Functional specificity and hierarchical control of trunk muscles in complex rhythmic movements

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List of Abbreviations

3-D, 3D	three dimensional
A	asynchronous pattern
A-P	anterior-posterior
abd	abduction (as in joint motion)
add	adduction (as in joint motion)
Adj. Sig.	adjusted significance
Age init.	age at beginning of training
alt	alternating
BC	British Columbia
BF	biceps femoris
BMI	body mass index
CCW	counter clockwise
CNS	central nervous system
CO-HF	high frequency component of the combination movement
CO-LF	low frequency component of the combination movement
COMBO	combination movement (hip slide plus fast hip shimmy)
COMBO-HF	high frequency component of the combination movement
COMBO-LF	low frequency component of the combination movement
CPG	central pattern generator
CW	clockwise
D	diagonal pattern
D-cau	D-caudal (diagonal pattern in which activity at L1 is synchronous with L2/3 and L4).
D-ros	D-rostral (diagonal pattern in which activity at L1 is synchronous with T10).
EMG	electromyography
EO	external oblique
ES	erector spinae
ESA	erector spinae aponeurosis
ext	extension (of a joint)
FAP	as fast as possible (hip shimmy tempo condition)
flex	flexion (of a joint)
FQRNT	Fonds de recherche du Québec – Nature et technologies
freq	frequency
FWDBND/FwdBnd	forward bend
GM	gluteus medius
GrpMean%	group mean of lag as a percentage of cycle time
Hf	high frequency
HIPSLD	hip slide

HIPSLD-D, HIPSLD D	hip slide case having a diagonal activation pattern
HIPSLD-S, HIPSLD S	hip slide case having a simultaneous activation pattern
Ht	height
Hyp	hypothesis
ID	subject identification code
id	insufficient data
IL	iliocostalis lumborum
ILL2-3	iliocostalis lumborum, level midway between second and third lumbar vertebrae
ILpL	iliocostalis lumborum pars lumborum
ILpT	iliocostalis lumborum pars thoracis
L ASIS, LASIS	left anterior superior iliac spine
L ES	left erector spinae
L2/3	mid-way between second and third thoracic vertebrae
Lag%T	lag between two muscle signals as a percentage of cycle time
Lagdiff%	difference between lags as a percentage of cycle time
LASIx	x translational displacement of reflective marker on left anterior superior iliac spine
Lf	low frequency
LT	longissimus thoracis
LTL1	longissimus thoracis, first lumbar vertebral level
LTL4	longissimus thoracis, fourth lumbar vertebral level
LTpL	longissimus thoracis pars lumborum
LTpT	longissimus thoracis pars thoracis
LTT10	longissimus thoracis, tenth thoracic vertebral level
MAYA/Maya	maya (a version of the frontal plane figure 8 pelvic isolations)
MC	movement condition
mdn	median
medio-lat	medio-lateral
ML, M-L	medio-lateral
MULT	multifidus
nd	no data
NMDA	N-Methyl-D-aspartate (an amino acid derivative used to stimulate glutamate receptors in the CNS, mimicking the action of the related neurotransmitter)
NOV, N, No	novice (subject group)
NSERC	Natural Sciences and Engineering Research Council of Canada
Pats chgd	patterns changed
PELV	pelvic (plane derived from pelvic reflective markers)
PELVy	rotational motion of pelvic segment in the frontal plane (y axis)
PiG	Plug-in-Gait (VICON validated reflective marker placement locations for 3-D motion capture)

plant	plantar
R ASIS, RASIS	right anterior superior iliac spine
R ES	right erector spinae
RLS	réseau locomoteur spinal
RMS	root-mean square
ROM	range of motion
S	simultaneous pattern
SD	standard deviation
SEMG, sEMG	surface electromyography
SENIAM	Surface Electromyography for the Non-Invasive Assessment of Muscles
SERP/Serp	serpentine (a version of the frontal plane figure 8 pelvic isolations)
SFU	Simon Fraser University
SHIM	hip shimmy
SIDBND/SidBnd	side bend
Sig.	significance
SM	soleus medius
SNC	système nerveux central
SPSS	Statistical Package for the Social Sciences
T	T statistic from Wilcoxon signed rank test
T (alone)	cycle period
T10-L4	difference in activation timing between tenth thoracic and fourth lumbar vertebral levels (of the ES)
T10-L4%T	same as T10-L4, but as a percentage of cycle time
TA	tibialis anterior
TFL	tensor fascia latae
TH1	Marker frame placed at first thoracic level
Th10	tenth thoracic vertebral level
TH10	Marker frame placed at tenth thoracic level
TH12y	rotational motion of twelfth thoracic segment in the frontal plane (y axis)
TH1y	rotational motion of first thoracic segment in the frontal plane (y axis)
TRD, T, Tr	trained (subject group)
TRG	training (level)
UVIC	University of Victoria
Vert	vertical
VM	vastus medialis
w	weeks
W_s	Wilcoxon signed rank statistic
Wt	weight
x-vel	x-velocity
yrs	years

Abstract

Belly dance was used as a novel paradigm for exploring motor control of voluntary trunk movements. Motion capture and electromyography were combined to record segmental motion and muscle activation patterns. A variety of different trunk isolation movements varying in tempo, range of motion and pelvic movement trajectories, were recorded to explore how the human nervous system controls complex, segmentally specific rhythmic trunk motion.

Results from the first study confirmed predictions from anatomical studies that different portions of the lumbar spine extensors could have independent functions, and established that belly dance could serve as a useful paradigm for exploring paraspinal muscle function and neural muscular specification in segmental spine motion. In the second study the previous findings on compartmental control of lumbar spine extensor muscles were extended to explore how muscle activation timing changes with tempo and training. Three different patterns were observed based on this capability for neuromuscular specificity of paraspinal muscles at different vertebral or segmental levels. The activation patterns resembled those corresponding to different gaits or locomotor modes observed in lamprey, salamander, humans and other mammals. Pattern selection and switching were dependent on task, training and tempo, with an interaction amongst these factors. Differences between novice and trained performers were seen in the selection of different patterns at low frequencies, but convergence toward a common pattern in higher frequency oscillations, findings which supported the proposal that the lower frequency variations are under voluntary descending control while the higher frequency versions involve lower, more automatic levels of control.

Finally, the third study explores hierarchical control further using two rhythmic trunk tasks of different frequencies performed separately and simultaneously. High and low frequency movements performed separately appear to be controlled by different mechanisms and require no previous experience, merely correct pattern selection to make use of innate neural circuits. However, combining the two requires extensive practice to achieve integration that preserves both frequencies to produce polyrhythmic kinematic and muscle patterns. The low frequency patterns are under voluntary control via descending supraspinal commands, whereas performance of the fast shimmy (above 3 Hz frequency) likely involves selective access to spinal central pattern generators (CPGs). Combining low and high frequency movements requires training in order to generate two distinct control signals, corresponding to different mechanisms/ levels of control. Successful integration likely requires a learned capacity to modulate CPG output for generation of polyrhythmic activation patterns in axial muscles. Thus, the well studied phenomenon of coupling in limbs that creates hybrid patterns when different rhythms are specified for each limb, also operates within single effectors and axial muscles. This common central nervous system (CNS) strategy for simplification of the control problem of dual tasks can be overridden with practice.

These results extend knowledge on motor control of voluntary multi-segmental tasks in general, and of rhythmic movements of the trunk in particular, as well as of compartmentalization of neuromuscular control and the integration of posture and movement. Additionally, they lend supporting evidence for the existence of spinal CPGs in humans, adding to the growing body of literature espousing the phylogenetic conservation of neural circuitry.

Résumé

La danse du ventre a été utilisée comme un nouveau paradigme pour explorer le contrôle moteur des mouvements volontaires du tronc. La capture de mouvement et l'électromyographie ont été combinées pour enregistrer le mouvement segmentaire et les patrons d'activation musculaire. Une variété de différents mouvements d'isolement du tronc variant dans le tempo, la gamme de mouvement et les trajectoires du mouvement pelvien, ont été enregistrés pour explorer comment le système nerveux humain contrôle les mouvements rhytmiques complexes et spécifiquement segmentés du tronc.

Les résultats de la première étude ont confirmé les prédictions des études anatomiques selon lesquelles différentes parties des extenseurs de la région lombaire pourraient avoir des fonctions indépendantes et ont établi que la danse du ventre pourrait servir de paradigme utile pour explorer la fonction musculaire paravertébrale et la spécification musculaire neurale dans le mouvement segmentaire de la colonne vertébrale. Dans la deuxième étude, les résultats précédents sur le contrôle compartimenté des muscles extenseurs lombaires de la colonne vertébrale ont été étendus pour explorer comment la synchronisation d’activation musculaire change avec le tempo et la formation. Trois patrons différents ont été observés sur la base de cette capacité pour la spécificité neuromusculaire des muscles paravertébraux à différents niveaux vertébral ou segmentaire. Les patrons d'activation ressemblent à ceux correspondant à différentes allures ou modes locomoteurs observés chez la lamproie, la salamandre, les humains et d'autres mammifères. La sélection des patrons et la commutation dépendaient de la tâche, de la formation et du tempo, avec une interaction entre ces facteurs. On a observé des différences entre les artistes novices et les artistes expérimentés dans la sélection des différents patrons à basses fréquences, mais la convergence vers un patron commun dans les oscillations à fréquence plus élevée, ces résultats appuyant la proposition que les variations de fréquence inférieures sont sous contrôle volontaire descendant tandis que les versions de fréquences plus élevées impliquent des niveaux réduits de contrôle plus automatiques. Enfin, la troisième étude explore le contrôle hiérarchique en utilisant deux tâches rythmiques de différentes fréquences réalisées séparément et simultanément. Les mouvements de hautes et basses fréquences effectués séparément semblent être contrôlés par des mécanismes différents et ne nécessitent aucune expérience préalable, il suffit de corriger la sélection des patrons pour utiliser les circuits neuronaux innés. Cependant, la combinaison des deux nécessite une pratique poussée pour réaliser une intégration qui préserve les deux fréquences pour produire des patrons polyrhythmiques cinématiques et musculaires. Les patrons à basse fréquence sont sous contrôle volontaire via des commandes supraspinales descendantes, alors que la performance du shimmy rapide (au-dessus de la fréquence 3 Hz) implique probablement un accès sélectif aux générateurs de réseau locomoteur spinal (RLS). La combinaison de mouvements de basse et de haute fréquence nécessite une formation afin de générer deux signaux de commande distincts, correspondant à différents mécanismes / niveaux de contrôle. Une intégration réussie nécessite probablement une capacité acquise pour moduler la production de RLS pour la génération de patrons d'activation polyrhythmiques dans les muscles axiaux. Ainsi, le phénomène bien étudié de couplage dans les membres qui crée des patrons hybrides lorsque des rythmes différents sont spécifiés pour chaque membre, fonctionne également au sein d'effecteurs simples et de muscles axiaux. Cette stratégie commune du système nerveux central (SNC) pour simplifier le problème de contrôle des tâches doubles peut être outrepassé par la pratique.

Ces résultats étendent les connaissances sur le contrôle moteur des tâches multi-segmentaires volontaires en général et des mouvements rythmiques du tronc en particulier, ainsi que de la compartimentation du contrôle neuromusculaire et de l'intégration de la posture et du mouvement. En outre, ils apportent des preuves à l'appui de l'existence des RLS dans la colonne vertébrale chez les humains, ajoutant à la masse croissante de la littérature épousant la conservation phylogénétique des circuits neuronaux. Ces résultats peuvent avoir une pertinence clinique dans le diagnostic et la rééducation suite à une blessure au muscle ou au système nerveux central lié spécifiquement à l'intégration des patrons locomoteurs et du tronc et à la restauration des mécanismes normaux d'activation et de coordination musculaire. En outre, ils peuvent améliorer les modèles biomécaniques de la fonction du tronc et informer les systèmes de conception et de contrôle pour les robots humanoïdes.

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While completion of a PhD thesis may produce many interesting advancements in a field, it also necessarily leaves open questions. For me, these include, “Would I have been able to finish without the benefits of chocolate and coffee?” “Has living several years in the McGill student ghetto been a factor in delayed onset of menopause?” Surely, one could never make it through such an arduous journey without an abiding sense of humour and appreciation for the palliative effects of absurdity. Even more surely, it could never be achieved with out the help and support provided by so many, and for which I will always remain deeply grateful. The many types of support I received and depended on, took different forms, but I they can be categorized into four types: academic, financial, technical/resource and moral.

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I don't think I ever quite made the adjustment going from running my little belly dance empire in Vancouver - teaching upwards of 120 students per week, performing hundreds of shows per year, conceiving and choreographing evening-long dance recitals, hosting the world leaders of belly dance in workshops - to sitting alone in a room with my laptop. This transition didn't involve just a geographical move and ended marriage, but a reformulation of my identity and complete restructuring of my financial, physical and social life, spanning the ages 46 to 52. Above and beyond the support of friends, I benefitted from many services offered by McGill: attending PhD support group, where students from diverse fields and backgrounds shared challenges and strategies, and many workshops and panel discussions on academic life, and career gave energy to perseverance and helped to keep one's "eye on the prize". I am very grateful also to Ruth Mencow at McGill Counseling and Mental Health Services who helped me regain perspective and reclaim my self-confidence during a period of mid-degree, mid-life confusion.

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Marilee Nugent, January, 2017, Firenze, Italy

Contributions of Authors

Dr. Theodore Milner co-authored the three articles in Chapters 3-5, provided guidance on data analysis methods and statistical testing, and assisted in revision of the manuscripts. Dr. Paul Stapley gave guidance on preparing the first article manuscript, provided the laboratory, equipment and technical assistance for the first stage data collection, was involved in discussion of results for the first study, and provided guidance on displaying and visualizing the data. As the first author on all three articles, I was the main person responsible for conceiving of the experimental paradigm, elaborating the hypotheses, designing the experimental protocol, pilot testing for feasible results, collecting and processing the data, analyzing the results, and writing the articles.

Preface

This is a manuscript-style thesis comprised of three research articles connected by the common theme of hierarchical control in the coordination of complex rhythmic segmental trunk motion. Each article chapter contains specific Introduction, Methodology and Discussion sections. In addition this manuscript begins with a General Introduction explaining the genesis of the project and rationale for the experimental paradigm, as well as background in the form of description of the movements studied, literature reviews on the relevant functional anatomy and rationale for electrode placement, previous research using dance to investigate motor control, overview of the neural mechanisms underlying the control of the motor patterns studied and project overview. The General Methodology section does not go into detail about the experimental protocol, since this is covered in depth in the three articles. It is included to provide some additional details about the overall data collection and rationale for the methods. It also includes mention of additional trial data intended for future studies and collected at the same time, but which has not yet been examined. The General Discussion provides a summary of the conclusions and knowledge gained, and interprets the findings in Chapters 3-5 in the context of the neural circuitry that likely underlies control of the movements studied. In addition, it discusses possible further analyses using the existing data set and directions for future research. The methodological limitations and possible applications of the results are discussed.

Chapter 1

Introduction

Introduction

1.1 BELLY DANCE AS A RESEARCH PARADIGM FOR HUMAN MOTOR CONTROL

Investigation of the generative mechanisms underlying axial motor patterns in humans during rhythmic tasks and locomotion is relatively recent. Balance and gait research initially focused on understanding responses controlling more distal joints before moving to investigate the balance responses in the more proximal pelvic and axial muscles. It is almost as though research efforts mirror the differing levels of conscious awareness typically accorded to the control of different body segments - i.e. limbs and hands versus axis. Indeed, an important impetus for improving the understanding of trunk function came from the failures in the early bipedal robots built with jointed lower limbs but inflexible spines, which easily toppled when moving on other than flat terrain.

To a movement scientist who is also a dancer, dance provides both a logical and appealing paradigm on which to base investigations into understanding how the central nervous system (CNS) controls and coordinates full-body, voluntary movement, and how it adapts existing neural patterns to learning novel tasks. The neural circuitry underlying centrally generated axial motor patterns in animals such as the lamprey, salamander and mud puppy has been well documented. More recent work has demonstrated parallels and elaborations of this functional neural organization in rats. Investigation of the neural circuits underlying coordination of human rhythmic motor patterns poses ongoing challenges due to the complexity and experimental inaccessibility of our neural circuitry. Consequently, underlying control structures and mechanisms must be inferred from behavior and through comparisons with animal models.

By recording muscle activity from multiple sites chosen to represent key joint motions during complex movement, we can obtain a good picture of the spatio-temporal muscle patterning that underlies the coordination of multi-segmental movement. Due to the role of the motor neuron as the "final common pathway", these patterns of neuromuscular excitation are indicative of the combined control output coming from multiple interacting levels of the nervous system.

My research approach began with the general notion that belly dance can tell us something about motor control of the trunk that the examination of global spine bending patterns cannot. Being a professional dancer and teacher for almost three decades, the theoretical decomposition of complex full body movements has been both a fascination and an occupation. Being a constantly evolving dance form, the ongoing manipulation and variation of the root vocabulary is an exploration of control possibilities for aesthetic and musical expression through the body. Because I had developed a pedagogical approach to teaching which breaks complex movements down into specific joint actions, practicing these in parts, and then flexibly combining them in different ways, it was not a big leap to see how this movement repertoire could be used as a paradigm for studying motor control. The repertoire represents a set of defined, constrained rhythmic tasks, amenable to experimental manipulation as a set of "motor primaries" that can be varied, combined and compared/contrasted/differentiated. Thus trunk control can be investigated by comparing the changes in muscle coordination patterns across voluntarily controlled variations in segmental specificity, tempo, and axis of rotation or translation direction. In addition, these cyclic movements can be performed continuously in place, allowing relatively easy acquisition of a large number of trials and samples (cycles) in a short period of time. Last but not least, the prevalence of trained dancers in virtually every city provides the opportunity for making comparisons between trained and untrained performers, with the potential of providing insights into discerning between the types of movements that are controlled by innate circuitry versus those that are accessible to modulation or reorganization, and even long-term adaptation through deliberate practice. Overall, this investigation brings more specific detail to the picture of the incredible capacity of the human nervous system to flexibly modify existing motor patterns or construct new ones.

