms and $246 \pm 68$ ms, respectively.

**Finger Tapping.** There was a significant difference in rates during the fast tapping condition only between the young and older adults ($F_{1,112}=6340.17, p<0.001$). For this condition, the young adults tapped at a faster maximal rate ($5.22 \pm 0.89$ Hz) compared to older adults who tapped at a slower maximal rate ($4.77 \pm 0.97$ Hz). No age-related differences were observed for the preferred tapping tasks (old: $2.89 \pm 1.19$ Hz, young: $3.04 \pm 1.73$ Hz).
Figure 4.1.
Average Rates for Chewing (A), Reaction Time (B), Finger Tapping (C), and Walking Velocity (D) For the Young and Older Adults.

Note. For chewing, mean rates are shown for the slow, preferred, and fast conditions. For tapping, average rates for the preferred and fast tapping conditions are shown. For all graphs, error bars represent one SD of the mean. Significant age differences are denoted with an asterisk (*) and significant condition differences are denoted with a hash mark (#).
Gait. Significant group effects were noted for both gait velocity ($F_{1, 112}=10.07, p<.001$) and step length ($F_{1, 112}=13.97, p<.001$). Overall, the older individuals walked slower (old: $128.60 \pm 16.5$ cm/s, young: $138.28 \pm 16.96$ cm/s) with decreased step length (old: $67.39 \pm 6.60$ cm, young: $71.75 \pm 6.19$ cm) compared to the younger adults.

Age-Related Effects of Chewing on RT, Gait, Balance and Tapping

Reaction Time and Chewing. For the average group RT responses, there was a significant age-by-condition interaction effect ($F_{3, 78}=8.16, p<.0001$). Planned contrasts demonstrated that the older participants had significantly slower reaction times compared to the younger participants. In addition, significant differences were found between the preferred and no chewing (control) conditions compared to the slow or fast conditions. For these comparisons, there was a slowing of reaction time during the paced chewing conditions (i.e. slow or fast chewing) compared to the other conditions (all $p$’s<0.001). The differences in the reaction time data as a function of age group and chewing condition is highlighted in Figure 4.2.
Figure 4.2.

*Figure Illustrating the Effect of Chewing on Reaction Time for Both Young and Older Adults.*

![Bar graph showing the effect of chewing on reaction time for both young and older adults.](image)

*Note.* Average values for simple reaction time are shown across the four conditions. For all graphs, error bars represent one SD of the mean. Significant age differences are denoted with an asterisk (*) and significant condition differences are denoted with a hash mark (#).
**Finger Tapping and Chewing.** Due the inherent differences in speed, analysis of the tapping data was performed for the fast and preferred speed conditions separately. For the preferred tapping speed task, no significant effects for chewing conditions or age were observed (p>0.10). However, for the fast tapping task, significant main effects for age group (F_{1,28} = 4.60; p<0.05) and chewing condition (F_{3,28} = 11.15; p<0.01) were observed. For the age effect, subsequent analysis revealed that the older adults were slower than the young persons (young=4.95±1.73 Hz, old=4.41±1.36 Hz). For the condition effect, the tapping rates for all individuals decreased significantly when they chewed compared to tapping rates when persons did not chew (all p’s <0.05). Figure 4.3 shows the pattern of results for the young and older adults when chewing and finger tapping were performed together.

**Chewing and Walking.** A significant age-by-condition interaction effect was observed for both gait velocity (F_{3,83}=3.69, p=0.02) and step cadence (F_{3,83}=4.40, p=0.01). Subsequent analysis demonstrated that both measures changed significantly with the designated chewing rates. For example, slower chewing was associated with slower gait speed and slower cadence while fast chewing was associated with faster gait speed and faster cadence. Further, older adults walked with a slower speed and a slower step cadence than younger adults during the slow chewing condition.

A significant condition effect for step length was also observed (F_{3,83}=25.48, p<.0001) with planned contrasts revealing that significantly shorter step lengths were taken during slow chewing compared to the control and other chewing conditions. No significant main effects for age were observed for step length (p>0.08). Figure 4.4 displays the pattern of results for the gait data as a function of age group and chewing condition.
Figure 4.3.  

*Mean Finger Tapping Frequency for the Preferred (top) and Fast (bottom) Tapping Tasks.*

**Preferred Tapping**

![Preferred Tapping Graph]

**Fast Tapping**

![Fast Tapping Graph]

*Note.* Both age groups are visualized across chewing and non-chewing conditions. For all graphs, error bars represent one SD of the mean. Significant age differences are denoted with an asterisk (*) and significant condition differences are denoted with a hash mark (#).
Figure 4.4.

Changes in Selected Gait Metrics (e.g., Step Cadence, Velocity, and Step Length) for Both Age Groups Across All Chewing Conditions.

Note. For all graphs, error bars represent one SD of the mean. Significant age differences are denoted with an asterisk (*) and significant condition differences are denoted with a hash mark (#).
4.4 Discussion

The current study was designed to investigate: 1) how aging effects the performance of chewing, reaction time, finger tapping, and gait, and 2) whether simultaneous chewing would affect an individual’s reaction time, finger tapping, and gait. Overall, the results demonstrated that the healthy older adults performed the majority of motor tasks slower as compared to the younger adults. No differences between the two age groups were seen during the chewing only task. Further, chewing while performing an additional motor task led to changes in the speed of the secondary movement. Specifically, walking, and finger tapping rates increased or decreased in line with the designated chewing rate (i.e. fast, slow) while reaction times were consistently slower when chewing concurrently, irrespective of the speed at which the person chewed.