1.2 PREVIOUS STUDIES USING DANCE TO INVESTIGATE MOTOR CONTROL

The motor control literature includes only a handful of studies on dance. Ballet dancers have been subjects in the investigation of stability control during complex full body movement (Lepelley et al. 2006; Mouchnino et al. 1992) or in response to unexpected perturbations (Simmons 2005a; b). These studies highlight the effect of training on the ability to predict and provide advance corrections or compensations for the perturbing effects of voluntary movement (Mouchnino et al. 1992), or on the establishment of shorter long-latency neuromuscular response times (Simmons 2005a). Given its trademark aesthetic of segmental spine isolations, belly dance has been used to show compartmental specificity of control in trunk muscles in the upper and lower rectus abdominus (Moreside et al. 2008), and in the erector spinae muscles above and below the third lumbar segmental level (Nugent et al. 2012; Nugent and Milner in press). Or (2006) proposes a belly dance-based control algorithm for flexible-spine humanoid robots to solve the problem of integrating locomotor movements and balance. Or’s proposed control structure was modeled on the central pattern generator (CPG) of the lamprey to produce the spinal isolations and undulations in a simulation of a robot belly dancing.

The lack of what I call “embodied knowledge” about the control capabilities of the nervous system (i.e. actual movement training) may be the reason dance has yet to be fully exploited as a research paradigm. Unfortunately, research involves an inordinate amount of time spent sitting, ignoring the body while all attention is focused on reading, typing, and thinking. From early in my undergraduate studies I have had an underlying concern that, by limiting our focus to simplified tasks, we run the risk of overlooking the kinds of complicated movement goals that the CNS is capable of realizing, leaving unexplored, important mechanisms that may not be evident in other contexts. It is true that whole body motor skills are difficult to define and are methodologically problematic to analyze. How do we evaluate the outcome of a movement goal that has no external target or speed or time outcome but has as its objective, some abstract kinematic pattern? The researcher must choose movements that utilize the functions she wishes to elucidate, and have an understanding of how to translate between aesthetic and functional criteria to determine objective measurements of performance.

It is the job of dancers to work with and manipulate the many functions and parameters of motor control that researchers theorize about and test: posture, stability, dynamics, sequencing, flow, movement quality, precision - all these can be understood in motor control terms - pattern selection, specificity, net generated torque, modulation of joint stiffness, control of total and segmental center of mass, exploitation and control of momentum, dynamic and static stability, freezing and freeing degrees of freedom. Dancers train continuously to improve segmental specificity, to fine-tune parameterization (speed, amplitude, tension), optimize automaticity, decouple stable coordination patterns and construct novel ones. Belly dance in particular focuses on the trunk - not to maximize stability and provide support for outstretched limbs, as in ballet, but to facilitate segmental oscillations and emphasize independent movement of proximal joints and pelvic, lumbar, cervical and thoracic trunk segments around different axes of rotation and in different planes, combinations and rhythmic variations. Often there is no tangible goal other than to explore and expand our own movement capabilities.

1.3 NEURAL MECHANISMS IN THE CONTROL OF BELLY DANCE MOVEMENTS

In 1884 Hughlings Jackson (Jackson 1884) proposed that movements can be categorized along a continuum between least automatic to most automatic. The line between these two modes of control is not so distinct. Implicit in the concept of hierarchical control of voluntary movement is the interaction between conscious and unconscious processes. The will to move and the choice of overall movement plan/goal originate in higher cognitive centers. More automatic mechanisms specify the spatiotemporal patterning of multi-joint coordination, ensure postural stability or make adjustments for incorrectly predicted movement outcomes and unexpected perturbations. Sensory feedback operates on a non-conscious (spinal) level to correct or refine the ongoing movement and is used in memory consolidation and more abstract processes via long-term learning, as well as being utilized during cognitive appraisals of one’s own performance. Thus, the concept of “hierarchical control” does not refer only to the production of control signals of different types and levels of complexity from different parts of the CNS. It also encompasses the interaction and mutual modulation amongst many control centers and mechanisms involved in producing coordinated, purposeful motor behavior. The different “levels” of control are broadly categorized as supraspinal (brainstem and above), spinal (including reflexes, pattern generation networks, and propriospinal and neuromodulatory interneurons) and peripheral (sensory afferent and motor efferent activity). Supraspinal structures - cortex, basal ganglia, cerebellum - perform such functions as selection, initiation and termination, movement sequencing, control of dynamics and updating of commands through error evaluation of movement outcomes (Shik and Orlovsky 1976). At this level, commands may be specific to individual muscles, or may be more abstract, specifying, for example the coordinated activity among multiple joints or limbs. Supraspinal output is conveyed through the brainstem to the spinal cord via corticospinal tracts. At the level of the spinal cord, descending inputs from vestibular and visual areas are integrated with commands to control of balance, steering and head/body orientation, while regulatory output from reticulospinal tracts adjust postural tone of axial muscles and excitability of limb flexors and extensors, modulated according to task requirements.

There is growing evidence that a wide range of cyclic activities such as locomotion and scratching are patterned and driven by spinal CPGs, even in humans. Animal models have been used extensively to investigate their functional properties. CPGs are oscillatory neural ensembles located in the spine which generate alternating flexor-extensor activity as in locomotion and scratching. Being under the influence of both afferent and supraspinal inflow in the shaping and tuning of their output, CPGs represent a physiological nexus of higher and lower level control. In vertebrates, descending input from the mesencephalic locomotor region of the brainstem initiates and regulates speed, turning and pattern switching of rhythmic activity, without specifying the selection or phasing between limb muscles, which are determined by the coupled CPG networks. Bilaterally asymmetric drive produces turning (Le Ray et al. 2011; Ijspeert 2001; Ijspeert et al. 2007). To summarize these interactions using gait as an example, the various roles of supraspinal input to CPGs include (1) activating and deactivating of the locomotor automatisms, (2) regulating the intensity of activation (muscle force and power), (3) defining the pattern of interlimb coordination (i.e. walk, run, crawl), (4) maintaining equilibrium, (5) adapting movement to the support surface (e.g. obstacle avoidance, slippery surfaces), (6) modifying gait through integration with sensorimotor, visual and other cortical areas in the service of voluntary movement goals (Shik & Orlovsky, 1976).

As far back as 1914, T.G. Brown (Brown 1914; McCrea and Rybak 2008) proposed a model of an oscillating spinal circuit capable of independently generating rhythmic movement patterns as in locomotion. His model has since been supported by many animal studies and is still accepted as descriptive of the basic neural circuitry capable of rhythmic movement generation. In this model, a unit CPG (Grillner 1985) is formed by a pair of excitatory interneurons or “half-centers” that are subject to fatigue, coupled with mutually inhibiting connections. The intrinsic properties of this basic neural circuit ensure that only one of these interneurons is active at a time. The reciprocal activation is what drives the antiphasic alternating activity of muscle antagonist pairs - the fundamental coordination pattern of joint rotation. Sustained descending drive activates these unit CPGs, while their intrinsic properties produce the oscillating activation. Networks of these oscillators are presumed to underlie the multi-segment and multi-limb coordination patterns in locomotion. Deafferentation studies have shown that sensory input is not required for their rhythmic pattern generation (Grillner and Zangger 1975), although it serves to shape and coordinate limb movement with the mechanical consequences of their actions (Grillner 1985). Rossignol et al. (2006) provide a comprehensive overview of the mechanisms and pathways: “Feedback originates from muscles and skin afferents as well as from special senses (vision, audition, vestibular) and dynamically adapts the locomotor pattern to the requirements of the environment. The dynamic interactions are ensured by modulating transmission in locomotor pathways in a state- and phase-dependent manner" (Rossignol et al. 2006). The influence of afferent feedback on locomotion can be global. It can allow, prevent and even select motor patterns through dynamic interaction with CPGs (mutual influence). The effects may be state or task dependent, via inhibitory or excitatory modulation of pattern generating networks. For example the influence of a tonic input can change throughout a motor cycle and may also evolve with time (learning). Sites of interaction include motorneurons, interneurons and descending input via supraspinal structures (Rossignol et al. 2006).

Rossignol et al. (2006) explain the interaction of CPGs with afferent input from the key sensory receptors important in shaping pattern output to enhance control. Tonic inflow from cutaneous receptors can trigger, enhance, or inhibit pattern generation (e.g. an itch triggers scratching). Phasic stimulation from cutaneous receptors produces spatial adjustments, producing necessary alterations in kinematic patterns, for example to modify or correct foot position in relation to an uneven support surface or limb trajectory in relation to obstacles. The joints and muscles affected are specific to the site of stimulation (e.g. as in a corrective stumble) and the phasing of activity is dependent on both the locomotor phase and the intensity of stimulus. Signals from proprioceptors - via type I afferents of muscle spindles (stretch receptors) and Ib afferents from Golgi tendon organs (force receptors) can trigger or block transitions between extensor/flexor phases to help regulate muscle activation phasing and amplitude, producing speed and timing adjustments such as changes in cycle durations. These ongoing adjustments improve movement efficiency by ensuring joint ranges of motion are maintained within effective muscle lengths for adequate force production. Muscles of proximal joints (i.e. hip muscles) are particularly influenced by sensory input from proprioceptors, related to their role in initiation of limb motion during locomotion.

The human motor system is remarkable in its versatility and ability to learn novel movement patterns. Grillner (1985) points out that this versatility is possible because of the interaction between voluntary and innate control processes: voluntary supraspinal input to spinal networks can influence genetically inherited patterns, as in modifying the locomotor pattern to perform the Monty Python “silly walk”. Conversely, depending on the context or movement goal, a voluntary movement can become part of an automatic motor program, as in learning to ride a bicycle. Thus, the motor programs determined and generated at the spinal level are not limited to stereotyped movement patterns, but can be decomposed and combined in a myriad of ways. Sensory input modifies their output in both short-term adaptation to immediate environmental circumstances, and long term adaptation to repeated practice. Grillner (1985; Grillner et al. 2008) proposes that the site of this adaptability is the unit CPG, which, through the interactions of descending and ascending input can be flexibly recruited for both voluntary and automatic (innate) generation of rhythmic muscle patterns. The degree of voluntary vs. automatic functionality depends on the context and amount of experience (degree of learning).

Lamprey and salamander have been studied to understand the functional connectivity of spinal rhythm generating networks. The investigations in this thesis focus on the motor patterns of the spinal muscles during a selection of belly dance movements. Across phylogenetic levels of complexity, we see a conservation of the spinal locomotor networks responsible for generating axial motor patterns (Falgairolle et al. 2006). The basic functional component is the unit CPG, a neural circuit with oscillating output responsible for the alternating flexion/extension patterns of muscle activity which seems to underlie all rhythmic motion in vertebrates. The neural organization follows a plan of bilateral networks of CPGs coupled longitudinally along the spinal cord which mutually influence each other. In lower vertebrates such as the lamprey, these CPGs have the property of independent segmental rhythmic generation. Intersegmental coordination of muscle activity is possible by virtue of this pattern of functional coupling between unit CPGs that produces a constant phase lag in segmental output, allowing for the sequential activation in ipsilateral axial muscle segments. In addition, crossed propriospinal inhibitory premotor interneurons send alternating excitatory or inhibitory signals through bilateral pairings of oscillators to coordinate right and left side activity.

Chevallier et al. (2008) found that isolated salamander spinal cord sections generate rhythmic patterns of activity very similar to those of the intact swimming lamprey: “the ability to generate coordinated activity with appropriate phase lag along the spinal cord is distributed within the entire spinal cord, since any part of the cord can be subdivided into pieces of two to three segments that retain the ability to produce rhythmic alternating activity.” Delvolve et al. (1997) discussed the similarities and differences in pattern generation between lamprey and salamander to illustrate the evolutionary alterations in neural circuitry in the transition from aquatic to terrestrial locomotion. The salamander swims and travels on land in the sprawled tetrapodal mode representing the transition in both form and function between anguilliform and mammalian quadrupedal locomotion. In salamanders, the undulating body axis still drives terrestrial locomotion, with the legs acting as struts to support the weight (Fischer and Witte 2007). Delvolve et al. (1997) observed the gait change in salamanders, in the switch from the traveling wave of epaxial muscle activation for propulsive swimming movements, to standing wave patterns of land trotting that accommodates the diagonal alternating limb motion with each half stride. The authors describe the intersegmental coordination of axial motion in the swimming salamander as a modification of the lamprey pattern: three time-offset metachronal waves of activation rather than one continuous one. The authors interpret the phase shifts occurring at each limb girdle as resulting from the mutual influence between leg and spinal CPGs that produces a hybrid *lamprey-like* pattern. The interaction between limbs and trunk neural circuitry is the source of coordination between the two. At lower locomotor speeds (i.e. on-land trotting) the leg CPGs dominate and ispilateral axial muscle activity becomes synchronous between limb girdles. Increased descending drive produces the gait transition to the swimming pattern. Even in very fast over-ground trotting, output from the axial CPGs become dominant under increased descending drive, and a metachronal descending wave as in swimming emerges, with a concomitant decrease in lateral movement amplitude as the animal "runs" (Chevallier et al. 2008; Crespi et al. 2013; Delvolve et al. 1997; Ijspeert et al. 2007).

Evidence suggests the further evolutionary modification of these same circuits - as opposed to them being discarded and replaced in phylogenetically later vertebrates (Lacquaniti et al. 2012; (Falgairolle et al. 2006). Changes in quadrupedal locomotion from sprawled stance to the parasagittal limb orientation of mammals was accompanied by another reorganization of limb and spinal circuitry (Fischer and Witte 2007). However, elements of the prior neural organization remained. Using in vitro spinal cord preparations from neonatal rats, Falgairolle and Cazalets (2007) found evidence of both segmental independence in rhythm generation and mutual influence through intersegmental coupling. Distinct rhythmic patterns were apparent in three regions of the cord: thoracic, lumbar and sacral (tail). Both thoracic and sacral regions produced slower rhythms than the lumbar, which seemed to dominate and entrain (both in frequency and direction) the other two when active. As a further example of segmental specificity in rhythmogenesis, the authors found reciprocal (antagonistic) bursting between ipsilateral L2 (flexor) and L5 (extensor) segments (Falgairolle and Cazalets 2007). Beliez et al. (2015) also found intrinsic rhythomgenic properties in both lumbar and thoracic portions of rat spinal cord. Additionally, they found that long and short propriospinal connections allowed triggering of distant thoracic segments by lumbar networks. However, this pattern switched to in-phase for complete hemicord preparations. They interpreted these results as confirmation of the existence of cross-cord connections at different segmental levels that function in reciprocal bilateral organization by mediating intersegmental phase shifts.

In light of these established neural arrangements in the spinal cords of vertebrates, Grillner (1985) describes how the activities of these innate control systems can be modified to produce many different behaviors. In fish, the default rostral-caudal phase lag between unit CPGs that produces forward swimming can be reversed for backward swimming or burrowing. Thus, descending signals may specify which set of oscillators receive higher drive to become the leading ones, thus setting the order of activation (e.g., caudal vs. rostral) and frequency by entraining adjacent segments. In this way, different behaviors (i.e. kinematic patterns of different segmental specification) can be generated using the same neural circuits. Different gaits in quadrupeds are achieved by activating different combinations of the coordinating neurons which changes the phase relations between muscles. In a similar manner, output from the locomotor circuits can be activated to produce scratching patterns, with additional modulation from the location of the scratch stimulus on the body to specify the target of the kinematic response. Grillner also notes the necessary capacity for flexible recruitment of single limb CPGs to adapt locomotion to direction and gait changes, terrain, and voluntary variations via altered phasing between muscle activity and joint motion. Grillner posits that descending access to individual unit CPGs would allow voluntary modification through selective control of individual muscle groups and joints. Descending control via corticospinal tracts "might have become progressively more specific, so that particular descending fibers could call on small specific fractions of the spinal networks to generate specific movements." Such a capability for voluntary "fractionation" of CPG locomotor networks could explain the ability of humans to perform the range of segmentally specific rhythmic motions characteristic of belly dance.

Indeed, Matsushima and Grillner (1992) have investigated mechanisms of intrinsic intersegmental coordination in the lamprey. By partitioning in vitro spinal cord preparations, they recorded chemically induced local excitability changes from segmental applications of NMDA (commonly used to substitute for descending drive from brainstem locomotor regions to produce fictive locomotor patterns). Such segmentally localized responses point to a descending neuromodulating (i.e. reticulospinal) mechanism with the capacity to modify the phase coupling between oscillators along the spinal cord in order to produce changes in the shape and timing of intersegmental motion of the body axis. To sum up, activating the entire network produces default (innate) locomotor patterns, but selection of subunits provides the means to specify submovements of the spine, in the service of a variety of behavioral goals. Preferential selection and modification of subunit output through experience is implicated in the formation and learning of novel spine motions.

1.4 SELECTED MOVEMENT CONDITIONS

The segmental motions of the trunk characteristic of belly dance include lateral undulations and translations, sagittal undulations, pelvic tilts and chest lifts, and horizontal twists of the pelvis and various multiplanar combinations of these (see videos on www.facebook.com/Shimmylab). The kinematic variety of these movements and their amenability to modulation, specification and combination make this movement form an ideal study object and source of experimental task conditions for investigating the capacity of the human nervous system to produce complex, segmental movements of the trunk.

For the three studies described in this thesis, the movements selected were vertical hip figure 8s in two different directions (maya and serpentine), the hip (or piston) shimmy performed slow and fast, the horizontal hip slide, and the combination movement of hip slide and shimmy. For all of these movements, the predominant motions occur in the frontal plane for the trunk and the sagittal plane for the legs. Hip joint action for these movements involves all three rotational axes to accommodate movements of spine, pelvis and legs. Overall, the movements have in common lateral trunk undulations of varying amplitudes and both standing and traveling waves of motion. In the first study, forward bends and side bends were also used for comparison movements of global spine motion. Table 1.1 provides details on the movements used in the three studies including details on their characteristics.

Previous EMG recordings from an undergraduate directed studies project had shown non-synchronous timing at different ipsilateral ES levels during frontal plane pelvic figure 8 movements. This was also seen in transverse plane figure 8s but the frontal plane versions were chosen for this investigation in order to try to simplify the role of the trunk muscles - i.e. to try to limit rotation around the longitudinal spine axis.

Table 1.1 Movement specifications for each task

Description of task	Primary plane of action	Joint motions	Active muscles	Movement amplitudes *frontal*
FWDBND in 4 counts Bend trunk forward as low as possible Return to upright posture	*sagittal*	Trunk and hips: *alt flex/ext*	ES, all levels bil; ham, glut (eccentric). ES, all levels bilaterally (concentric); ham, glut.	Full ROM *sagittal* *(no frontal)*
SIDBND both sides in 4 counts Bend trunk sideways as low as possible Return to upright posture	*frontal*	Trunk: *alt lateral flex*	All levels of CL ES, uni (eccentric). All levels of CL ES, uni (eccentric).	Full ROM
HIPSLD R Lateral translation of pelvis (head remains over feet) L Lateral translation of pelvis (head remains over feet)	Trunk: *frontal* Hips: *frontal* Legs: *mvt minimal*	Thoracic: *r lat flex* Lumbar: *l lat flex* Hips: *r add; l abd* Thoracic: *l lat flex* Lumbar: *r lat flex* Hips: *l add; r abd*	ES: **S** (rT10 + rL1 + rL2/3 + rL4) **D** (rT10 + rL1 + rL2/3) + lL4 EO R leg ES: **S** (lT10 + lL1 + lL2/3) + rL4 **D** (lT10 + lL1 + lL2/3) + rL4	**TRD** 10-27 cm *Mdn*: 16 cm *medio-lat* **NOV** 11-21 cm *Mdn*: 16 cm *medio-lat*
SHIM (2Hz, 3Hz, FAP) Counterclockwise (+) rotation of pelvis (L hip rises, L leg extends, R hip drops, R leg flexes) Clockwise (-) rotation of pelvis (R hip rises, R leg extends, L hip drops, L leg flexes)	Trunk: *frontal* Hips: *frontal/ sagittal* Legs: *sagittal*	Thoracic & lumbar alt *lat flex (global or segmental)* R hip: abd, flex R knee: flex R ankle: dorsi flex R hip: add, ext R knee: ext R ankle: plant flex	ES: **S**: (lT10 + lL1 + lL2/3 + lL4) **D**: (rT10 + rL1) + (lL2/3 + lL4) OR (rT10) + (lL1 + lL2/3 + lL4) **A**: lT10 > lL1 > lL2/3 > lL4 EO: l (or r) R leg: GM, TA, TFL ES: **S**: (rT10 + rL1 + rL2/3 + rL4) **D**: (lT10 + lL1) + (rL2/3 + rL4) OR (lT10) + (rL1 + rL2/3 + rL4) **A**: lT10 > lL1 > lL2/3 > lL4 EO: r (or l) R leg: SM, BF (hip ext), VM	**2Hz** NOV: 9-19º *Mdn*: 13º TRD: 9-24º *Mdn*: 14º **3Hz** NOV: 5-14º *Mdn*: 10º TRD: 5-17º *Mdn*: 9º **FAP** NOV: 3-14º *Mdn*: 5º TRD: 2-12º *Mdn*: 4º

Description of task	**Primary plane of action**	**Joint motions**	**Active muscles**	**Movement amplitudes** *frontal*
COMBO (see details above for HIPSLD and FAP)	Trunk: *frontal* Hips: *frontal/ sagittal* Legs: *sagittal*	(see details above for HIPSLD and FAP)	(see details above for HIPSLD and FAP)	Low freq component **TRD** 9-20 cm *Mdn*: 14 cm *medio-lat* **NOV** 5-13 cm *Mdn*: 9 cm *medio-lat*
Pelvis describes a continuous infinity sign trajectory: up the middle in Maya, down the middle in Serpentine - *only muscles recorded: ES from L1 to L5* **MAYA** RASIS CCW circle with LASIS CW circle **SERP** RASIS CW circle with LASIS CCW circle (down medially, up laterally)	Trunk: *frontal* Hips: *frontal/sag* Legs: *sag*	Trunk alternating lateral flex Hips alternating add, abd with pelvic lateral translation R leg ext; l leg flex L leg ext: r leg flex	Only right side ES from L1-L5 recorded. MAYA R ES: (L4 + L5) > (L1 + L2) L ES: (L4 + L5) > (L1 + L2) SERP R ES: (L1 + L2) > (L4 + L5) L ES: (L1 + L2) > (L4 + L5)	Kinematic data were not collected from participants in first data collection.

Note: plantar flexors, knee extensors, hip extensors active for postural support, weight-bearing. Ankle inversion, eversion for hip slide (muscles not recorded). FWDBND - forward bends, SIDBND - side bends, HIPSLD - hip slide, SHIM - shimmy, FAP - fast as possible shimmy, add - adduction, abd - abduction, r - right, l - left, alt - alternating, GM - gluteus medius, TA - tibialis anterior, BF - biceps femoris (hamstring), EO - external oblique, CCW - counterclockwise, CW - clockwise. TRD - trained subjects. NOV - novice subjects. In the *Active muscles* column, S = simultaneous, D = diagonal pattern, and A = asynchronous patterns of activation timing of the erector spinae (ES) as determined in the second study. The > indicates that activations in the muscles on the left of the symbol precedes that of those on the right.

1.5 FUNCTIONAL ANATOMY OF THE SPINE EXTENSORS AND RATIONALE FOR ELECTRODE PLACEMENT

1.5.1 Muscles and movement analysis

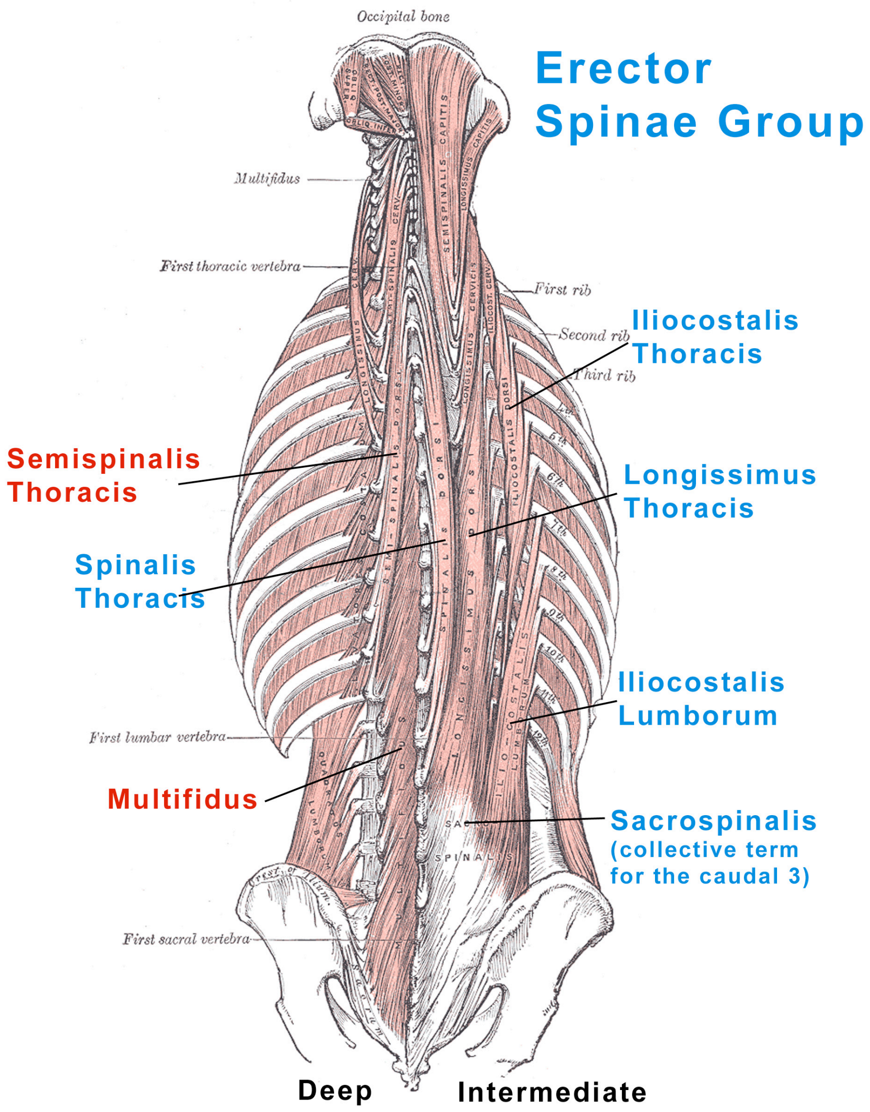
The prime movers for trunk include the abdominal muscles anteriorly and the spine extensors, posteriorly. Abdominals and spine extensors are antagonistic when activated bilaterally, but synergistic when activated unilaterally as in performing side bends and for each half cycle of the hip shimmy. The hip flexors/extensors, adductors/abductors are also important contributors to movements of the pelvis, especially for the movements which emphasize pelvic isolation mediated through full use of hip range of motion. Other important muscles involved in lumbo-pelvic relative motion include the quadratus lumborum, which has synergistic functions with the lumbar ES, and so assists lateral trunk flexion and ipsilateral pelvic rotation (hip upward), and iliopsoas (hip flexor) which assists in rotating the hip downward, but these are not accessible for recording of the surface electromyogram (SEMG). Tensor fascia latae (TFL) is a synergist with the gluteus minimus and medius in hip abduction, acting to rotate the femur medially (or assist pelvic obliquity when the foot is fixed) and also assists in hip flexion. TFL was recorded as representative of hip flexor activity. In the shimmy, hip flexion occurs with hip abduction as the ipsilateral knee and ankle flex to rotate the hip downward (Wikipedia source: Gray's Anatomy, public domain).

Across phylogeny, paraspinal muscles play a dominant role in control of the body axis during locomotion (de Seze et al. 2008; Falgairolle et al. 2006; Fischer and Witte 2007). In swimming vertebrates such as the lamprey, these muscles produce rhythmic lateral undulations for propulsion through water. In tetrapods they create the lateral undulating trunk motion that accommodates limb stride. In bipedal locomotion they stabilize the trunk sagittally and frontally and accommodate movements of the limbs. In locomotion studies, rhythmic activation patterns in paraspinal muscles have been observed. Unilateral alternating bursts once per cycle associated with lateral trunk motion during walking, appears to be overlaid with bilateral bursting twice per cycle associated with each heel strike (Anders et al. 2007; Thorstensson et al. 1982). These findings point out their dual role in control of sagittal and frontal plane rotation of the trunk in bipedalism. Only a few studies have assessed their role in producing segmentally specific trunk motion in humans (Nugent et al. 2012; Oddsson 1990; Thorstensson et al. 1985). In terms of lateral rhythmic pattern generation, this capacity has old phylogenetic roots, and is important for the coordination between trunk and limbs in both bipedal and quadrupedal gaits, and in direct production of locomotor propulsive forces in swimming vertebrates (Chevallier et al. 2008; de Seze et al. 2008; Delvolve et al. 1997; Falgairolle and Cazalets 2007; Falgairolle et al. 2006).

1.5.2 Overview of back muscle anatomy

There are three back muscle layers: *superficial*, *intermediate* and *deep*. The **superficial** layer includes those muscles that act on the scapula, humerus and ribs. These are the serratus posterior (inferior and superior), latissimus dorsi (spanning T6-lumbar fascia), rhomboids (medial border of scapula to C7-T5 and deep to trapezius), and the trapezius (occiput to lower thoracic vertebrae). The **deep** muscles of the back include the transversospinals, semispinalis, multifidi and rotatores. The **intermediate** layer includes the *erector spinae* (ES) group, consisting of spinalis thoracis, longissimus thoracis (LT), iliocostalis lumborum (IL) and iliocostalis thoracis. The extensors of the back (Fig. 1.1) are located in the intermediate and deep layers. In this study, muscle recordings were limited to regions of spine extensors accessible to surface electromyography, that is, where they are the most superficial of back muscles or are covered only by non-contractile aponeurotic tissue.

FIGURE 1.1 Back muscle anatomy

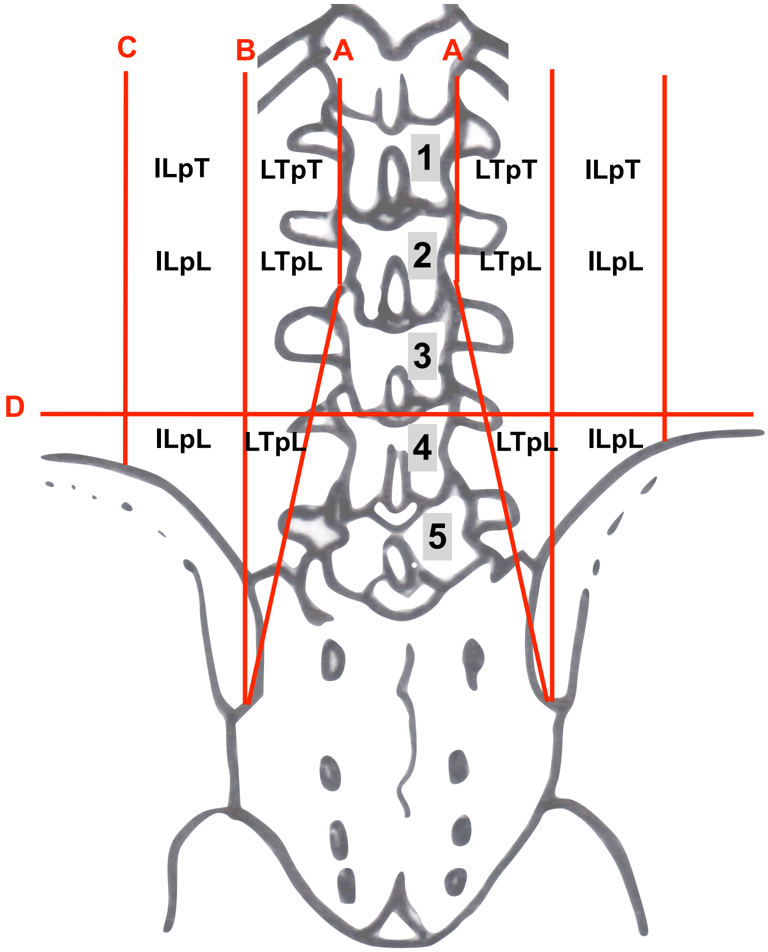


Source: http://www.bartleby.com - Gray's Anatomy, public domain.
Large text has been added.

Macintosh and Bogduk (1987) noted that in anatomical and functional descriptions, the lumbar erector spinae are frequently represented by a single fusiform muscle extending from the pelvis and iliac crest to thorax. Given this oversimplification and some inconsistencies in the literature on terminology and definitions, they undertook a detailed dissection study to establish greater anatomical accuracy which could enhance functional analysis and biomechanical modeling. The authors revealed the structural detail of the separate muscle fascicles, including precise determinations of origins and insertions, identifying in particular the insertions of the LT and IL into the lumbar aponeurosis, which they claim other authors had omitted or missed. They also showed that the LT and IL each have two distinct thoracic and lumbar portions, of which the latter had been poorly described in previous literature.

To aid future research into the functional specificity of different compartments of the lumbar spine extensors, the authors generated a grid to guide electrode placement for SEMG using surface anatomical landmarks. The result is shown in Figure 1.2. According to the authors, the lumbar ES consist of 4 components. The two main branches are the thoracic portions of the IL and LT. Deep to these are the *longissimus thoracis pars lumborum* (LTpL) and *iliocostalis pars lumborum* (ILpL). The thoracic portions both span the pelvis, lumbar vertebrae and ribs, thus acting on both the lumbar spine but named for their insertion location. The fascicles of the lumbar portions run from pelvis and iliac crest to the lumbar and lower thoracic vertebrae at roughly 90º to the thoracic fibers. The multifidus is the spine extensor lying closest to the spine and runs from the sacrum to the axis. The principal role of the multifidi is to produce extension torques to oppose trunk flexion and thus they function primarily as postural stabilizers (Macintosh and Bogduk 1986).The lumbar portion of the multifidi is more superficial and covered only by the lumbar aponeurosis and is accessible to SEMG in this region.

FIGURE 1.2 Electrode placement grid for selective recording from lumbar spine extensors.



Redrawn from MacIntosh and Bogduk (1987).

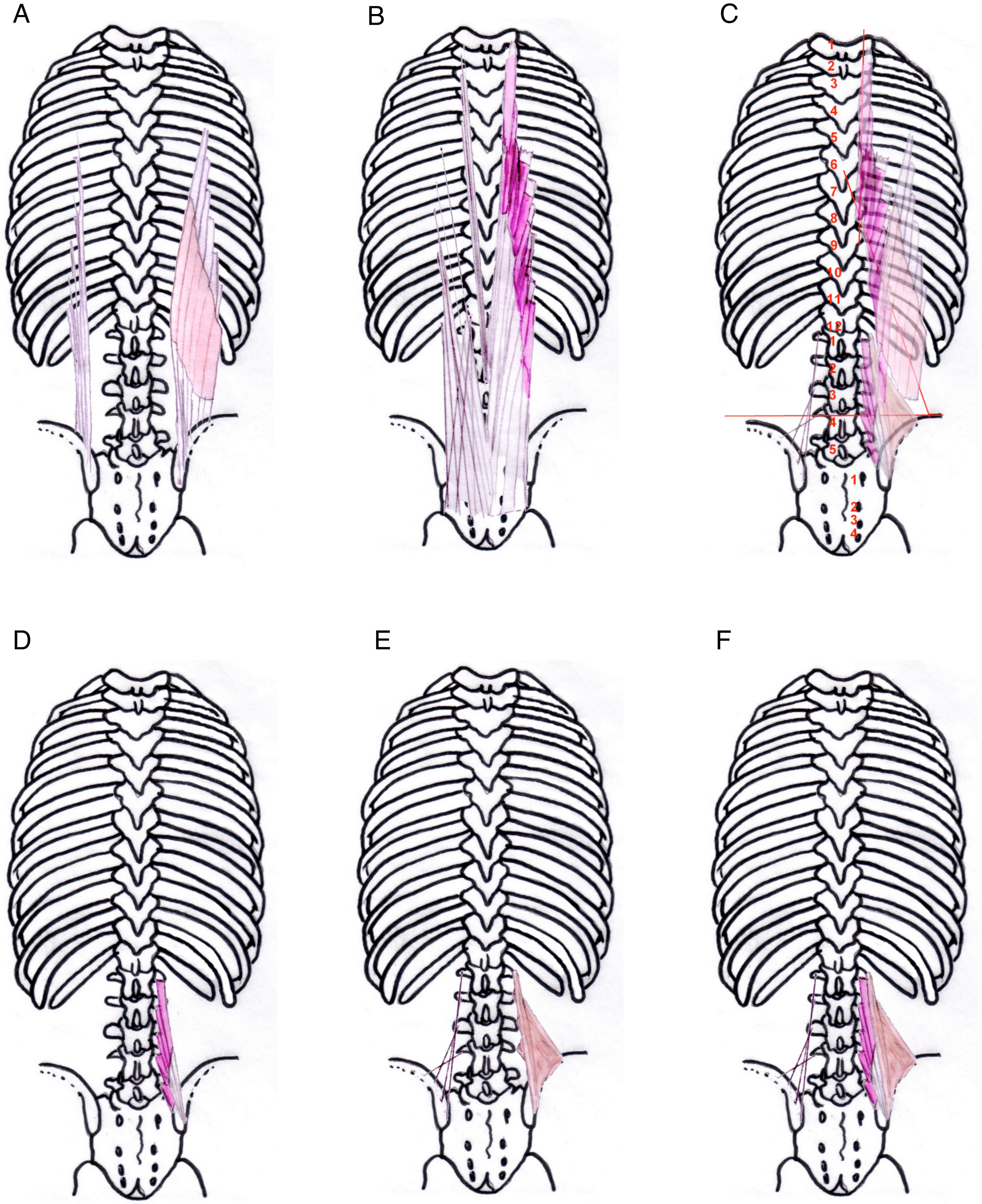
The most superficial structure in the lower lumbar region is the erector spinae aponeurosis (ESA). The caudal tendons of the Il and the LT form the lateral and medial portions, respectively, of the ESA. The most superficial and lateral portion of the ES is the thoracic portion of the IL which arises from its caudal tendons along the iliac crest to insert at the angles of the lower 8-9 ribs. (Fig. 1.3A). The thoracic portion of the LT lies medial to the IL and is deep to the

IL along its lateral border (Fig. 1.3B). The caudal tendons of the LT create a thick sheet forming the medial portion of the ESA along a horizontal line across the sacrum at the S4 level and along the posterior edge of the ilium. The LT inserts on the transverse processes at every thoracic level as well as on the ribs from T3 or T4 and below. The structure of LT is a combination of overlapping and convergent fascicles.