Changes in General Neuromotor Function with Age

The results from our study support the view that older adults tend to perform voluntary movements at a slower speed compared to young adults. More specifically, older adults walked at a slower pace, tapped at a slower frequency, and had increased (i.e. slower) simple reaction times in comparison to the younger individuals. For these measures, the results of the current study are consistent with previous research which have reported similar declines (Morrison & Newell, 2015; Newell et al., 2001; Newell et al., 2009). For gait, the slowing was driven by changes in step frequency and step length. Older adults took shorter steps, but exhibited similar stepping cadence to their younger counterparts, a finding consistent with previous studies (Maki, 1997; Samson et al., 2001; Winter et al., 1990). Physiologically, the slowing of movements has also been related to numerous changes which span both muscle and the nervous system. Additionally, the age-related changes in gait, tapping, and RT have also been linked to older
adults adopting a different, more conservative strategy during the specific movement task. During walking, older adults may employ this strategy to improve postural stability (Shkuratova, Morris, & Huxham, 2004) while for the RT and tapping tasks, older persons tend to prioritize accuracy over speed of movement within increasing age (Alexander, Ashton-Miller, Giordani, Guire, & Schultz, 2005). The consequences of adopting such a movement strategy is commonly manifested by slower movements.

However, this general pattern of slowing was not observed for all motor tasks performed, with the chewing rates being the same for both age groups. This result would appear to indicate that the motor task of chewing was less affected by the aging process, as there was no difference between the young and older adults irrespective of the designated chewing speeds selected. Typically, the pattern of slowing is more prominent when the older adults participate in motor activities that require performance at faster than preferred speeds.

The slowing of movements seen with aging has typically been linked with changes in neuromuscular function. For example, decreases in muscle cross-sectional area, reduction in muscle mass, increases in the variability of motor unit (MU) firing, atrophy and/or remodeling of fast twitch MU, and a decline in the number of alpha motor neurons (Erim, Beg, Burke, & de Luca, 1999; Morrison & Newell, 2012). The consequences of these muscle changes include a decrease in the rate at which a particular movement can be performed coupled with a decline in strength. However, the finding that chewing rates are not different between the two groups indicates that the general pattern of age-related changes in movement performance may not apply to the task of chewing. Indeed, based on function, it is plausible to expect differences to exist between masticatory and limb muscles as there are key neural and structural differences between muscles of mastication and muscles underlying trunk and limb control. The masseter, a
primary masticatory muscle, receives bilateral innervation from the brain which provides
tautology, thus increasing resilience against disease and effects of aging. In contrast, the muscles
of the upper and lower limbs receive neural input from a single hemisphere.

Further, there are inherent differences in the actual muscle architecture between those
involved in chewing compared to muscles which play a role in upper and lower limb movements.
Briefly, the muscles of mastication tend to have a greater proportion of Type II (fast-twitch)
fibers compared to muscles of the appendages. Further, the distribution of the fibers within the
specific muscles is also different, with the Type II fibers in the masseter/temporalis muscles
being grouped together rather than dispersed (Eriksson & Thornell, 1983). In contrast, the fibers
for the muscles of the upper and lower limbs tend to be organize in a mosaic pattern (Jennekens,
Tomlinson, & Walton, 1971). Consequence of these neural and structural differences is that the
masticatory muscles are able to exhibit finer force gradation as well greater control of fine
movements (Hannam & McMillan, 1994). These differences may describe why chewing rates
are more resilient to the effects of chronological aging than finger tapping, reaction time, and
gait.

Effect of Chewing on Secondary Motor Task Performance

To date, there has been considerable research conducted assessing the influence of
performing a cognitive and motor task simultaneously (Azadian, Torbati, Kakhki, & Farahpour,
2016; Bond & Morris, 2000; Hollman et al., 2007; Pashler, 1994; Riby, Perfect, & Stollery,
2004; Simoni et al., 2013), less emphasis has been on investigating the impact of performing two
motor tasks concurrently. One assumption would be that performing two motor tasks
simultaneously would lead to a similar pattern of performance decrement in the secondary task
(Oh-Park et al., 2013). Alternatively, performing one task may entrain the other movement—similar in context to performing the action of tapping your head while simultaneously rubbing your stomach (Ridderikhoff, Peper, & Beek, 2006; Smyth, Collins, & Morris, 1994). Previous research has shown that the second explanation would appear to persist when walking while chewing (Samulski et al., 2019). In our previous study, we reported that stepping rates increased or decreased in line with increases/decreases in chewing rates. Several of the results of the current study support this view, with chewing altering the performance of the secondary motor tasks. Briefly, gait and finger tapping were tightly coupled to the chewing, with the respective rates increasing or decreasing with similar changes in chewing rates. For gait, the average stepping rate for healthy adults is 1.8 Hz, whereas the mean chewing rate for healthy adults is approximately 1.2-1.3 Hz (Buschang, Throckmorton, Travers, & Johnson, 1997; Sekiya & Nagasaki, 1998). When individuals chewed at a slower pace (i.e. 1.0 Hz), stepping cadence decreased whereas when chewing was performed at a faster pace (i.e. 2.0 Hz), an increase in stepping cadence emerged. A similar pattern of results was observed for the influence on finger tapping where all tapping rates were driven down during the specific chewing condition. It should be noted that the fastest tapping rates were significantly higher (e.g. 5.22 ± 0.89 Hz for young adults and 4.77 ± 0.97 Hz for older adults) than the persons preferred chewing rates (e.g. 1.13 ± 0.11 Hz on average for young and older adults). These tapping rates dropped notably (e.g. 4.95 ± 0.89 Hz for young adults and 4.41 ± 0.52 Hz for older adults) when chewing for both the young and older adults.