Deep to the ESA, the LTpL and ILpL are visible, having no attachments to the ESA which moves freely over their fibers. Removal of the ESA and the thoracic fascicles of LT reveals the lumbar fibers of the LTpL (Fig. 1.3C). Five overlapping fascicles lateral to multifidus arise from the PSIS to insert on accessory and transverse processes of all 5 lumbar vertebrae. The caudal tendons of fascicles 1-4 form the lumbar intermuscular aponeurosis (LIA) which separates the LTpL from the ILpL. The ILpL is the deepest of the four lumbar ES components. Its structure is formed by 4 large fascicles arising from the transverse processes of L1 (most superficial) to L4 (deepest) (Fig. 1.3D). The more rostrally originating fascicles attach more medially along the posterior iliac crest and the more caudally originating fascicles attach more laterally to the iliac crest, with the result that these fascicles overlap and their fiber directions are not all parallel, but cross at angles.

Certain other anatomical details elucidated in the study are important to bear in mind when recording EMG in this region. Fascicles of thoracic LT and IL are distinct, separated by fat and areolar tissue, their fibers run at slightly different angles and have different insertion points (more medial and caudal on ribs in the case of IL) suggesting the possibility of different biomechanical functions. This fact combined with the segmental nature of contiguous fascicles points to the likelihood that differential activity at different levels may correspond to different muscles or muscle subvolumes, with different moment arms. Thus it is important to relate precise electrode positions to specific muscles, both rostro-caudally medio-laterally: the vertebral placement levels and medio-lateral placement distances of electrodes from midline are not arbitrary.

FIGURE 1.3 The four components of the lumbar erector spinae.



(A) ILpT, (B) LTpT, (C) all four layers, (D) LTpL, (E) ILpL, (F) Relative location of the lumbar components - LTpL superficial to ILpL.

1.5.3 Electrode placement grid of lumbar muscles surface Anatomy

> *Although seemingly academic, these specifications are not without functional significance. It is notable that very few electromyographic studies have recorded from the erector spinae below L3. Between L1-3 the strongest electromyographic signals would arise from the thoracic components of longissimus thoracis and iliocostalis lumborum and do not necessarily reflect the activity of those fibers of the erector spinae that attach to, and therefore act directly on, the lumbar vertebrae. The activity of these latter fibers remains unknown, and there is scope for electromyographic studies of the lumbar fibers of iliocostalis lumborum and longissimus thoracis, which morphologically are so different from their thoracic fibers and presumably have a different action and function.*
>
> - Macintosh and Bogduk 1987, p. 667.

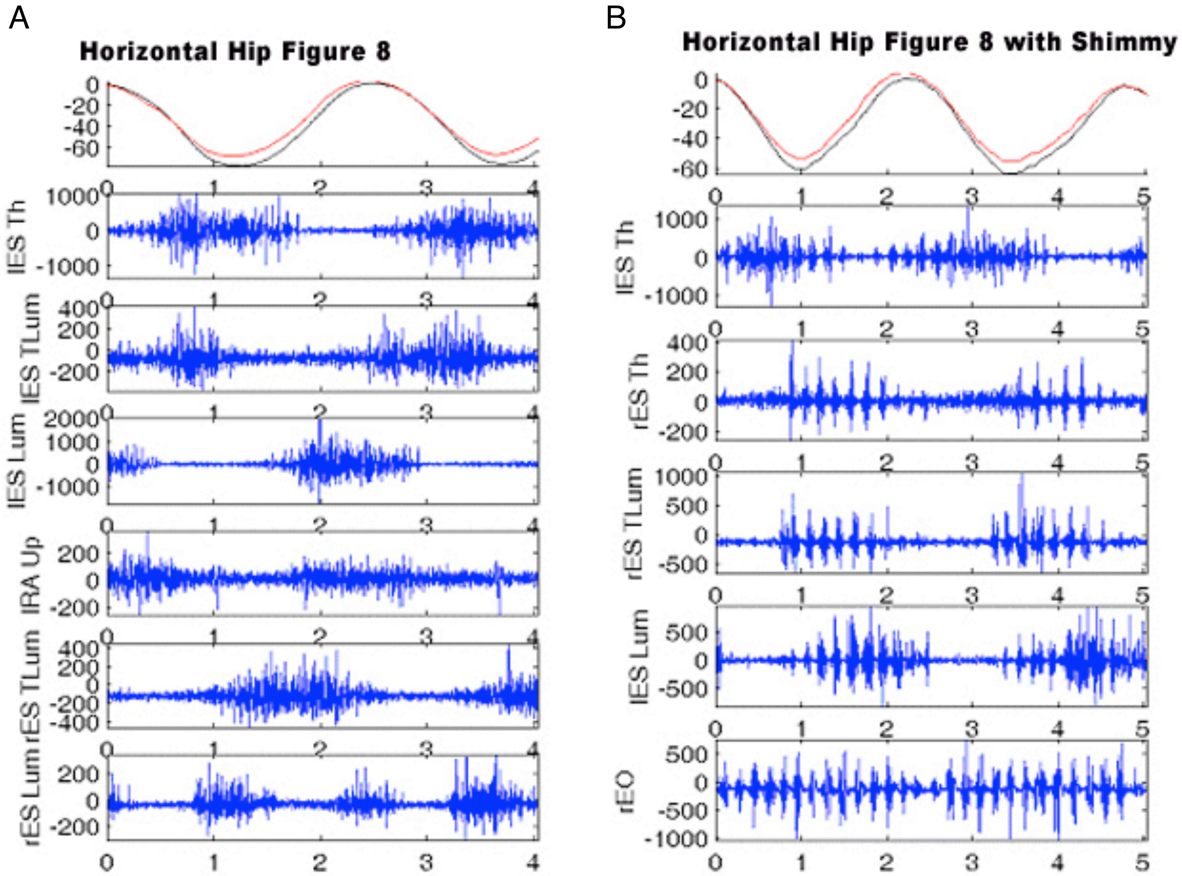
Figure 1.2 is a redrawing of the grid based on identification of surface anatomical landmarks created by Macintosh and Bogduk (1987) for specific electrode placement to record from the different portions of the ES and multifidus. To highlight the major points: *Line A* demarcates lateral margin of the lumbar multifidus, most accessible to SEMG at about the L4 to L5 levels medial to a diagonal line running from PSIS to 2 cm lateral of the L2 spinous process. *Line B* represents the longitudinal borders between the LT and the IL. *Line C* is meant to represent the palpable lateral border of the ES (i.e., that of IL). In reality, this border appears more diagonal, as the longitudinal muscle bulge can be seen to run rostro-laterally. *Line D*, running horizontally at the level of the bottom of the L3 spinous process represents the lower limit of thoracic fibers for IL and LT.

1.6 PROJECT OVERVIEW

This project began in a directed studies course for my undergraduate degree in kinesiology, in which I recorded kinematics and electromyography of myself performing a variety of belly dance movements. The objective was a general one: to characterize the kinds of muscle activation patterns during movements involving different numbers of body segments and levels of complexity, performed in different ways (e.g. slow vs. fast, continuous vs. rhythmic) and in different planes of motion. In that early study, one observation stood out and was particularly intriguing: the "layered" movement, such as when a slow, continuous movement figure is performed while overlaying the fast hip vibration, produced EMG patterns with distinct high *and* low frequency envelopes. It appeared that the high frequency activation was modulating the low frequency burst pattern, with periodic inhibition strong enough to reduce muscle activity to levels below baseline (Fig. 1.4). We postulated two separate control signals going to the same muscle, with the high frequency signal modulating the low frequency pattern. This observation raised some interesting theoretical questions: Can we verify that these component patterns originate from separate control signals? Through experimental manipulation can we infer the underlying mechanisms and origins within the CNS? By comparing the separate patterns with the combined ones, and patterns in trained versus novice performers, what can we infer about the integration of different levels of control in the coordination of complex movement? What are the neural circuits likely being utilized to produce these movements? How are these circuits modified by training?

The goal of the first study was to use belly dance movements to elucidate the functional compartmentalization within lumbar erector spinae muscles. The data collected for my undergraduate study showed that ipsilateral thoracic versus lumbar spine extensors could switch roles from synergists to antagonists, depending on the task. In the first study presented here, by recording muscle activity at specific sites spanning L1 to L5 during the performance of segmentally specific pelvic isolation movements, I expected to find greater rostral-caudal and medio-lateral specificity than had previously been shown. In addition, I expected to find a difference in lumbar ES muscle activation patterns between novices and trained dancers, at higher tempos if not at lower ones. The assumption was that novices would not be able to produce the same degree of activation timing difference across lumbar ES muscles as trained dancers.

FIGURE 1.4 Examples of first recordings of low frequency and polyrhythmic movements.



(A) Low frequency hip figure 8 and (B) composite movement of figure 8 and high frequency shimmy.

The second experiment extends the investigation of activation timing patterns in paraspinal muscles during rhythmic movement to elucidate hierarchical control mechanisms in a complex, multi-segmental trunk movement. The experimental conditions comprised the hip shimmy at different frequencies. Electrode placement spanned a wider range of segmental levels than in the initial study to allow elucidation of a more elaborate activation patterns, if such existed, and more detailed comparisons amongst different patterns. In this study, tempo was manipulated to evaluate the effect of movement frequency on coordination patterning in ES compartments. Trained and untrained performers were compared, with the expectation that higher frequencies of the hip shimmy can only be achieved with extensive practice. If low and high frequency versions of the shimmy are under the control of different mechanisms, as expected, this should be evident in differences in muscle coordination patterns. Initially it was unknown whether spine oscillations of the much smaller amplitude and higher frequency, which characterize the fast shimmy would also elicit asynchronous activation across lumbar muscle segments, or if there is a biomechanical limit which constrains timing specificity. I expected to find differences between trained and untrained performers in the specificity of the timing pattern. Considering that fast and slow versions of the same action have different dynamics, which imposes different constraints regarding the applicability of voluntary versus automatic control, I expected that different patterns would be elicited at different tempos. Comparisons between patterns and different speeds and between expert versus naive performers were expected to provide insight into the underlying control mechanisms. Assuming trained performers utilize more automatic control (a hallmark of expert skill levels), such as spinal pattern generators, muscle and kinematic patterns would be expected to breakdown when novices attempt the same movements at higher tempos, indicating an inability to modulate innate circuits. No difference between training groups would indicate that performance merely requires selection and activation of the correct innate motor program - supraspinal in initiation but automatic - spinal (pattern specification) and or brainstem (postural adjustment and maintenance) in execution.

The final study was an investigation into the simultaneous superposition of two different types of movements - a slow, large amplitude movement and a fast spine oscillation - to try to parse out the roles of different CNS levels in the control of a complex voluntary movement. Trained belly dancers are able to “layer” the fast shimmy over slower, continuous movements. Envelopes at both frequencies in one muscle activation pattern are clearly visible in EMG recordings. We hypothesized that this represents the integration of two separate control signals going to the same effectors. The premise of this study was that by comparing the patterns in the isolated movements with the decomposed versions from the combination movement, the forms in which the patterns change would distinguish between movements under more voluntary control versus those under more automatic control, as well as provide insights into how the CNS integrates two control signals from different hierarchical levels. Once again, novice versus trained performers were compared with the expectation of thereby being able to distinguish between motor patterns that utilize voluntary (supraspinal) versus more automatic (spinal and reflex modulation) mechanisms of control, or that appear to recruit innate circuits through selection (no prior experience needed) versus those that require learned modulation of circuits through extensive practice.

To summarize, the questions posed in each study are the following:

Study #1

Independent activation in adjacent lumbar extensor muscle compartments (published)

Given the assumption that previous studies of global trunk movements (typical belly dance movements) have not fully elucidated the ability of the CNS for segmental specification of trunk motion, what is the degree of compartmentalization in human spine extensors? Can specific trunk isolation tasks reveal functional differentiation within lumbar spine extensors? Do trained and untrained performers differ in the capacity for compartmental control (activation timing difference in adjacent ES compartments)? How does tempo affect activation timing differences within the lumbar ES? Are timing differences preserved at increased tempos? Specifically, are they preserved in experts and lost in naive performers, i.e. does practice have an effect on the capacity for compartmental control?

Study #2

Segmental specificity in belly dance mimics primal trunk locomotor patterns (in press)

Are slow versus fast tempo lateral spine undulations characterized by different muscle and kinematic patterns? Are segmental trunk motions of higher frequency and smaller amplitude characterized by asynchronous or synchronous activation of spine extensors? Are low frequency versus high frequency lateral trunk oscillations controlled by different mechanisms? Do ES activation patterns in belly dance resemble locomotor patterns in other animals or humans? Is the mechanism of control affected by training, i.e. to what degree is coordination the result of accessing or modifying genetically inherited circuits? Can elucidation of these patterns provide evidence of phylogenetic conservation of trunk locomotor circuits in humans?

Study #3

Hierarchical control in the coordination of multifrequency, multi-segmental spine motion in humans

Does the combination of two different kinds of rhythmic trunk motion result in two superposed patterns (original patterns preserved) or in a new, hybrid pattern? Are the two different patterns controlled by different levels of the CNS a) when performed separately? b) when combined? Does the combination of high and low frequency segmental trunk motion utilize two separate control signals originating from different levels of the nervous system? If so, where are the two signals likely integrated? Is training required for successful superposition of the two patterns? What are the likely mechanisms/control centers?

Chapter 2

General Methodology

General Methodology

2.1 ELECTROMYOGRAPHY

Surface electromyography (SEMG) is a non-invasive method for recording muscle activity by capturing the electrical potential difference between two passive electrodes, as a wave of muscle membrane depolarization during muscle contraction passes within range of their pickup volume. While SEMG is limited to recording from superficial muscles or those covered only by non-contractile aponeurotic tissue, it nevertheless gives a better picture of whole muscle contraction that needle electromyography when the overall activity of large muscles is of interest. Needle EMG is preferable for assessing the activity in small muscles or individual muscle fibers since recording range is very localized. While this approach might have yielded even higher indications of selective activation within spine extensor muscles, needle electromyography is susceptible to movement artifact, which, in the case of the movement tasks used in this study, would likely cause excessive corruption of the EMG signal. Additionally, the invasiveness can have negative consequences on subject recruitment. Thus, SEMG was chosen as the best option for this study.

Adequate knowledge of muscle functional anatomy is a requisite for acquiring high quality EMG data. If recorded muscles are not accurately identified the validity of functional interpretations could be suspect. Electrodes should be placed over the muscle bellies (usually the mid-point, longitudinally, and medio-laterally where the bulge is thickest when contracted), away from the non-contractile portions near joints (e.g. tendons) and in parallel with muscle fiber direction. Care should be taken not to place electrodes close to their borders with adjacent muscles to ensure the activity recorded corresponds to the specific actuators under investigation, thereby maximizing signal strength and limiting the pickup of interference signals (crosstalk) that may obscure or distort the activation profile. Ideally electrodes are placed near innervation zones if they are known, in order to maximize signal strength. The innervation zone or motor point is located by stimulating with active electrodes to determine the lowest stimulation strength required to activate the muscle fibers. This is a time-consuming and somewhat invasive procedure, and is not normally used in studies of muscle function and coordination patterns. As well, since the aim was to record from a number of specific muscle regions, with placement of electrodes fairly close together, localization of motor points might have compromised relative placements of electrodes. Due to these factors and additional time constraints of keeping the protocol under 4 hours (an ethics concern) this procedure was deemed non-viable and unnecessary.

2.2 EXPERIMENTAL PROTOCOL: MUSCLE IDENTIFICATION, ELECTRODE SITE LOCALIZATION AND PLACEMENT

For experimental recording of muscle activity in subjects of normal BMI, location of most of the superficial, large prime mover muscles is usually straightforward and easy to verify by viewing the EMG trace during simple muscle test contractions. Electrode placements have been well described in numerous clinical and research studies on human physical function. Accepted guidelines for optimal location based on anatomical landmarks have been provided (Hermens et al. 1999). However, the separate extensor muscles of the back are rarely visually obvious and can be difficult to identify. In studies on back muscle function in locomotion, investigators typically limit recording of the lumbar ES to one vertebral level. Guidelines for placement involve identifying the level of a specific vertebral spinous process and measuring a specified lateral distance from the midline of the spine (c.f. SENIAM guide). For both improved ease and accuracy of placement on lumbar spine extensors, MacIntosh and Bogduk (1987) offer a localization grid and detailed guidelines for muscle site localization on the posterior lumbar region of the trunk to selectively record from lumbar multifidus and erector spinae spanning L1 to L5 levels (see Figure 1.2 from Chapter 1). In addition, to furnish myself with a better understanding of muscle locations, origins, insertions and fiber directions, I viewed dissected cadavers at the McGill Anatomy lab. Additional information on fiber direction and electrode placement were found in (De Foa et al. 1989; de Seze and Cazalets 2008). I also referred to the classic anatomical reference, Gray's Anatomy, available online (see Bartleby.com) and of which many open source diagrams are also available.

All electrode localizations on subjects were based on anatomical reference landmarks through visual inspection and manual palpation: the spinous process of the seventh cervical (C7) vertebra - the most prominent protrusion at the base of the neck when the head is dropped, T8 - counting down via palpation, from the C7 and mark by noting the protrusions from the spinous processes of each vertebra and intervertebral spaces. T8 location can be confirmed according to the criteria of coincident level with the tip of the scapula when the subject's trunk position is upright. T10 location can be verified by viewing from the side while placing one finger on the spinous process and one at the base of the sternum - these should be at approximately the same level. The difference between T12 and L1 is visually and or tactilely apparent due to the difference in shape of the spinous processes. The lumbar vertebrae have spinous processes that are long and rectangular, compared to the more point-like (round bump) configuration of the spinous processes of the thoracic vertebra. This can be seen in the photo of electrode placements on subjects in Chapter 4 Figure 4.1.

L4 and L5 spinous process can be a little more difficult to locate as they may be hard to distinguish with those of the sacrum. Two additional cross-references are useful. Placing the fingers atop the iliac crests and joining the thumbs together, the L4-L5 space is located approximately where the thumbs indicate (Chakraverty et al. 2007). Additionally, the posterior superior iliac spines are easily palpated, and there should be no more or less than four finger-widths diagonal distance between each one and the middle of the spinous process of the L5 vertebrae. This helps to avoid the error of misidentifying L4 as L5, in cases where L5 is not easily palpable. Although abdominal, hip and leg muscles (right side) were also recoded in these studies, analysis was limited to the ES muscles in order to focus the scope of the investigations. Future analyses will be undertaken to evaluate the coordination between legs and trunk.

2.3 ADDITIONAL DATA TRIALS NOT YET ANALYZED

Because of the considerable amount of time required to localize electrode sites and instrument the subjects for data collection (2-2.5 hours), I recorded a number of additional movements for future analyses. These included sagittal plane undulations at 0.5 and 1 Hz frequencies, from both NOV and TRD subjects, forward bends, side bends, and in some subjects, hip twists. These movements were selected to answer the future questions on differences in multi-segmental muscle activation patterns in different planes of motion. Additionally, during data collection for the second and third studies, some of the experts were asked to perform trials of the maya and serpentine movements used in the first study. In that study, kinematics were not recorded, nor were other muscles recorded aside from the right side lumbar spine extensors spanning L1 to L5. These additional trials including kinematics, collected during experiments for the second and third study, will enable future analyses of the kinematic patterns of these movements and allow more direct comparisons with the muscle and kinematic patterns recorded in the second and third studies.

Chapter 3

Independent activation in adjacent lumbar extensor muscle compartments

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Preface to the first article

This study began as an investigation into the capability of the CNS for neuromuscular specificity in lumbar spine extensors, as revealed using segmental trunk tasks from belly dance. From my undergraduate directed studies project, I had data showing that ipsilateral ES regions at the T10 and L4 levels were activated antiphasically during large amplitude lateral hip slide movements, or in figure 8s and twists in the transverse plane, even showing non-synchronous activity between the T12/L1 and L4 levels. The aim of this study was to determine the level of selective activation within lumbar spine extensors, and to this end, 8 electrodes were placed over the right lumbar region. The movements used (vertical figure 8s), cyclic pelvic isolation movements in the frontal plane (see videos at www.facebook.com/Shimmylab), were chosen to limit the activity of spine extensors as much as possible to their role of producing spine lateral flexion (as opposed to a combination of lateral flexion and rotation around the longitudinal axis). Performers of different expertise levels were compared, and movements were performed at two different tempos (0.5 and 1 Hz) to evaluate the influences of training and increasing difficulty on neuromuscular coordination patterns (relative activation timing in ipsilateral ES).

The novice subjects were recruited mostly from the belly dance classes I was teaching in Montreal at the time. They had been studying for some weeks or months but had no prior experience with the movements studied. I had expected to find a difference between novices and trained dancers in the ability to specify the separate compartments, i.e. I predicted that timing asynchrony would be greater as a result of extensive practice. In fact, results pointed to the opposite conclusion, that the control mode involved was innate and not learned, dependent on the biomechanical requirements of the movement, and had only to be selected. This despite the fact that untrained blind raters could easily classify each subject as beginner, intermediate or advanced in skill, with good inter-rater consistency and correlation with amount of training.

The results of this study confirmed the feasibility of using belly dance movements to investigate the specificity of neuromuscular function in spine extensor muscles. It appeared that this paradigm could also be used to dig deeper into the underlying control mechanisms of complex voluntary trunk movements, i.e. by providing a means to distinguish between movements that are generated by innate neural circuity and those that require practice to learn how to modulate or reorganize existing neural pathways.

ABSTRACT

The purpose of this study was to examine compartmentalization in human lumbar spine extensors. Structure and innervation of these muscles would suggest the possibility of more segmentally specific biomechanical functions than have been found in previous studies examining muscle activation patterns during simple spine bending and twisting tasks. We selected specialized tasks to more effectively investigate the degree of independent control possible within lumbar spine extensors. We recorded surface electromyograms (SEMG) from the right posterior lumbar region during performance of two segmentally specific belly dance skills by seven novice and five trained subjects. These movements were performed at two frequencies (0.5 and 1 Hz). Cross-correlations were performed between pairs of rectified, low-pass filtered (6 Hz) SEMG signals to determine temporal lags between rhythmic bursts. Results showed a difference in the timing of muscle activation above and below the third lumbar vertebra. Temporal asynchrony was independent of either skill level or tempo, suggesting a hard-wired capacity for independent control of adjacent muscle compartments. The results have implications for understanding trunk control in the context of postural stability and postural adaptation during locomotion, as well as for lower back functional assessment and rehabilitation.

3.1 INTRODUCTION

Proponents of the partitioning hypothesis (English et al., 1993) or neuromuscular partitioning (Stuart et al., 1988) contend that the fundamental control units of the central nervous system (CNS) are not whole muscles but muscle compartments innervated by their own primary nerve branches, with localized stretch reflexes and distinct biomechanical functions (English et al., 1993). Support for this hypothesis is extensive, including a range of studies using different methods to identify distinct neuromuscular compartments via evoked EMG mapping (English and Weeks, 1989), glycogen depletion (English and Letbetter, 1982; English and Weeks, 1984), response to perturbations (Chanaud and Macpherson, 1991), compartmental specificity of single motor unit activation (English and Weeks, 1984, 1989), associated stretch reflex circuits (Liddell and Sherrington, 1924; Cohen, 1953), and compartmental specification based on mechanical advantage (ter Haar Romeny et al., 1984; van Zuylen et al., 1988; Herrmann and Flanders, 1998; Wickham and Brown, 1998; Staudenmann et al., 2009). A number of studies have examined compartmentalization in the muscles of the upper and lower limbs in animals (see English et al., 1993) and humans (as referenced above), but research on compartmentalization in human trunk muscles is limited. Differential activation of muscle compartments has been found in such trunk muscle as the external obliques (Mirka et al., 1997), rectus abdominus, (Moreside et al., 2008), and lumbar multifidus (Moseley et al., 2003) but to the best of our knowledge there have been no studies that have investigated functional compartmentalization in lumbar erector spinae (ES).

The structure and innervation of lumbar spine extensors suggests the possibility of a more segmentally specific biomechanical function (Bogduk, 1980; Bustami, 1986; Macintosh and

Bogduk, 1987) than has been found in previous electromyographic analyses of simple spine bending and twisting tasks. The multi-articulated design of the spine allows for flexible specification of the number of functional units depending on task requirements. An outstanding question is the degree to which segmental specificity is possible through selective activation of muscle compartments. Considering the paraspinals as a group of muscles with different functions (Jonsson, 1973), MacIntosh and Bogduk (1987) described the anatomy of superficial muscles within the posterior lumbar region: the multifidus (MULT), and the medial longissimus thoracis (LT) and lateral iliocostalis lumborum (IL) divisions of the ES. They also identified a deeper portion of the ES, which they contend is often overlooked by anatomists. This compartment is comprised of partially overlapping fascicles running rostro-medially from the iliac crest to insert on each of the lumbar vertebrae. It is sufficiently superficial to be accessible to surface EMG (SEMG) caudal to L3 where it is covered only by aponeurosis. The fascicles of the superficial compartment run rostro-laterally from the aponeurosis to the lower costal area, thus acting indirectly on the lumbar vertebrae as they do not insert on the spinal processes. The authors predicted that these two portions of the lumbar ES, superficial and deep, would be capable of different biomechanical functions by virtue of their distinct locations and fiber directions and created a grid to guide the placement of surface electrodes to record differentially between MULT, LT and IL and between the deep and superficial portions of the lumbar ES, accessible to SEMG below and above L3, respectively (Macintosh and Bogduk, 1987).

Studies using a variety of static and dynamic postural tasks in different planes of motion have examined activation patterns of the spine extensors to determine biomechanical functions of individual muscles at different spinal levels (Floyd and Silver, 1955; Morris et al., 1962; Jonsson, 1970; Donisch and Basmajian, 1972; Jonsson, 1973; Pope et al., 1986). None of these studies showed independent activation of adjacent ES muscle bundles within the ipsilateral lumbar region, although differential activity between thoracic and lumbar regions was recorded during a variety of spine bending and twisting tasks (Morris et al., 1962; Donisch and Basmajian, 1972). Since these initial studies, a plethora of research has been conducted on muscle activation patterns, particularly as applied to low back pain and work-related loading of the spine. In several of these studies SEMG has been recorded over the bilateral lumbar region using large arrays of evenly spaced monopolar electrodes in static postures (Finneran et al., 2003; Reger et al., 2006) and during dynamic flexion–extension tasks (Hu et al. 2010). The objective of these studies was to determine whether topographical and amplitude differences in the spatial gradient of muscle activity could distinguish between low back pain patients and healthy individuals. No attempt was made to relate the spatial gradient of activation to specific muscle compartments or to their biomechanical function, nor was the temporal organization of the muscle activation analyzed.

Differential recording from specific compartments of the lumbar spine extensors during dynamic, segmentally specific tasks would provide more insight into the neuromechanical potential of these compartments. In pilot studies using specific belly dance movements, we found temporal asynchrony in the activation of ES at lower thoracic vs. lumbar vertebral levels. Certain movements elicited anti-phase antagonistic activation in contralateral spine extensors at different segmental levels, while others showed temporal asynchrony in ipsilateral ES muscles at different segmental levels. We chose frontal plane pelvic ‘figure eight’ movements, which can be performed in two different directions, as the movement paradigm expected to elicit separate, asynchronous compartmental activation.

The goal of the present study was to determine the degree of independent compartmental control, assessed by quantifying temporal asynchronies in muscle activation, across different segmental levels of the lumbar paraspinals. We predicted that whereas global spine bending would show synchronous activation, the lumbar spine extensors above and below L3 would be activated at different phases of the figure eight movement cycles, respectively. We further predicted that the difference in activation timing between these regions would vary with the type (simple bend vs. figure eight) and direction (maya vs. serpentine) of movement.

The study also addressed the question of whether the ability to independently activate muscle compartments would depend on skill level (degree of learning) or increased movement tempo (task difficulty). We predicted that less trained subjects would activate muscles more synchronously and that muscles would be activated more synchronously for movements performed at faster tempos (loss of independent control).

3.2 METHODS

3.2.1 Subjects

Fourteen healthy female subjects aged 19–56 years (mean 34.8 ± 11.8) participated voluntarily and signed an informed consent form. The study was approved by the Research Ethics Board Office, McGill University. Subjects were classified as novices (0–1 year of training, N = 7, mean = 0.3 ± 0.23, range 0–0.6 years) or trained (more than 1 year of training, N = 7, mean = 14.3 ± 10.3, range 3–29 years). All subjects were without musculoskeletal disability or injury, however, one subject had an obvious lumbar scoliosis. In an initial data collection session, EMG only was recorded from 12 subjects (subjects 1–12 in Table 1). Subjects 11Tr and 2No from the first collection session and two new novice subjects participated in a second session several months later, during which kinematic data were collected in addition to EMG.

3.2.2 Kinematics

Kinematics were recorded from the four subjects in the second data collection session using the VICON 6 camera system and standard Plug-in-Gait full body marker set. Kinematic data were sampled at 200Hz. The subject was oriented such that lateral displacement to the right was in the positive x direction, forward sagittal displacement was in the positive y direction, and upward vertical displacement was in the positive z direction.

3.2.3 EMG

Muscle EMG patterns were recorded using custom-made differential bipolar surface electrodes with circular stainless steel contacts of diameter 3 mm, and inter-contact distance 13.5

mm (center–to–center). These electrodes have high selectivity due to their small size. The gain was adjusted between 100 and 1000. Input impedance was 10 ohms, with 2 pF capacitance. Slope of the cut-off was –15 db per decade. Electrodes had internal 30–500 Hz first order band-pass filters. EMG was sampled at 2000 Hz and stored in a computer for digital processing. Signals were recorded from the extensors of the lumbar spine accessible to surface EMG (Macintosh and Bogduk, 1987). Electrode placement was based on the grid created by MacIntosh and Bogduk (1987) to differentially record from thoracic (superficial) vs. lumbar (deep) portions of the lumbar ES where their fibres are accessible to SEMG above and below L3, respectively. Additionally, placement locations were selected to record separately from MULT, LT and IL. Fig. 3.1 illustrates electrode placement on a representative subject. Specific lumbar vertebrae and other anatomical landmarks were determined through manual palpation.

Prior to EMG recording the skin was shaved where necessary and cleaned with alcohol swabs. A small amount of electrode gel was applied to the contacts prior to securing the electrodes to the skin with double-sided medical grade tape. Eight electrodes were placed over the right lumbar region. Electrodes 1 and 2 were positioned to record activity from MULT at L5 and L4 levels, respectively. Electrodes 3, 5 and 7 were positioned to record from LT at levels L4, L2–3 and L1, respectively. Electrodes 4, 6 and 8 were positioned to record from IL at levels L4, L2–3 and L1, respectively. Electrodes were aligned with the estimated fibre direction as indicated by anatomical diagrams and cadaver dissections. After placement, electrode signals were tested while recording lumbar alternating flexion/extension motions.

FIGURE 3.1

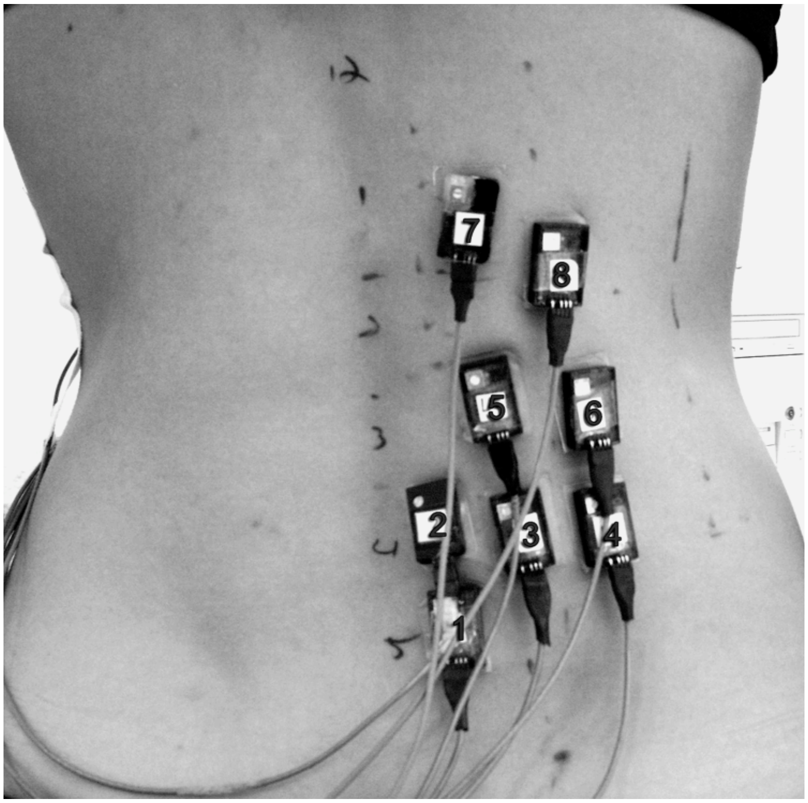


FIG. 3.1 Electrode placement on a representative subject (based on the grid from MacIntosh and Bokduk, 1987).

3.2.4 Procedure

Two types of common intermediate level belly dance movements, maya (Maya) and serpentine (Serp) were chosen based on pilot data showing asynchronous activation between lower thoracic and lumbar levels of the ES during these movements. Two comparison tasks were chosen for which activation of the ES at these two levels was expected to be synchronous: alternating spine flexion/extension in the sagittal plane (FwdBnd) and alternating spine lateral flexion/extension in the frontal plane (SidBnd).

The performance of maya and serpentine movements involves moving the pelvis in a figure eight pattern (similar to an infinity sign) in the frontal plane using anti-phase hip and leg motions. This is achieved by combining mediolateral pelvic translations with rotations of the pelvis around an anteroposterior axis (pelvic list). Spine motion is predominantly lateral flexion. Lower limbs alternately flex and extend, with alternating adduction/abduction of the hips. The two movements differ in direction, e.g. during the right-hand loop of the maya, the right anterior superior iliac spine moves clockwise, whereas during the serpentine, it moves counterclockwise. Subjects were instructed to avoid twisting, but depending on skill level, rotation of the spine and pelvis in the transverse plane was present to varying degrees. The movement cycles were performed at frequencies of 0.5 and 1 Hz in time with a metronome set at 60 and 120 beats/min respectively (one beat per half cycle). Each trial consisted of 10–13 cyclic repetitions recorded continuously for 12 to 40 s durations, depending on tempo. Although up to six trials could be analyzed for some subjects, due to technical problems and poor performance of the figure eight movements, only one trial could be analyzed for others. One trial was recorded for each of forward bends and side bends, for two to three repetitions (4 s cycle period).

3.2.5 Data processing

EMG records without a clear rhythmic bursting pattern were excluded from analysis. These were sometimes seen in the case of subjects with thicker skinfolds in the region of the recording electrodes. The data from two subjects had to be excluded entirely for this reason (see Table 3.1). To distinguish between synchronous and asynchronous activation of adjacent muscle compartments, we defined synchrony as a difference of less than 60 ms in the time of the cross-correlation peak between rectified, low-pass filtered SEMG at two recording sites: the choice of

60 ms was based on the presumed twitch rise time of a fast-twitch motor unit since sequential activation of two muscle compartments within this interval would tend to produce a synchronous buildup of force. Although a smaller time difference could have been chosen, 60 ms was adequate for our purposes since there was a marked contrast with asynchronous patterns which differed in timing by several hundred milliseconds.

Subject demographic data, as well as the number of usable trials by condition are listed in Table 3.1. Custom Matlab (The Mathworks, Natick, MA, USA) script was written for processing and plotting the raw data.