However, this pattern of entrainment was not evident for all tasks assessed with chewing appearing to have a detrimental effect of the secondary movement task performance. Most notable was the reaction time responses which slowed significantly while chewing (e.g. from 257
+ 77ms to 290 + 86ms), irrespective of the actual chewing rates selected. What this result illustrates is that chewing can have a detrimental effect on secondary movement performance although the immediate effects would appear to be task dependent. One possible explanation is that chewing - a cyclical action - would entrain the performance of other rhythmic actions like tapping and walking. Alternatively, performing a rhythmic chewing action negatively affects the performance of more discrete, time dependent actions (i.e. reaction time).

Overall, the contrasting effects of chewing on reaction time, finger tapping, and gait indicates that a traditional dual task paradigm does not fully describe the observed behaviors for these concurrent motor tasks. Previous studies investigating the coordination dynamics of bimanual finger tapping assert that performing two motor tasks may not always result in an interference phenomenon. The rhythmic movements of the two fingers are controlled by coupled neural oscillators and despite perturbations to tapping, the resultant movements often return to one of two stable rhythms (Yamanishi et al., 1980). The timing of the two motor tasks is key to eliciting a coupling effect (Klapp, 1979). Investigating movements performed together using a coupled oscillator approach may augment understanding of coordination patterns and mechanisms behind simultaneous performance of two rhythmic motor tasks.

**Limitations**

While the results of this study demonstrate important differences between young and older adults with regards to slowed patterns of performance during motor tasks, there are limitations that should be considered when interpreting the findings. One limitation was that there were unequal representations of gender, hand dominance, and preferred chewing side in the sample. The effect of gender on chewing performance is yet unknown. There have been small documented differences in simple reaction time between the genders that is narrowing with each
generation (Der & Deary, 2006; Silverman, 2006). Future investigations should reflect a more even distribution of both genders. The effects of hand dominance and preferred chewing side on the studied motor tasks also remains unclear. There has been no clearly described relationship between hand dominance and chewing side preference (Martinez-Gomis et al., 2009). Chewing side preference appears to be centrally selected (Nissan, Gross, Shifman, Tzadok, & Assif, 2004). A metronome was used to manipulate and set slow and fast chewing speeds. To minimize the effect of the metronome on outcomes, it was turned off prior to all data collection for each trial. Despite efforts to limit the effect of the metronome during the dual task activities, it could have influenced the findings of the study as participants were asked to match chewing to an external auditory stimulus. Subsequent investigation would eliminate the metronome to allow participants to freely chew at self-selected fast and slow rates to better understand natural chewing patterns and eliminate any influence of additional auditory cues.

4.5 Conclusion

The findings illustrated that healthy older adults walked slower, tapped slower, and had slower reactions times compared to young healthy adults. The one exception was for the motor act of chewing where no differences between the two age groups were found. The basis for these differences would appear to be neuromuscular in origin, with evidence pointing to greater age-related preservation of muscular and neural function related to chewing compared to the other motor tasks. In regard to the second question, chewing affected the performance of secondary motor tasks for all individuals, irrespective of age. More specifically, for cyclical actions (i.e. tapping, gait), the speed of the secondary movement changed in accordance with the designated chewing rate suggesting entrainment. The strong coupling between chewing and the gait/finger
tapping actions probably reflects some level of entrainment between the respective oscillators driving the respective actions. In contrast, RT responses slowed appreciably irrespective of the chewing rates performed, indicating that chewing interfered with the timing of the RT response. Taken together, these results illustrate the contrasting effects of chewing on a secondary motor tasks highlighting that a traditional dual task view does not fully describe the observed behaviors for these concurrent motor tasks.
CHAPTER 5

EXPERIMENT THREE: INFLUENCE OF TIMING ON CHEWING AND WALKING

5.1 Introduction

The human body exhibits many instances of self-organizing systems of coupled oscillators including the rhythmic coordinated beating of heart muscles, the coordination of breathing and swallowing movements, as well as the coordination of the limbs during walking. Gait patterns of animals have been shown to be heavily influenced by the self-organization of central pattern generators (CPGs) for each of the limbs located in the thoracolumbar section of the spinal cord (Duysens & Van de Crommert, 1998; Grillner, Brodin, Sigvardt, & Dale, 1986). Humans also have CPGs that influence gait patterns, but these are less developed in comparison to animals. People have also developed a bipedal gait pattern which allows for differentiation of movement between the upper limbs and lower limbs. The primary function for the lower limbs is related to walking and general locomotion, whereas the upper limbs are more commonly used to perform a range of discrete manipulation tasks. This evolution in coordination between the limbs is also associated with more corticospinal control of limb patterns in humans (Capaday, Lavoie, Barbeau, Schneider, & Bonnard, 1999; Schubert, Curt, Jensen, & Dietz, 1997). Descending drive from the cortical areas of the CNS interacts with the spinal CPGs to facilitate and fine tune voluntary control of gait. Cortical control of locomotion is most evident when sensory information indicates that gait behaviors must be modified to address challenges in the environment or of the task. Walking on more regular surfaces (i.e. flat, open, and firm) is likely to require less cortical resources than walking in an environment with narrow passages or uneven surfaces. Despite the major influence of higher motor centers on human gait, there is evidence that leg muscles are differentially activated when the limb is in different positions due to a
physiological phase-link in gait (Schubert et al., 1997). A major functional underpinning of the phase-linked movements is to maintain optimal balance during walking (Dietz, 2003).

Much like gait, the control of chewing is also believed to be driven by bilateral neural CPGs in combination with descending drive from the higher motor centers. Cortical involvement in the control of chewing is more evident when the size or consistency of the bolus is dynamic. The CPGs for chewing are located in the pons and medulla, rather than the spinal cord (Kandel et al., 2000; Lund & Kolta, 2006). Interestingly, chewing also exhibits phase-linking behavior. Rather than being related to postural stability, the phase-linked movements are thought to prevent injury to dentition (Lund et al., 1983). As gait and chewing are generally believed to share similar neural control, it is possible that chewing and walking movements may naturally entrain when performed concurrently. Previous research has demonstrated that chewing can influence the performance of a secondary movement but there appears to be a degree of task dependency to this relation. For example, chewing tends to interfere with performance of discrete motor tasks (i.e., reaction time), but entrains with other cyclic tasks to enhance performance of both tasks (Samulski, Prebor, Armitano-Lago, & Morrison, 2020).

Aging has been characterized by a general slowing of the neuromotor system related to a number of physical and functional changes in the body. Previous studies have indicated that chewing and walking patterns do entrain, regardless of age (Samulski et al., 2019). Preferred and maximal gait velocity slows with age, whereas chewing appears more resilient against the effects of aging. The influence of slowed gait patterns on the interaction of chewing and walking should also be considered, especially if stepping rates have the potential to drive the coupled movement.

In many studies, chewing rates have been set with an external stimulus (i.e., auditory metronome cue) so there is little known about natural chewing and stepping patterns that emerge
when each movement is performed individually or together. Previous research has reported that rhythmic movements that entrain interact in one of three ways: combining to form an entirely novel rhythm with components of both maintenance tendencies, competing and adjusting to the stronger maintenance tendency, or cooperating to form a new hybrid frequency (Von Holst, 1937). Chewing appears to influence walking by acting as a dominant maintenance tendency that drives coupling when chewing is introduced first (Samulski et al., 2019). The dominance of the chewing pattern when it is initiated after walking has not been tested. It is possible that the strong influence of chewing noted in previous research may have been due to the timing of when chewing was initiated.

This study was designed to examine the influence of chewing on step rates when chewing is initiated after walking. It was predicted that chewing will affect the stepping rates regardless of when it is initiated relative to the walking task. Specifically, it is hypothesized that chewing does not need to occur prior to initiation of walking to influence the stepping rate. When chewing is initiated prior to walking, previous research has shown that the stepping rates change in accordance with the chewing rates (i.e., faster chewing rates are associated with faster step rates, and vice versa for slow chewing). Replication of these previous findings is expected for the chewing-before-walking task. Describing the effect of chewing on stepping when chewing is introduced mid-walk or is eliminated after performing concurrent chewing and walking will be the focus of the other two tasks.
5.2 Methods

Participants

Fifteen young adults (24.5 ± 4.6 years) and fifteen older adults (66.3 ± 3.8 years) participated in this study. Information on participants’ age, height, weight, and preferred chewing side was collected. Patients were excluded from the study if they had orthopedic, neurological, cognitive, arthritic conditions or loss of vision or hearing that interfered with their ability to walk or chew gum safely. Written consent was obtained prior to inclusion in the study. All procedures complied with university IRB guidelines.

Experimental Design

Participants were asked to participate in tasks that varied the timing of when chewing or walking were initiated. There were three tasks: chewing-before-walking, walking-before-chewing, and concurrent chewing and walking. Within each of these tasks, chewing speed was also manipulated. Volunteers chewed at slow, preferred, and fast rates for each of the tasks. For all trials, chewing pace was not set by external cues other than the verbal direction to “chew slowly” for the slow pace, “chew at your most comfortable pace” for the preferred pace, and “chew as fast as you can” for the fast pace. All participants were given a piece of Trident gum to standardize chewing consistency and were asked to specify a preferred chewing side at the start of the study (Wintergerst et al., 2008). They were then instructed to chew primarily on that side during all trials. Participants were able to exchange the gum bolus between each trial; however, bolus size was kept consistent across all trials. All walking was performed at a self-selected speed. This resulted in an overall design of nine task-condition combinations, in addition to a
Table 5.1.
*List of All Baseline and Task-Condition Combinations That Were Measured.*

<table>
<thead>
<tr>
<th>Combinations</th>
<th>Task</th>
<th>Condition</th>
<th>Number of trials</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(timing of chewing or</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>walking initiation)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B1: Chewing baseline</td>
<td>Chewing only</td>
<td>Slow Chewing</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Preferred Chewing</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fast Chewing</td>
<td>3</td>
</tr>
<tr>
<td>B2: Walking baseline</td>
<td>Walking only</td>
<td>None</td>
<td>3</td>
</tr>
<tr>
<td>T1: Chewing first</td>
<td>Chewing-before-walking</td>
<td>Slow Chewing</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Preferred Chewing</td>
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<td></td>
<td></td>
<td>Fast Chewing</td>
<td>3</td>
</tr>
<tr>
<td>T2: Walking first</td>
<td>Walking-before-chewing</td>
<td>Slow Chewing</td>
<td>3</td>
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<td></td>
<td></td>
<td>Preferred Chewing</td>
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<tr>
<td></td>
<td></td>
<td>Fast Chewing</td>
<td>3</td>
</tr>
<tr>
<td>T3: Chewing elimination</td>
<td>Chewing and walking</td>
<td>Slow Chewing</td>
<td>3</td>
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<tr>
<td></td>
<td></td>
<td>Preferred Chewing</td>
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<td></td>
<td></td>
<td>Fast Chewing</td>
<td>3</td>
</tr>
</tbody>
</table>

*Note.* Number of trials collected for each combination noted.
chewing only control condition and walking only control condition. Three trials were collected for each task-condition combination, resulting in a total of 45 trials for each participant. Each of the task-condition combinations are listed in table 5.1 for clarity.