3.2.6 Activation timing

Raw EMG was full-wave rectified and low-pass filtered using a digital third order Butterworth filter with a 6 Hz cutoff frequency. The Matlab function ‘filtfilt’ was used to avoid introducing time lags. Cross-correlations between simultaneously recorded EMG signals from pairs of electrodes were performed using the Matlab function ‘xcorr’. The time of the peak of the cross-correlation function lag was used to represent the difference in timing of the command to the muscle compartments under the electrodes. The electrode at the top right corner of the grid (electrode 8) by virtue of its rostral location would record either leading or lagging activation compared to the more caudally situated electrodes. It was, therefore, selected to be the reference electrode for determining relative differences in the timing of muscle activation between recording sites. A negative lag indicated that bursts were initiated first at the L1 level (electrode 8) and later at the site being compared, whereas a positive lag indicated the reverse. Lags for each site were averaged across trials by condition and subject. For some novices, only portions of a trial contained a regular bursting pattern because the subject was unable to maintain the rhythmic movement pattern for more than a few cycles. In these cases, the sections where the rhythmic pattern was lost were excluded from the cross-correlation analysis. Sections retained for analysis were at least 15 s in duration, representing 6–14 movement cycles.

TABLE 3.1 Subject data.

						Number of trials used in analysis					
Subject	Ht (m)	Mass (kg)	BMI	Age (yrs)	Training (yrs)	Fwd Bnd	SidBnd	Maya .5 Hz	Serp .5 Hz	Maya 1 Hz	Serp 1 Hz
1No[1]	1.54	45.0	18.97	33	0.08	1	1	3	1	-	-
2No	1.64	44.5	16.73	19	0.21	2	2	5	6	2	3
3No*	1.50	37.8	16.80	29	0.5	1	1	2	-	-	-
4No	1.60	52.6	20.55	33	0.5	1	1	-	-	-	-
5No	1.72	61.8	20.89	24	0.33	1	1	-	3	-	-
6Tr[2]	1.60	62.4	24.38	33	7	-	-	-	-	-	-
7Tr	1.62	62.7	23.89	51	3	-	-	-	-	-	-
8Tr	1.76	65.6	21.18	52	14	1	1	1	-	1	-
9Tr	1.72	55.4	18.73	23	9	1	1	1	1	1	1
10Tr	1.69	65.5	22.92	37	10	1	1	3	2	2	1
11Tr	1.65	55.5	20.39	45	28	2	2	5	5	4	4
12Tr	1.62	56.4	21.49	56	29	1	1	1	1	1	1
13No	1.63	55.3	20.81	26	0	-	1	4	3	3	4
14No	1.77	66.2	21.13	26	0.6	1	1	3	2	4	3
Mean	1.65	56.19	20.63	34.79	7.30	$N = 11$	$N = 12$	$N = 10$	$N = 9$	$N = 8$	$N = 7$

*Subject with scoliosis

[1]No: novice; [2]Tr: trained.

2.7. Statistical analyses

Significance level was established as $p < 0.05$. To test the assumption that differential activation occurs at different locations within the lumbar region, all movement conditions were pooled and a Kruskal–Wallis rank test of independent samples was performed across the eight electrodes in which the pooled lag values for each electrode were first compared to the others. Subsequently, the electrodes were partitioned into two groups based on the a priori hypothesis of differential activation of functionally distinct muscle compartments below (electrodes 14) and above L3 (electrodes 5–8). If the quality of the data for a given electrode did not allow for accurate lag values to be calculated, for a given trial it was not included in the analysis. This amounted to 7% of the data. Timing of EMG relative to the reference was compared between electrodes to determine if the muscle fibres within the recording volume of the respective electrodes could be considered as a functional unit, i.e. activating simultaneously under all movement conditions. A one-way ANOVA with electrode location as a factor was performed on the lags from electrodes 1–4 (region below L3). Post hoc Bonferroni comparisons were performed between each pair of electrodes (6 tests, adjusted $p < 0.0083$). The lags from electrodes 5–7 (region above L3) were not normally distributed so a Kruskal-Wallis rank test was used followed by post hoc Mann-Whitney U tests (3 tests, adjusted $p < 0.017$). Since electrode 8 served as the timing reference for all other electrodes its lag was identically zero.

To test the hypothesis that compartments of the lumbar ES above and below L3 were functionally distinct, the mean lag for each electrode group was represented as a percentage of the corresponding movement oscillation period, calculated individually by subject. The resulting parameter, GrpMean% collapsed across all six movement conditions, was compared for electrode groups above and below L3 using the non-parametric Mann–Whitney U test.

Lag difference was calculated by taking the difference between mean lags from above vs. below L3 and then normalising this value as a percentage of oscillation period (Lagdiff%). Lagdiff% between the two electrode groups was used to test the hypothesis that relative timing of activation above and below L3 would indicate differences between movements. Mann–Whitney U tests were performed between: maya vs. serpentine (Maya–Serp); forward bending movements vs. figure eight movements (FwdBnd–Maya and FwdBnd–Serp); forward bending vs. side bending, (FwdBnd–SidBnd); and side bending vs. figure eight movements (SidBnd–Maya and SidBnd–Serp) (six tests adjusted p = 0.0083). Tempos and training levels for Maya and Serp were combined in the above tests. To test the hypothesis of greater temporal separation in trained subjects compared to novice subjects, one-way ANOVAs were performed on each of the four figure eight conditions with skill as a factor and Lagdiff% as the dependent variable (adjusted p < 0.0125 for four tests). The grouped data used in testing for effect of tempo (difficulty level) was not normally distributed so Mann–Whitney U paired tests were performed separately for maya and serpentine at each skill level using Lagdiff% adjusted $p < 0.0125$ for four tests.

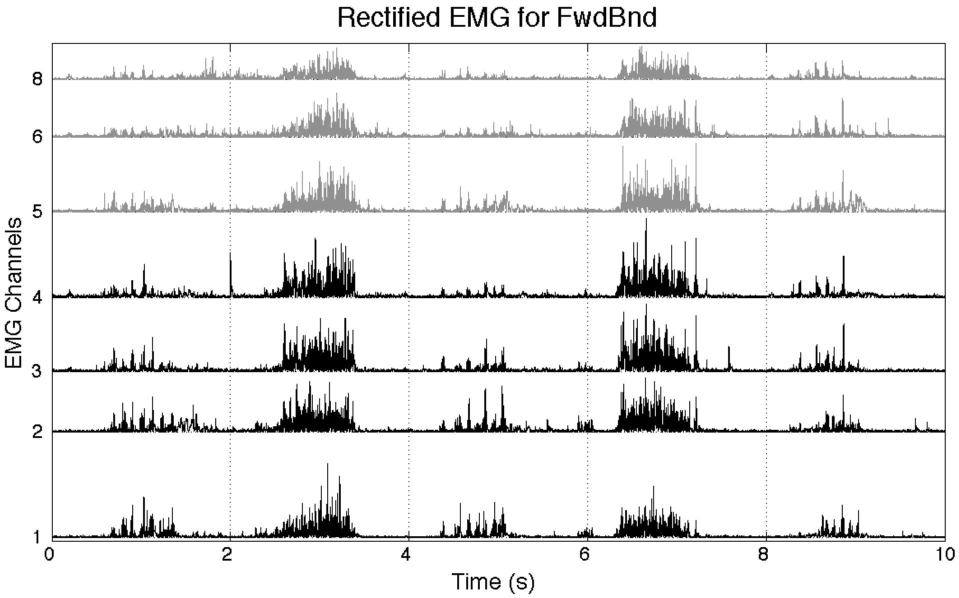
3.3 RESULTS

3.3.1 Activation timing patterns

Plots of rectified EMG (Fig. 3.2) and mean lags (Fig. 3.3) showed four distinct temporal patterns corresponding to the four different movements, consistent across subjects and training levels. The FwdBnd displays very similar EMG bursting patterns (Fig. 3.2a) and synchronous activation (Fig. 3.3a) across all eight electrode sites. In comparison, SidBnd EMG shows earlier burst onsets and longer burst durations at sites 1–4 compared to sites 5–8 (Fig. 3.2b), with a tendency towards earlier activation at the most caudal site (Fig. 3.3a, electrode 1). Fig. 3.2c displays the typical EMG pattern for Maya 0.5 Hz, with electrodes 1–4 (group 1, below L3, dark traces) showing earlier onsets and burst peaks compared to electrodes 5 and 6 (group 2, above L3) and electrodes 7 and 8 (reference signal, at L1). The EMG pattern for Serp 0.5 Hz (Fig. 3.2d) shows the reverse sequence of activation to the Maya, with the onsets and burst peaks occurring later for electrodes 1–4 (dark traces) compared to electrodes 5–8 (lighter traces). For the figure eight conditions at the lower tempo, in all cases but three (5No for Maya; 8Tr and 3No for Serp) an asynchronous activation pattern was used. Because we were primarily interested in the ability to independently control muscle compartments we used asynchrony at the lower tempo as our performance criterion. The fact that these subjects appeared to be using an activation pattern more similar to side bends in these three cases suggests they had selected a motor pattern different from that which was the focus of our study. These three cases were consequently treated as a distinct group and excluded from the comparative statistical analysis. The lag values for this group are plotted in Fig. 3.3b clearly showing the marked difference.

FIGURE 3.2 EMG patterns for each movement condition.

A



B

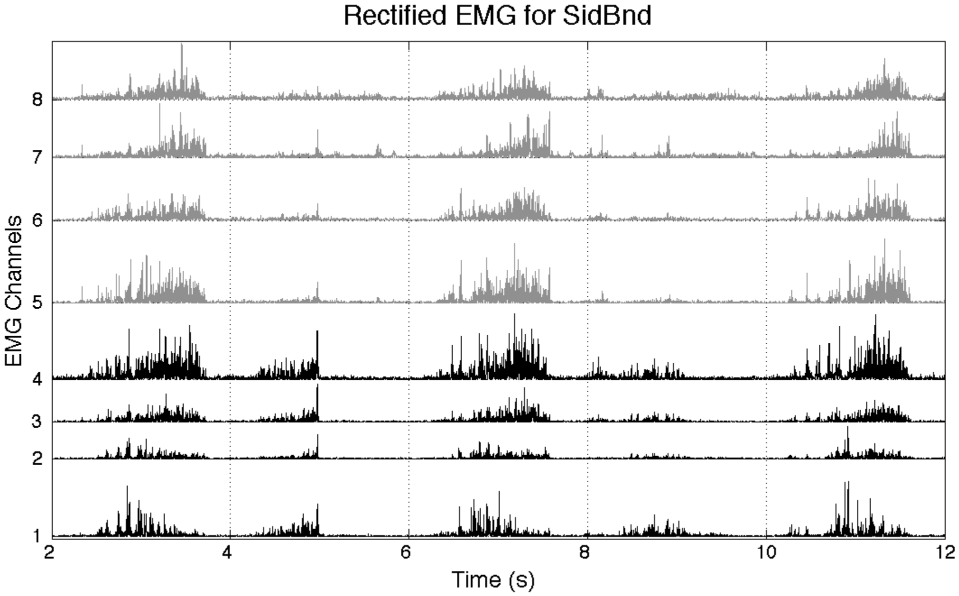
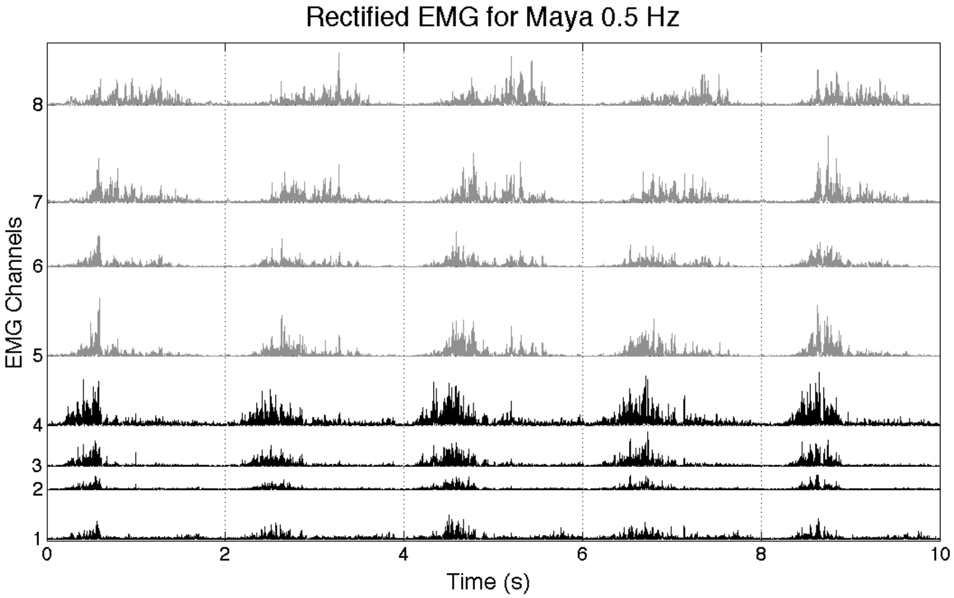


FIG 3.2A and B Non-normalized rectified EMG patterns from one representative subject (trained). The black traces are from electrodes positioned below the third lumbar vertebral level; the grey ones from those above. a) Forward bend, b) Side bend.

FIGURE 3.2

C



D

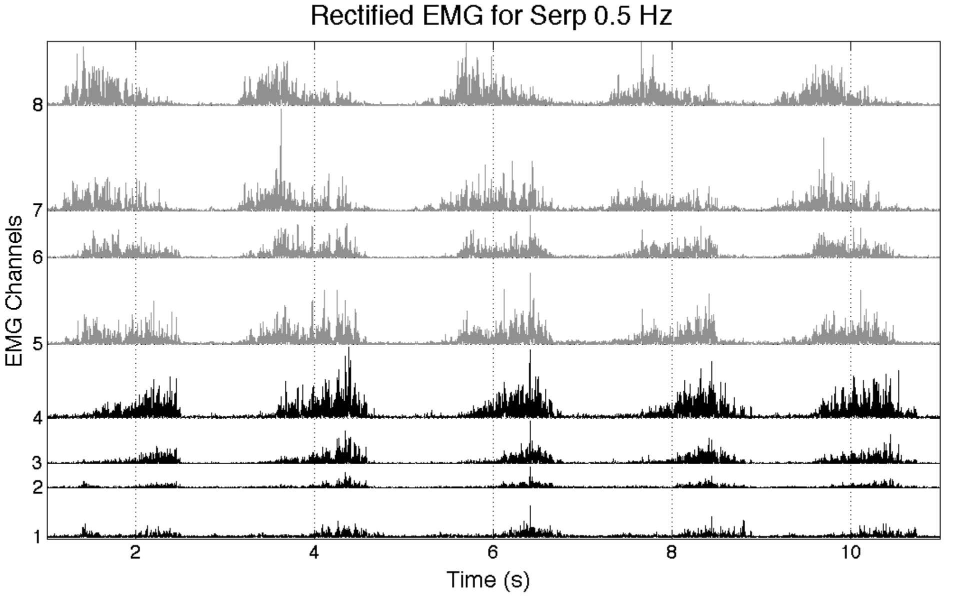


FIG 3.2 C and D Non-normalized rectified EMG patterns from one representative subject (trained). The black traces are from electrodes positioned below the third lumbar vertebral level; the grey ones from those above. c) Maya .5 Hz, d) Serpentine .5 Hz.

FIGURE 3.3

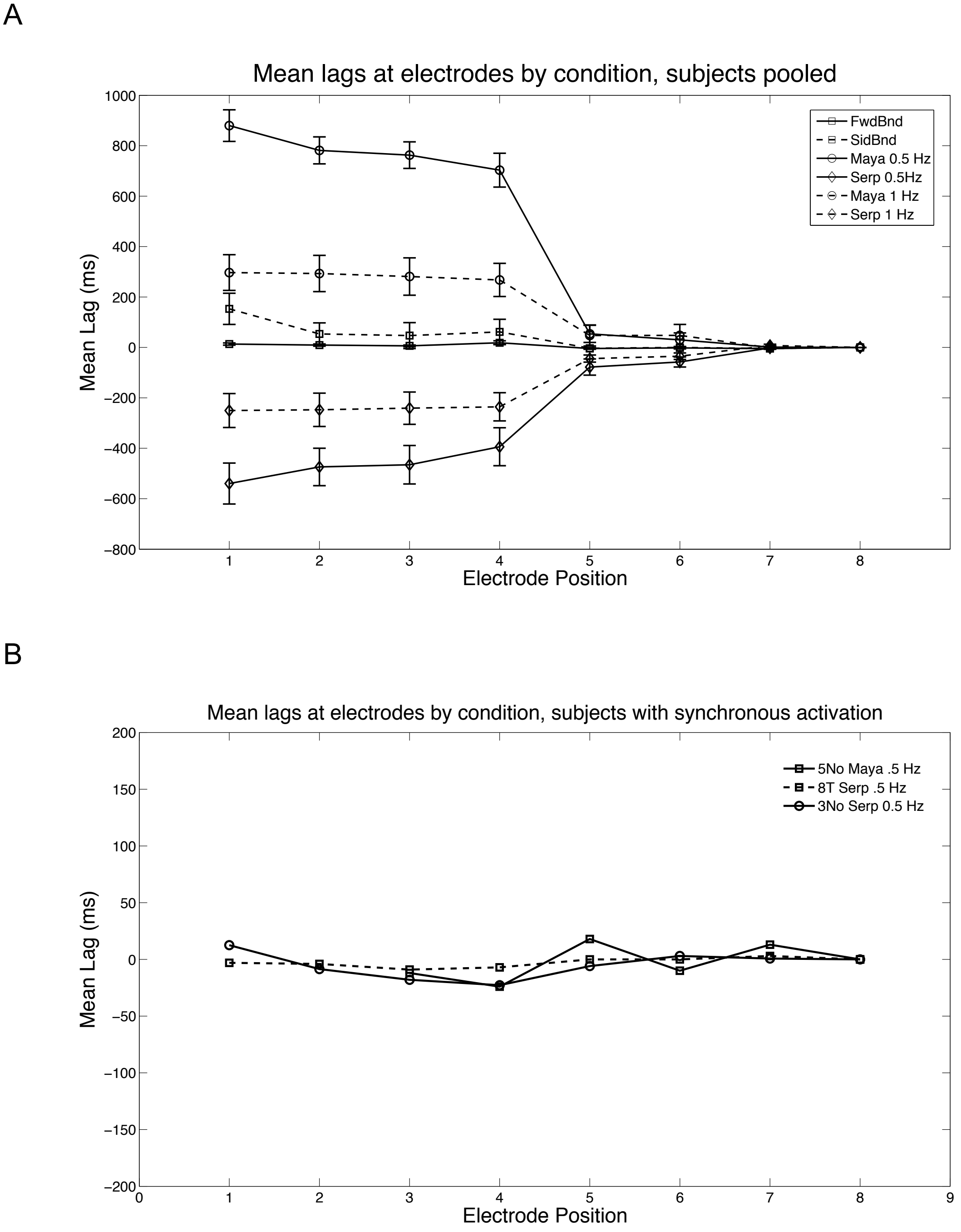


FIG. 3.3 Lags plotted by electrode position. a) Included subjects. The two lines around zero correspond to the bending tasks. The traces with positive values for electrodes 1-4 correspond to the maya conditions, those with negatives correspond to the serpentine conditions, indicating that the order of firing rostro-caudally was opposite for the two figure 8 tasks. Bars represent standard error. b) Three cases (one Maya 0.5 Hz and two Serp 0.5 Hz) showed synchronous patterns and were excluded from movement condition analyses.

Fig. 3.4 shows the EMG signals recorded from IL at L4 and L1 levels for one representative subject, as well as the x, y and z positions of markers which underwent the largest displacements. The movements are shown beginning from rest. In the forward bend (Fig. 3.4a), synchronous lumbar ES activity occurred in phase with vertical displacement of the tenth thoracic vertebra related to flexion and extension of the spine. During trunk forward flexion, smaller amplitude bursts associated with eccentric contraction were recorded by all electrodes, and larger amplitude bursts were recorded during extension back to upright posture. In the side bend (Fig. 3.4b), muscle activity across all recording regions appeared to be associated with reversal of movement in both the x and z directions, i.e. the right lumbar ES was active eccentrically to control lateral lowering of the trunk, and then active concentrically to laterally extend the trunk to upright posture. In the maya (Fig. 3.4c), reversal of movement of the right hip (z increasing/R ASIS rising) preceded reversal of movement in the mediolateral direction (x increasing/ R ASIS shifting towards the right). The pattern was opposite in the serpentine: reversal of R ASIS movement in the x–direction preceded that in the z–direction. Thus, in both conditions, the vertical displacement of the hip was out of phase with the mediolateral displacement.

3.3.2 Electrode groupings

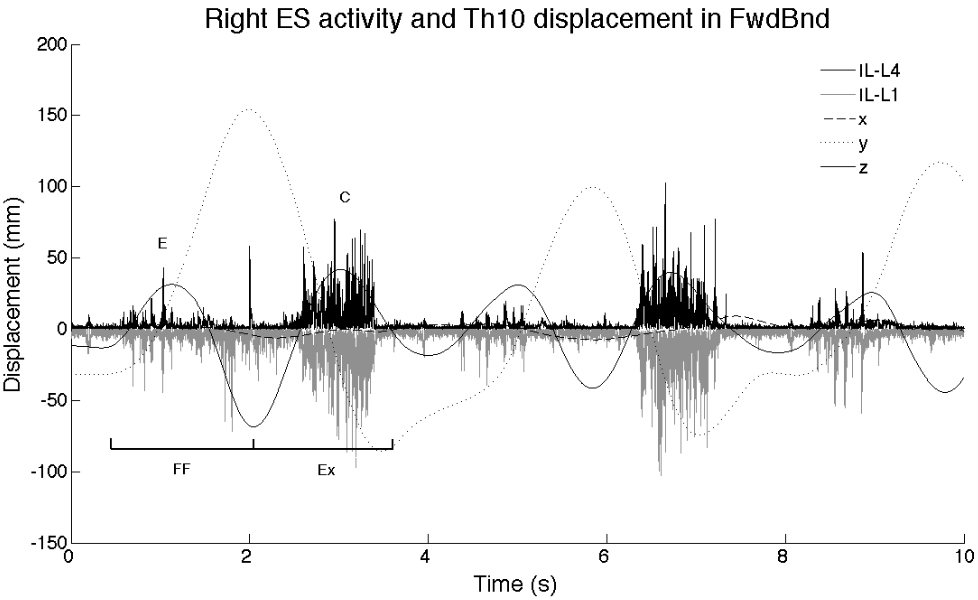
The non-parametric test showed that overall, the lags recorded across the eight electrode sites were not the same ($\chi^2 = 17.37$, $p = 0.15$). Muscle compartments represented by electrodes 1–4 were activated in synchrony, whereas activation of compartments represented by electrodes 5–7 was asynchronous. Lack of significant differences in lags among electrodes 1–4 ($F = 0.015$, $p = 0.998$), across conditions, provided justification for using a single lag group average in subsequent analyses. There was a main effect of electrode location ($\chi^2 = 33.05$, $p = 0.000$, $p < 0.005$) for lags among electrodes 5–8. Post hoc Mann–Whitney tests showed no difference between lags for electrodes 5 and 6 ($z = –0.137$, $p = 0.891$), but significant differences between lags for electrodes 5 and 7 ($z = –2.809$, $p < 0.005$) and between lags for electrodes 6 and 7 ($z = –3.876$, $p = 0.000$, $p < 0.005$). Since there was no significant difference in lags between electrodes 7 and 8 ($z = –0.165$, $p = 0.869$) the signal recorded by electrode 7 was not included in subsequent analyses as it did not appear to provide information which was different from that of the reference electrode. The mean lag for electrodes 1–4 is hereafter referred to as group 1 lag and that for electrodes 5 and 6, as group 2 lag.

Overall, with all movement conditions and skill levels pooled, the timing of muscle subvolume activity above and below L3 was not synchronous. There was an overall main effect of electrode group (recording site), on the relative timing of EMG bursts ($z = –2.122$, $p = 0.034$). Furthermore, this asynchrony did not have the same relative timing for all movements. The mean electrode group lags for the different conditions are depicted in Fig. 3.5. Comparison of movement conditions showed that the FwdBnd did not differ from SidBnd ($z = –0.033$, $p = 0.974$, N = 11) mean difference in activation asynchrony between FwdBnd and SidBnd as a percentage of cycle period, 2.3%). However, FwdBnd was significantly different from Maya ($z = –3.283$, $p < 0.001$, $N = 7$) and Serp ($z = –3.372$, $p < 0.001$, $N = 7$; mean difference for FwdBnd–Maya 30% of cycle period; FwdBnd–Serp 21% of cycle period). SidBnd was significantly different from Maya ($z = –3.368$, $p < 0.001$, $N = 8$ and Serp ($z = –3.356$, $p < 0.0005$, $N = 7$) conditions with the difference in asynchrony between SidBnd–Maya being 26.7% of cycle period and for SidBnd–Serp, 22.5% of cycle period. Maya and Serp had different temporal activation patterns ($z = -4.503$, $p < 0.0005$, $N = 7$) with the mean difference in asynchrony between them being a lag of 51.1% of the cycle period.

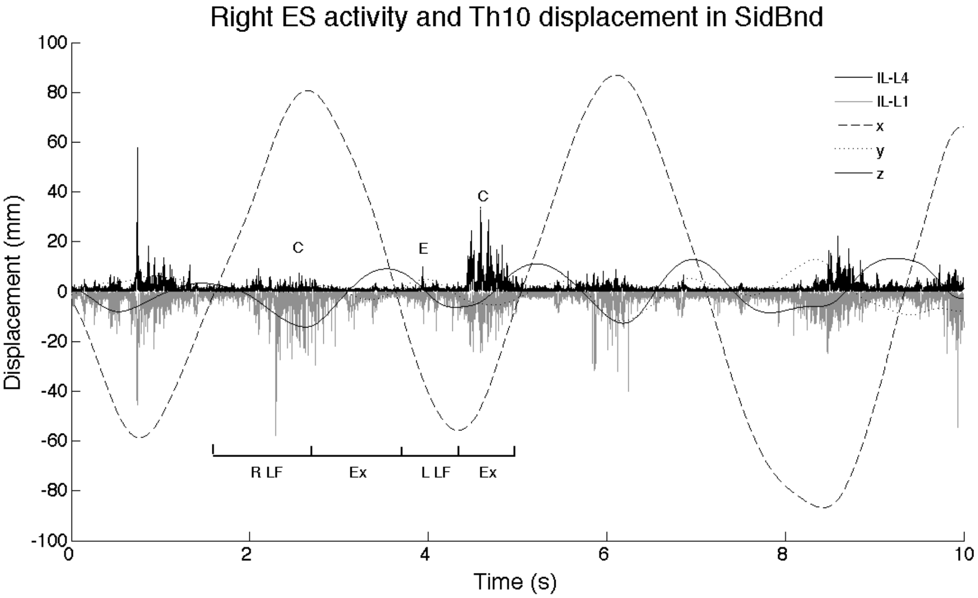
Contrary to our hypothesis, we did not find any significant difference in lag as a percentage of cycle period (Lagdiff%) between tempos for either Maya ($z = -1.05$, $p = 0.294$, $N = 8$) or Serp ($F = 0.038$, $p = 0.848$, $N = 7$). Nor did we find that novice subjects used muscle activation patterns that were more synchronous than trained subjects. In fact, the only effect of training which we were able to show was for Maya 0.5 Hz where novice subjects actually demonstrated greater asynchrony since activation recorded by group 1 electrodes occurred 17.7% of the cycle period earlier for novices than for trained subjects ($F = 48.51$, $p < 0.0005$).

FIGURE 3.4

A


Right ES activity and Th10 displacement in FwdBnd
Displacement (mm)
Time (s)
IL-L4
IL-L1
x
y
z
E
C
FF
Ex
200
150
100
50
0
-50
-100
-150
0
2
4
6
8
10

B


Right ES activity and Th10 displacement in SidBnd
Displacement (mm)
Time (s)
IL-L4
IL-L1
x
y
z
C
E
C
R LF
Ex
L LF
Ex
100
80
60
40
20
0
-20
-40
-60
-80
-100
0
2
4
6
8
10

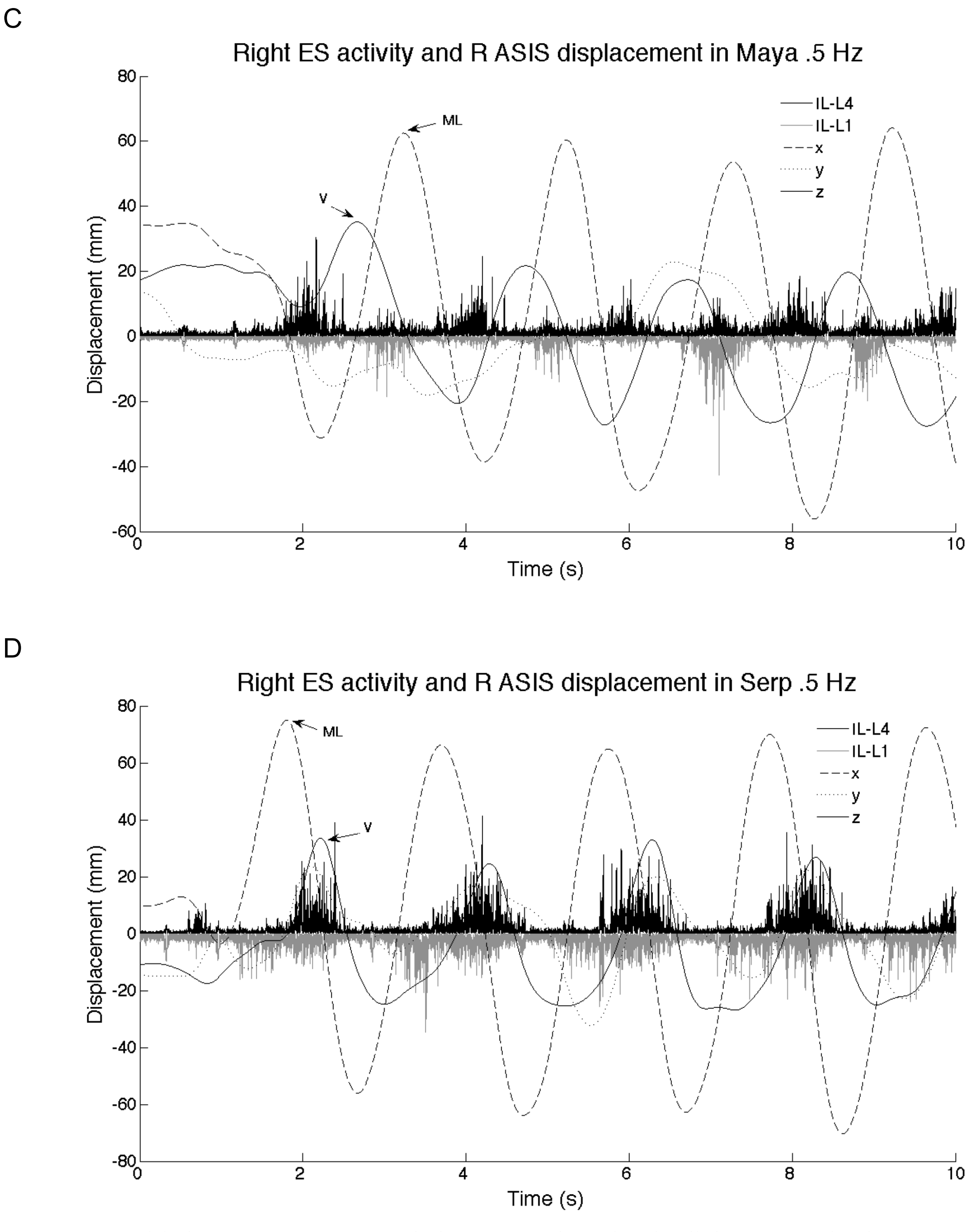
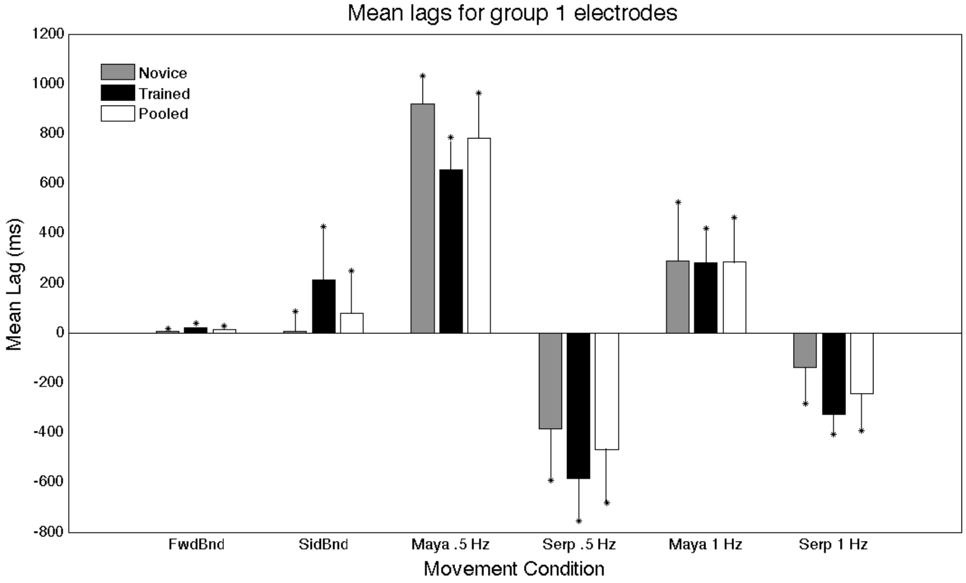


FIG 3.4. Rectified EMG of IL at L4 (dark trace) and L1 levels (lighter trace) in the four movement patterns. In a) FwdBnd and b) SidBnd, lines indicate displacement for the marker at the 10th thoracic vertebra (Th10) in x, y, z dimensions. In c) Maya .5 Hz and d) Serp .5 Hz, lines indicate displacement in x, y, z dimensions of the marker on the right anterior superior iliac spine (R ASIS). EMG amplitudes have been scaled for plotting with kinematic data and do *not* show relative activation amplitudes dependent on movement condition. The data are all from one novice subject. Forward flexion (FF), extension (Ex) right lateral flexion (R LF), left lateral flexion (L LF), eccentric contraction (E), concentric contraction (C), R ASIS vertical direction change (V), R ASIS mediolateral direction change (ML).

FIGURE 3.5

A



B

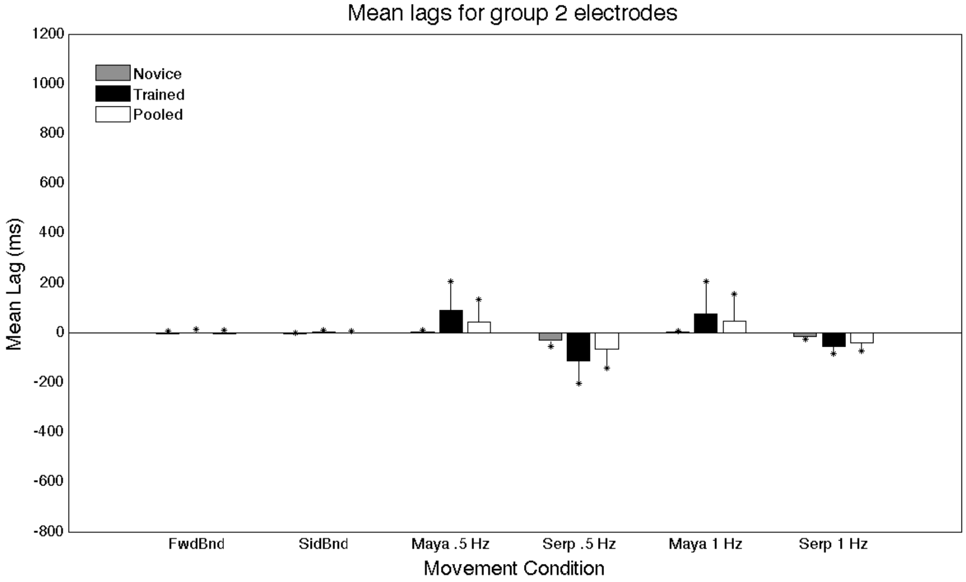


FIG. 3.5 Mean lags (with respect to electrode 8) by electrode group and condition for novice, trained and pooled subject data. a) Group 1 electrodes (1, 2, 3, 4); b) group 2 electrodes (5 and 6). The positive values indicate activation in that electrode group preceded activation at the reference electrode, whereas negative lags indicate activation in that group followed activation at the reference. Lines and stars represent standard deviations.