**Chewing only.** Individuals were asked to stand quietly and chew gum for three 30-second trials at three different self-selected speeds (slow, preferred, and fast) to obtain baseline chewing measures. None of the participants were asked to multi-task during the baseline chewing task. All subsequent trials involving chewing were collected using the same methods.

**Walking only.** To collect baseline walking data, individuals were asked to walk a distance of 90 feet on a flat, straight surface. In the center of the walking path was a 20-foot pressure-sensitive walkway (Protokinetics, Haverstown, PA). Participants were asked to walk at a self-selected pace for all trials. Timing gates were positioned at the beginning and end of the walking path to record overall walking time. Accelerometry data was collected using the Delsys triaxial accelerometers which were placed on the head, neck, low back (L3 spinous process), and bilateral lower leg (distal Achilles tendon) per previous research (Armitano, Morrison, & Russell, 2017). All subsequent trials involving walking were collected using the same methods. Figure 5.1 depicts a diagram of the walkway set-up for all trials in the study.
Figure 5.1.

Diagram of Walkway Set-up For All Measured Trials.

Note. Location of where participants were cued to start or stop a task are noted for each task.

Abbreviations: B2 = Walking only baseline task, T1 = Chewing-before-walking task, T2 = Walking-before-chewing task, T3 = Chewing and walking, then stopping chewing mid-walk.
**Chewing-before-walking task.** Participants were asked to begin chewing for at least 15 seconds, then cued to walk for 50 feet at their preferred speed. Chewing patterns were collected via EMG, and walking was recorded via accelerometry and pressure-sensitive walkway as previously described. All chewing was performed at self-selected, but varied speeds based on the cue to chew slowly, at a preferred speed, or as fast as possible to reflect the slow, preferred, and fast chewing conditions, respectively. All walking was performed at a self-selected speed.

**Walking-before-chewing task.** Participants were asked to hold their gum under their tongue or in their cheek until cued by the researcher to begin chewing mid-walk. The researcher verbally cued the participant walk 40 feet without chewing, then told to begin concurrent chewing and walking for the remaining 50 feet. The participant did not stop walking once chewing began. Chewing patterns were collected via EMG, and walking patterns were recorded via accelerometry and a pressure-sensitive walkway as previously described.

**Concurrent chewing and walking task.** Participants were asked to begin chewing and walking at the same time for 40 feet, then verbally cued by the researcher to stop chewing mid-walk. The participant then walked the remaining 50 feet of walkway and did not stop walking when the chewing was stopped. Chewing patterns were collected via EMG, and walking was recorded via accelerometry and pressure-sensitive walkway as previously described. All chewing was performed at self-selected speeds based on the cue to chew slowly, at a preferred speed, or as fast as possible to reflect the slow, preferred, and fast chewing speeds, respectively. All walking was performed at a self-selected speed.

For each of the task-condition combinations, chewing rates and stepping rates (step cadence) were calculated by taking the number of signal peaks over a time period. Chewing frequency and stepping frequency were calculated for all trials based on the accelerometry (stepping) and EMG
(chewing) data. For the task timing trials, chewing and stepping frequencies were calculated for the first half and second half of the trial to reflect changes in the movement patterns before and after introduction or removal of chewing or walking based on the relevant trial. Accuracy of calculated stepping frequency was verified by comparing data to cadence measures from the pressure-sensitive mat. The following statistical analyses were performed on the calculated chewing and stepping frequencies.

Statistical Analysis

A 2-way mixed design analysis of variance (ANOVA) was used to assess differences in step rate between the two age groups, the two parts of the walk (first half, second half) and as a function of the chewing speed (slow, preferred, fast). Separate analyses were done for each of the tasks. Using step rates from the first and second half of the walking trial allowed for comparison of stepping rates when chewing was either added or stopped. Mauchly’s test was used to assess sphericity of each model. If sphericity was not met, an epsilon adjustment was made by using the Greenhouse-Geisser corrected value to avoid a type 1 error. Bonferroni post-hoc comparisons were used to determine significant differences between step rates for each chewing speed condition. All tests were performed using SPSS statistical software (IBM, New York, NY) with a significance level of \( p<0.05 \).

5.3 Results

**Chewing-before-walking task.** The mean stepping rate at baseline (i.e. not chewing) was \( 1.87\pm0.13 \) steps per second for the young adults and \( 1.82\pm0.15 \) steps per second for the older individuals (\( p>0.10 \)). A comparison of the stepping rates while chewing and not chewing reveal a
Figure 5.2.

Changes in the Mean Step Rates From Baseline Walking Condition and During the Chewing-Before-Walking Condition Task.

Note. Data are shown for both the young and older adults. Error bars denote one SD of the mean.
significant time-by-condition interaction, (F_{1,26.31.542}=16.798, p<.001). The step rates while chewing were significantly different from the step rates when not chewing and are shown in Figure 5.2. Contrasts revealed that participants had slower step rates when chewing slowly and had faster step rates when chewing quickly (p<.005) compared to step rates during single task walking.

**Walking-before-chewing task.** Pre-chewing stepping rates were significantly slower than the stepping rates while chewing (F_{1,28}=27.228, p<.001). The changes in step rate for the walking before chewing task are shown in Figure 5.3. There were significant main effects for chewing speed (F_{2.56}=22.071, p<.001) on step rates. Contrasts revealed that the step rates during the fast chewing condition were significantly faster than the slow and preferred chewing conditions (p<.005). No age-by-condition interaction effects were noted.

**Chewing and walking task.** Step rates were significantly faster after chewing was stopped compared to step rates during the concurrent chewing and walking portion of the task, (F_{1,28}=19.38, p<.001). Differences in the step rate while performing the dual task (chewing and walking) and the single task (walking) are displayed in Figure 5.4. There was a significant condition effect for chewing speed condition on step rates (F_{2.27}= 24.375, p<.001). Contrasts revealed that stepping rates during the fast chewing condition were significantly faster than during the preferred and slow chewing conditions, (p<.005).
Figure 5.3.

Mean step rates during walking before chewing task.

Note. Data are shown for both the young and older adults. Error bars denote one SD of the mean.
Figure 5.4.

Mean step rates during chewing and walking task.

Slow Chewing, Young

Preferred Chewing, Young

Fast Chewing, Young

Note. Data are shown for both the young and older adults. Error bars denote one SD of the mean.
5.4 Discussion

The aim of the current study was to examine whether chewing influences stepping rates based on when it is begun relative to the walking task. Overall, the results demonstrated that chewing changes stepping rates regardless of when it occurs. Differences in step rates between each of the chewing conditions for all tasks also confirms an oromotor connection to gait timing. When chewing occurred first, the step rate increased for all conditions except the slow chewing condition which slowed step rates. This effect supported previous findings (Samulski et al., 2019) and confirmed that the coupling effect emerges even in the absence of an auditory metronome. When walking occurred first either as a single or dual task, step rates increased during the subsequent walking period. Interestingly, when chewing is removed from walking, step rates still increase.

A central finding from the study was that changes in chewing rate significantly impacted on stepping rates for both the young and older adults. For example, step rates declined when individuals chewed at a slower rate. Conversely, step rates increased when persons chewed at a faster rate. This finding validates the influence of chewing on gait patterns and points to a flexible “top-down” organization of the movement patterns. Given the entrainment relationship between chewing and walking, it is likely that there is an underlying physiological connection between their timing structures. The rhythmical characteristics of chewing are driven by neural oscillators (central pattern generators or CPGs) within the pons and medulla (Kolta, Morquette, Lavoie, Arsenault, & Verdier, 2010). Similar cyclical characteristics of gait are also influenced by CPGs or oscillators in the spinal cord (Takakusaki, 2013). The results of the current study seem to indicate that there is a clear interplay between these two oscillatory centers, but that the CPGs in the hindbrain related the chewing more strongly influence the centers in the spinal cord
than vice versa. The chewing rate appears to drive the stepping rate regardless of when it is introduced. Stepping rates consistently speed up or slow down based on similar changes to chewing rate.

One explanation may be that biting or chewing has a neuromodulatory effect on the pyramidal tracts which include the corticobulbar and corticospinal tracts. It has been shown that sustained clenching of the teeth can lead to increased excitability of the alpha motor neurons of the muscles for the limbs (Boroojerdi et al., 2000; Miyahara, 1991). Repetitive chewing may activate the neural oscillator in the brain which interacts with the lower neural oscillator in the spinal cord and results in consistent upregulation of timing in both. This phenomenon is similar to the commonly used Jendrassik maneuver, where teeth clenching, and co-contraction of limb muscles are used to elicit a more noticeable tendon reflex response (Boroojerdi et al., 2000; Sugawara et al., 2005). This could explain the finding that step rate increases when chewing is introduced. Obviously both the chewing and stepping timing centers are also modulated by descending neural inputs from higher motor centers, such as the motor cortex or cerebellum. This allows for flexibility of the system despite a default organization to these rhythmic centers. When chewing is performed as a single task before walking, the step rates can be entrained to a faster or slower rhythm that more closely matches chewing frequency. However, when walking is performed first, the modulation of step rates by chewing is less specific. Instead the entrainment could be exemplified by a more general activation of the entire system.

When classifying behavior of coupled oscillators, the two rhythms combine to result in one of three patterns (Latash & Turvey, 1996). These patterns are referred to as rhythmic synergies and they either compete and favor one or the other (i.e., the maintenance tendency), combine to create a novel rhythm with components of both maintenance tendencies (referred to
as superimposition), or cooperate to create a novel hybrid frequency (i.e., the magnet effect) (Latash, & Turvey, 1996). The results of the study indicate that elements of these behaviors are noted when performing chewing and walking simultaneously. Chewing performed before walking results in chewing being the dominant maintenance tendency which drives the coupling of stepping rate. When chewing is initiated or stopped mid-walk, the step rates increase. Increasing step rates when chewing is stopped is more indicative of a magnet effect occurring during walking and chewing. When the low frequency chewing maintenance tendency ceases, step rates speed back up toward a higher frequency similar to single task stepping rates. It is likely that the resultant output is reflective of a more complex system than just two neural oscillations interacting, which would account for the varied findings across each of the tasks. Though there are auditory sensory components related to the action of chewing, the addition of proprioceptive sensory information from the opening and closing of the jaw into the system appears to be associated with effects lasting at least 20 seconds or the duration of the walking trial. Future investigations should include longer distance performance of chewing and walking dual tasks to better appreciate the interaction of the coupled oscillators to assess phase shifts or offsets, as well as the duration of effects of gum chewing on gait patterns.

In summary, the main findings of this study were that chewing influenced stepping rates regardless of when chewing is initiated during the walking activity. Chewing appears to be more influential on stepping rates when it is initiated prior to walking, but regardless seems to cause step rates to increase. The interaction of the neural oscillators underlying chewing and walking does not appear to follow locked-in behaviors (i.e. superimposition, magnet effect) but rather are more flexible, which may indicate further research is needed to fully appreciate the complexity of this system.
CHAPTER 6

CONCLUSION

The overall aim of this study is to examine the coordination of chewing and walking throughout adulthood and determine how chewing influences other motor tasks when performed concurrently. Prior to this line of research, little was known about natural chewing patterns and their impact on general motor function. It was anticipated that findings would improve understanding of how various motor functions like chewing and walking change with increasing age. It was also expected that chewing influences patterns of movement in the limbs when the two actions are performed together. The exact effect of chewing in a dual task paradigm had yet to be examined. Finally, it was expected that chewing would drive the frequencies of other rhythmic movements due to the bilateral, internal sensory feedback, as well as its central function being highly linked to survival. A summary of the findings from the three experiments are discussed.

Chewing effects gait patterns

Chewing is a fundamental motor skill that must be performed on a daily basis and is central to an individual’s survival. Despite the importance of chewing, little is known about natural chewing patterns or the motor control of chewing. Much of the knowledge regarding chewing physiology and associated neural mechanisms are derived from animal models due to unique challenges associated with accessing the chewing centers in the hindbrain. The primary goal of chewing is to breakdown food in preparation for digestion, but that means there is no ideal way to perform chewing. Rather chewing patterns are dynamic in response to the task (i.e.,
most efficient way to breakdown the food, changes in bolus consistency) (Po et al., 2011; Quintero et al., 2013; Yamashita et al., 1999).

Interestingly, chewing exhibits many similarities to walking in regards to the underlying movement characteristics and neural control mechanisms. Both tasks are cyclic in nature and exhibit a defined order to movement defined by phases (Begg & Sparrow, 2006; Minami et al., 2012). Both tasks require the right and left sides of the body to coordinate so that there is always an active side/stance side where the muscles are engaged in a task requiring stabilization and power while the contralateral side is engaged in orbiting/swing movements focused on coordinated mobility (Schubert et al., 2012). Chewing and gait also both have similar neural control components, including central pattern generators and higher conscious cortical control (Kandel et al., 2000). The presence of both types of neural control allows for flexibility of the system. For chewing, when a bolus size and consistency are familiar, there is less cortical involvement. In contrast, when a bolus consistency is variable (i.e., a hard seed in a generally soft substance) more cortical activity is noted (Quintero et al., 2013). Both chewing and walking also exhibit phase-dependent reflex mechanisms associated with safety (Forssberg et al., 1975). The jaw-opening reflex is more strongly stimulated during the mouth closing phase because this is believed to be a mechanism to prevent injury to dentition when a hard substance is sensed in the mouth. This same jaw-opening reflex is less strongly activated during the mouth opening phase of chewing by the same stimulus (Lund, Rossignol, & Murakami, 1981; Van der Glas, Van der Bilt, Abbink, Mason, & Cadden, 2007). A similar phase-dependent reflex is noted during gait when advancing the limb in swing phase. It is associated with a strong limb flexion reflex, which is thought to prevent tripping and loss of postural stability during gait (Baken, Dietz, & Duysens, 2005; Yang & Stein, 1990).
An individual must be able to move to a food source, as well as process and breakdown food to take in nutrition. Understanding how an organism coordinates and prioritizes these two tasks is central to this work. Though previous findings have revealed mixed outcomes when performing two motor tasks concurrently, experiment 1 and experiment 3 solidly confirmed that chewing effects gait patterns. Initial findings from experiment 1 highlighted that chewing at different speeds appears to be linked to similar changes in gait. That is, if someone chews slowly, then their gait pattern slows significantly. Increases in stepping rate and gait velocity were also noted when chewing quickly. Experiment 1 used an auditory metronome to set chewing speeds, which may have influenced this relationship. Consequently experiment 3 was designed whereby participants were allowed to chew and walk freely according to simple directions, such as “Chew quickly.” Although the methodology was changed to eliminate effects of the metronome, the findings from experiment 1 were replicated in experiment 3. Also, naturally selected chewing rates were found to be close to the rates set in experiment 1 (i.e., 1 Hz for slow chewing and 2 Hz for fast chewing). The exact neural mechanism and function behind a mouth-leg connection remain unclear but are likely related to the principle of parsimony. Given the neural and physical similarities between chewing and walking, the two neural oscillators can couple and optimize to a particular variable or per a set goal, thus resulting in the need for less energy-expensive cortically based control.

*Chewing patterns appear resistant to age-related slowing*

To date, much of the research has focused on describing chewing patterns in young adults, or older adults with a neuropathology (Ferrario et al., 2006; Plesh et al., 1987; South, Somers, & Jog, 2010), but there is less direct research specifically designed to describe chewing
in healthy older adults. Aging has traditionally be associated with a general slowing of movement across a number of motor tasks, including fast finger tapping, reaction time, and walking (Fozard, Vercruyssen, Reynolds, Hancock, & Quilter, 1994; Prince et al., 1997; Ruff & Parker, 1993). While changes in chewing with age have been described, these have been limited to decreased bite forces, and self-reports of “slower eating” (Mioche, Bourdiol, & Peyron, 2004). Consequently, few studies have objectively and directly measured the temporal nature of chewing in the elderly. The results of all three experiments demonstrated that the chewing rates of healthy elderly were similar to healthy young adult chewing rates. Chewing is controlled both via ipsilateral and contralateral innervations to bilateral chewing musculature (Kolta, Morquette, Lavoie, Arsenault, & Verdier, 2010; Kandel et al., 2000). The redundancy of mechanisms controlling chewing may underlie the resistance of chewing to degradation of temporal chewing patterns as observed for other motor tasks with age. Though there are changes in the muscle activation, food selection, and other aspects that influence eating, the chewing rate appears a consistent goal for the system (Mioche et al., 2004; Samulski et al., 2019).

**Chewing exhibits contrasting effects on secondary motor tasks**

Most studies investigating the effects of chewing on a secondary task are focused on cognitive-motor interactions. Dual task interference (DTI) is a common outcome when a cognitive and motor task are performed simultaneously (Al-Yahya et al., 2011). DTI is generally associated with poorer overall performance on one or both tasks. Cognitive tasks, such as the Stroop test or serial subtraction, have shown to consistently interfere with walking tasks (Patel et al., 2014). In the past, less was known about how simultaneous performance of two motor tasks changes movement patterns in healthy adults. Much of the research on dual motor task effects
were on patients with Parkinson’s disease as this is a commonly used intervention (Fritz, Cheek, & Nichols-Larsen, 2015; O'Shea, Morris, & Iansek, 2002). Past studies have also investigated chewing’s effect on secondary tasks from a cognitive resource utilization perspective, rather than from a coupled oscillators or neurophysiological perspective.

The results of experiment 2 highlighted a dichotomy regarding the effects chewing has on the performance of a secondary motor tasks. Chewing appeared to significantly slow reaction time, regardless of the speed at which the chewing was performed. Theoretically, there should be less cortical control of chewing for the preferred chewing pace as this rate requires less conscious control. Alternatively, the paced chewing tasks probably require increased cognitive involvements, as reflected by the discrepancies between the desired and actual chewing paces. Combining chewing, which is characterized by a cyclicity, with a finite task, like reaction time, appears to be differentiating element. When combining chewing with other cyclic tasks, like walking or finger tapping, the chewing appears to entrain the secondary motor task. Again, the mechanism behind this may indicate a parsimony principle where the brain couples pattern generators that are close in frequency for efficiency. This same coupling of CPGs in the upper and lower limbs of humans during crawling and walking at various speeds has been documented (MacLellan, Ivanenko, Catavitello, La Scaleia, & Lacquaniti, 2013; Webb, Tuttle, & Baksh, 1994).

**Top-down organization of neural oscillators**

The results of experiment 3 build upon the findings in experiment 1 by highlighting the widespread role chewing has on motor tasks and that there appears to be a hierarchy to the oscillators involved in chewing and walking. The findings indicate that chewing influences gait regardless of when it is initiated. A top-down organization of the coupled neural oscillators could
allow for greater flexibility within the system. The cortex allows for coordination of movement based on efficiency with the ability to adjust to incoming sensory information to allow accommodations to the environment or task goals. The interplay of the conscious and subconscious control of both walking and chewing exemplifies this flexibility by facilitating cognitive parsimony in less challenging situations. Bilateral innervation of the chewing musculature makes it a prime driving CPG of the system as its redundancy (i.e. bilateral cortical innervation) ensures intact mechanisms despite injury or damage. If the limb-associated CPGs in the spinal cord were to function as the primary driving components, injury would disrupt the entire system.

Understanding the mechanisms driving the coupling between chewing gum and walking are paramount. Not only does this information help to build a better understanding of motor control in organisms that multi-task, but also drives understanding of the organization underlying natural neural mechanisms. Chewing gum is a cheap and socially acceptable activity that could have powerful implications for cuing gait and other voluntary cyclical actions during rehabilitation. Recognizing the potential and gleaning consistent principles that drive this coupling relationship opens new doors for developing an oral sensory intervention for altering walking and other movements of similar features. Rhythmic auditory and visual cues have been popular for addressing gait abnormalities in patients who suffer from Parkinson’s disease, stroke, and other neurological diseases or injuries. Rhythmic chewing may tap into a primitive, fundamental motor process to aid in rehabilitation of cyclical movements including gait.
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VITA

Brittany S. Samulski, PT, DPT
4211 Monarch Way
Norfolk VA 23529

FORMAL EDUCATION

Post-Graduate
2016-2020 Ph.D. Old Dominion University, Norfolk, VA
School of Rehabilitation Sciences
Major: Kinesiology and Rehabilitation

2008-2011 D.P.T. Old Dominion University, Norfolk, VA
School of Physical Therapy
Major: Physical Therapy

Undergraduate
2004-2008 B.A. University of Virginia, Charlottesville, VA
Department of Psychology
Major: Psychology
Major: Spanish Language

PROFESSIONAL APPOINTMENTS

2019- present Assistant Professor, School of Rehabilitation Sciences, Old Dominion University, Norfolk, VA

2016-2019 Graduate Teaching Assistant and Adjunct Faculty, School of Physical Therapy and Athletic Training, Old Dominion University, Norfolk, VA

2010 Graduate Teaching Assistant, School of Physical Therapy, Old Dominion University, Norfolk, VA

RESEARCH AND PUBLICATIONS

Referred Publications


Published Abstracts