3.4 DISCUSSION

The aim of the present study was to demonstrate independent neuromuscular control of adjacent muscle compartments of the lumbar erector spinae. Previous studies which have examined the topographical variation in EMG amplitude and frequency spectrum across the lower back described global patterns without attempting to link them to specific muscles (Finneran et al., 2003; Reger et al., 2006; Hu et al., 2010). Furthermore, they did not relate the EMG patterns to biomechanical function or investigate the temporal coordination of different lumbar ES compartments. In the present study, specialized, segmentally specific movements from belly dance were performed by novices and trained subjects, and temporal activation asynchrony elicited by these tasks was used to demonstrate compartmentalized separation of control within the lumbar ES. The study also demonstrated that compartmentalized control of deep and superficial ES motor units above and below L3 is an innate, hard-wired capability that is not related to task-specific training, that is, it does not require learning as it was produced by both novice and skilled subjects at both medium and fast tempos.

We found that in contrast to simultaneous activation of ipsilateral lumbar ES compartments above and below L3 during global spine bending tasks, asynchronous activation occurred during figure eight movements. According to MacIntosh and Bogduk (1987), these regions represent separate superficial and deep subvolumes of the lumbar ES. We found that the rostro-caudal order of activation in these subvolumes differed depending on the direction of the figure eight movements. Further, we found that this pattern of asynchrony was, in general, independent of amount of training or difficulty (increased tempo), and that contrary to the expectation that trained subjects would show a larger temporal difference in activation of these muscle compartments, novices performed the Maya 0.5 Hz with greater temporal separation. Therefore, we cannot conclude that a greater temporal separation results from more practice. In the only other study to date examining temporal activation patterns in belly dance, Moreside et al. (2008) found independence in upper vs. lower rectus abdominus in a group of trained dancers during certain belly dance movements (abdominal waves). However, they did not include a novice group in the study, so it was not determined whether the segmental separation of the rectus is also innate or can only be achieved through practice. All eleven subjects in our study were able to activate the two lumbar ES compartments asynchronously for at least one of the two 0.5 Hz figure eight movements with eight subjects activating them asynchronously for both movements. Interestingly, four of the subjects had never attempted the figure eight movements other than during a brief practice period at the beginning of the data collection session. Nevertheless, their activation patterns were clearly asynchronous.

Previous research has not shown the ability to independently control the temporal activation of adjacent lumbar ES muscle subvolumes, although differential activity between thoracic and lumbar regions has been recorded (Morris et al., 1962; Donisch and Basmajian, 1972). In assessing the possible differential biomechanical roles of portions of the lumbar multifidus, Moseley et al. (2003) also found temporal asynchrony, seen as a 20 ms earlier activation of deep multifidus compared to lateral and superficial compartments at one vertebral level (~L4), for predicted vs. unpredicted trunk loading conditions. In the present study, we observed a tendency towards pre-activation in MULT compared to ES during side bends but this was not significant. Jonsson (1970, 1973) made early attempts to record at more than two different levels within the posterior lumbar region, both medially and laterally. However, only relative activation levels were compared and no temporal analyses of activation patterns were performed. More recent studies using large array surface electromyography spanning the entire bilateral lumbar region have examined regional muscle activity but did not perform temporal analysis (Finneran et al., 2003; Hu et al., 2010). Hu et al. (2010) noted a sequential caudal to rostral (L5 to L2) increase in activation level during flexion and the opposite pattern during extension, but the authors were careful to state that muscle coordination or synergies are not what is represented by the SEMG topographies: the analysis involved a topographical comparison of muscle activation based on RMS levels, in contrast to the temporal comparison of individual muscle compartment onsets investigated in our study.

Our results support the assumptions made by MacIntosh and Bogduk (1987) regarding electrode placement according to the specific muscle anatomy in order to record differential activation between thoracic vs. lumbar portions of the lumbar ES. We did not observe any differences in activation mediolaterally, i.e. no differences in activation between the medial longissimus thoracis vs. the lateral iliocostalis lumborum compartments of the lumbar ES at any of the tested vertebral levels. However, surface EMG may not be amenable to detecting differential activation between these two compartments because of cross-talk, or the movements investigated may not require functional specificity of these compartments. Alternatively, these two partitions may receive common motor innervation at a given segmental level and thus, may not have the capacity for differential activation. Synchrony between MULT and caudal IL and LT in the figure eight movements suggest a synergistic role for MULT in lumbar lateral flexion during these tasks, as opposed to acting to stabilise against flexion, which Ward et al. (2009) described as its primary function.

In the first study to look at multifidus and longissimus activation patterns during gait, Thorstensson et al. (1982) concluded that the primary role of lumbar paraspinals during walking is to counteract movements in the frontal plane. Alternating right-left lower lumbar lateral flexion with concurrent stabilisation of upper lumbar and thoracic levels accommodates cyclic pelvic obliquity during gait while minimising overall trunk center of mass displacement in the frontal plane. In the present study, the innate ability to perform isolated frontal plane lumbar-pelvic movements via independent compartmental activation above and below L3 (deep vs. superficial lumbar ES) is an expression of the neuromechanical capacity for segmentally specific spinal motion. In locomotion, pelvic obliquity is adapted to changing gait cycle kinematics and terrain, whereas in belly dance the range of motion of pelvic obliquity (normal range approximately 5° (Rose and Gamble, 2006) is voluntarily maximized (21° in maya, 35° in serpentine).

Bergmark (1989) distinguished between the thoracic portion of the lumbar ES being a global trunk muscle (spanning pelvis to ribs) and producing lateral bending of the rib cage on unilateral action, and the lumbar portion (deeper compartment) being a local muscle spanning pelvis and lumbar vertebrae and causing lateral bending of the lumbar spine in unilateral action. Our findings support the differential mechanical roles of each during volitional movement, showing that they can act as synergists for global movements of the trunk (as in side bending) or as antagonists for more isolated, localized actions (as in the maya and serpentine). We are currently conducting studies to further explore the relationship between muscle patterns and kinematics of segmentally specific movements of the trunk as these relate to biomechanical control.

The ability to independently activate these specific muscle compartments by selecting appropriate movements could be exploited for interventions to improve postural stability in the elderly and for developing muscle specific exercises to relieve low back pain or restore erector spinae function. The present results provide additional support for the partitioning hypothesis, extending this principle to include the neuromuscular region of the posterior lumbar spine.

Acknowledgements

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Chapter 4

Segmental specificity in belly dance mimics primal trunk locomotor patterns

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Preface to the second article

This paper looks deeper into the control of rhythmic undulatory spine movements, exploring the possibility that different control mechanisms dominate for faster vs. slower tempo oscillations, and for trained vs. untrained performers. Following from the first article, I first asked, can the same neuromechanical specificity observed in low frequency, medium amplitude spine/pelvis isolations be seen in those of higher movement frequency and smaller amplitude? For the second and third studies, ES electrode placement in the lumbar region was simplified, given that in the first study we found no difference in activation timing medio-laterally, and the only significant differences in relative timing was with respect to regions above the third lumbar vertebra and below. With a reduction in the number of ipsilateral ES placements to three lumbar vertebral levels, I had enough electrodes to enable bilateral recording in the second and third study, to provide greater elaboration of timing patterns. Adding to these another longitudinal position at T10, I hoped to be able to record a more complex activation timing patterns. Verification of this would form the basis for a classification method of activation timing patterns. By making pattern comparisons between experimental conditions and training groups, I expected to be able to infer differences in control requirements, and thus identify the control mechanisms as more voluntary (supraspinal) or more automatic (spinal) depending on movement frequency and training.

Do coordination patterns differ between naive performers and those who have had extensive practice? The hip shimmy was chosen for its flexibility as to speed manipulation, and the requirement of extensive practice to acquire the ability to perform it at the highest frequencies. Performed at a 2Hz tempo, it is easily controlled and monitored. When performed as fast as possible, it feels as though it takes on a “life of its own”, and so seems to require tapping into more automatic mechanisms for generation and maintenance. I chose a third frequency condition of 3 Hz in the expectation that this would represent a transitional tempo, as from a subjective sense of difficulty, it seems to represent a threshold frequency between more stable states of high and low shimmy tempos, not unlike the unstable states described prior to state changes in dynamical systems theory. Thus, I predicted that depending on training and tempo, we would see switches in patterns similar to gait transitions in locomotion.

Indeed, the patterns observed were very similar to the centrally generated spinal locomotor patterns of lower vertebrates, providing evidence for the phylogenic preservation of centrally generated spine locomotor patterns in humans. This study provides insights into the interplay between innate circuits and voluntary modulation and modification of their output in the construction of novel skills. This also implies that trunk movement itself can be a product of skill, not merely a mediator of posture and movement.

ABSTRACT

Belly dance was used to investigate control of rhythmic undulating trunk movements in humans. Activation patterns in lumbar erector spinae muscles were recorded using surface electromyography at four segmental levels spanning T10 to L4. Muscle activation patterns for movement tempos of 2 Hz, 3 Hz and as fast as possible (up to 6 Hz) were compared to test the hypothesis that frequency modulates muscle timing, causing pattern changes analogous to gait transitions. Groups of trained and untrained female subjects were compared to test the hypothesis that experience modifies muscle coordination patterns and the capacity for selective motion of spinal segments. Three distinct coordination patterns were observed. An ipsilateral simultaneous pattern (S) and a diagonal synergy (D) dominated at lower frequencies. The S pattern was selected most often by novices and resembled the standing wave of activation underlying the alternating lateral trunk bending in salamander trotting. At 2 Hz, most trained subjects selected the D pattern, suggesting a greater capacity for segmental specificity compared to untrained. At 3-4 Hz, there emerged an asynchronous (A) pattern analogous to the rostral-caudal traveling wave in salamander and lamprey swimming. The neural networks and mechanisms identified in primitive vertebrates, such as chains of coupled oscillators and segmental crossed inhibitory connections, could explain the patterns observed here in humans. Training allows modification of these patterns, possibly through improved capacity for selectively exciting or inhibiting segmental pattern generators.

NEW AND NOTEWORTHY

Belly dance provides a novel approach for studying spinal cord neural circuits. New evidence suggests that primitive locomotor circuits may be conserved in humans. Erector spinae activation patterns during the hip shimmy at different tempos are similar to those observed in salamander walking and swimming. As movement frequency increases, a sequential pattern similar to lamprey swimming emerges, suggesting that primal involuntary control mechanisms dominate in fast lateral rhythmic spine undulations even in humans.

4.1 INTRODUCTION

Fundamental to the coordination of human movement is the control of the body axis. Trunk control as it relates to meeting challenges to stability imposed by upright, bipedal posture has been previously investigated (Henry et al. 1998; Oddsson and Thorstensson 1987; Kung et al. 2009; Vernazza-Martin et al. 2006). However, the trunk's multi-functionality extends beyond its role in facilitating static balance to include dynamic stability during locomotion (Bouisset and Do 2008; Cappellini et al. 2010; Carlson et al. 1988; Ceccato et al. 2009; Thorstensson et al. 1982, 1984), steering and head/trunk orientation (Courtine et al. 2006; Mouchnino et al. 1992; Schmid et al. 2005), configuration changes to negotiate environmental obstacles, and facilitate focal tasks (Frank and Earl 1990; Ivanenko et al. 2005) and expression of emotions or aesthetic principles as in dance (Bartenieff 1965; Daprati et al. 2009; Nugent et al. 2012; Riskind and Gotay 1982). In the absence of pathology, the hierarchical control structure of the central nervous system (CNS) allows for seamless integration of voluntary control and automatic postural adjustments. While control of trunk movements during gait, target-directed movements of the upper limb and automatic postural responses to loss of balance have been extensively studied, studies of simple rhythmic movements of the trunk (e.g. cyclic flexion/extension) as goals in themselves are limited (Andersson et al. 1996; Carlson et al. 1988; Nugent et al. 2012; Oddsson and Thorstensson 1986, 1987). Little has been published on the possible mechanisms of control in skilled rhythmic trunk movements, such as those employed in dance (Nugent et al. 2012; Or 2006). The common finding among studies of isolated trunk movements is task dependent specificity of activation at different segmental levels and in different compartments of epaxial spine extensor muscles which is predicted from functional anatomy (Macintosh and Bogduk 1987). Several studies have investigated lumbar extensor patterns in gait by recording EMG at a single segmental level (Cappellini et al. 2010; Carlson et al. 1988; Ivanenko et al. 2004; Saunders et al. 2005; Thorstensson et al. 1982). However, recording at only a single level may not be sufficient to characterize complex coordination patterns such as those associated with intricate undulations of the spine employed in dance.

Several studies have shown that trunk movements during locomotion and other types of rhythmic trunk motion in humans involve differential timing in paraspinal muscles at different segmental levels (Anders et al. 2007; Ceccato et al. 2009; de Seze et al. 2008; Ivanenko et al. 2006; Nugent et al. 2012; Winter 1991). De Seze et al. (2008) recorded erector spinae (ES) activity from four electrodes at spinal levels C7, T3, T12 and L4 in male subjects during forward and backward walking as well as crawling on hands and knees, revealing a complex rostral-caudal sequence of epaxial muscle patterning in these tasks, whereas an ascending wave characterized arm swinging and hands only walking on a treadmill while kneeling behind the treadmill. Ceccato et al. (2009) found the same pattern in both walking and gait initiation. This descending metachronal wave closely resembles the traveling wave of activation recorded in lamprey and salamander swimming while a caudal-rostral wave produces backwards swimming (Delvolve et al. 1997; Grillner 1985). These rhythmically generated spine oscillations are considered models of the earliest form of vertebrate locomotion. In interpreting the functional significance of this patterning in humans, de Seze et al. (2008) and Falgairolle et al. (2006) propose that the coordination mechanism behind the lateral undulation patterns that evolved to propel aquatic animals continues to be exploited in humans for the coordination between trunk and legs to maintain dynamic stability in locomotion and possibly other rhythmic movements. Among the variety of human trunk movements, belly dance may involve movements most similar to the lateral trunk undulations of primitive vertebrates.

A previous study (Nugent et al. 2012) used belly dance movements as a paradigm for exploring functional and neurological specificity in the lumbar ES during voluntary, segmental spine motion. Differences in the activation timing of adjacent, ipsilateral muscle compartments above and below the level of the third lumbar vertebrae during 0.5 and 1 Hz isolated rhythmic pelvic motion were taken as evidence for segmental control of lumbar extensor muscles. Both novice and trained dancers were able to sequentially control lumbar extensor muscles at different vertebral levels. The direction of activation sequencing (rostral-caudal or caudal-rostral) switched with a change in movement direction. We concluded that the separate innervation of these compartments corresponds to distinct biomechanical functions of different portions of the lumbar erector spinae, and that this capacity for neuromuscular specificity is innate and hard-wired.

To further investigate the structure of the paraspinal control system with the objective of elucidating the control mechanisms we focused on the belly dance hip shimmy, which can be performed at various tempos up to approximately 6 Hz, with performance at higher frequencies being associated with extensive practice. We hypothesized that there would be a pattern transition in the activity of lumbar spine extensors as the shimmy frequency increased. Patterns should differ with respect to the relative peak activation timing at different ES levels, and can be characterized accordingly. Furthermore, we expected that the characteristics of each pattern and the relative likelihood of a specific pattern occurring would be dependent on the amount of training.

4.2 MATERIALS AND METHODS

4.2.1 Subjects

Fourteen novice (NOV) subjects and sixteen trained (TRD) subjects were recruited. TRD were defined as those having engaged in 3 or more years of regular belly dance training and practice. NOV had no prior belly dance training. All participating subjects were free from injuries or medical conditions that might impair physical performance. Novices were selected such that their ages at the time of data collection were matched to the ages at which TRD subjects had initiated their belly dance training. The study was approved by the McGill Research Ethics Board and all participants gave written informed consent. Care was taken to select participants with a low-to-normal body mass index (BMI) to maximize signals recorded with surface electromyography (sEMG) (De la Barrera and Milner 1994). Subjects whose data set did not include a minimum of 5 trials of useable data for each movement condition were not included in the analysis. Reasons for data exclusion were: loss of signal due to excessive perspiration (one subject), incomplete data sets (two subjects), low signal amplitude due to high skinfold thicknesses (3 subjects). After exclusions, 12 NOV and 12 TRD subjects remained. Subject demographics are provided in Tables 4.1A and 4.1B. NOV age range was 18 to 32 years (25 ± 5 years), TRD range was 27 to 57 years (39 ± 9 years), with age at start of training ranging from 16 to 33 years (26 ± 5 years). For the TRD group, amount of training ranged from 3.5 to 32 years (12.4 ± 5.24) years. The first author was a professional belly dancer and one of the subjects.

4.2.2 Procedure

To probe the effects of training (TRG) and movement frequency on coordination pattern and to test the hypothesis of a frequency threshold for pattern change, three target frequencies for the hip shimmy were chosen as movement conditions (MC): 2Hz and 3Hz, performed to a digital metronome, and as fast as possible (FAP) with no auditory stimulus. Control in the 2Hz shimmy was assumed to be voluntary, being slow enough for cycle by cycle control and easily entrained with the metronome. We presumed further that the FAP shimmy, depending on individual ability, would reach frequencies too high for cycle by cycle voluntary control, thus requiring some other or additional control mode(s) for generation and maintenance. The 3Hz MC was chosen to test the possibility of a threshold frequency for switching from one control mode to another since performing at this tempo was difficult and could lead to switching to either a higher or lower frequency. For the FAP condition, the maximum achievable frequency was expected to vary widely from subject to subject, depending on individual ability and body mechanics. A functional stance width for performing these movements was established for each subject and marked on the platform with masking tape. Feet were aligned with the tape markings to standardize width of base of support across trials.

For each MC, subjects performed 3 practice trials while watching a videotaped demonstration (recorded with the metronome for 2 Hz and 3 Hz MC). Verbal cues and a brief demonstration on how to perform each MC were given before the practice trials and during rest periods between trials, as necessary. For the NOV group, this served to cue them on the necessary joint motions; for the TRD group, it served to constrain the options of their extensive movement repertoires to the task requirements. The three practice trials were followed by a block of 10 acquisition trials of the same condition. Practice and acquisition trial durations for the 2 Hz, 3 Hz and FAP conditions were 25 s, 15 s and 10 s, respectively, consisting of continuous, cyclic repetition alternating with approximately 10-20 seconds of rest (standing in place) between trials. Data collection thus yielded 400-500 cycles per task condition for a total of 1200-1500 cycles per subject.

Trial blocks by MC were ordered to alternate between more and less tiring tasks to prevent fatigue effects in muscle signals. Overall, level of physical exertion would be considered low to moderate. Since optimal performance was desired, positive transfer from one task to another was not a concern, rather, the order of progressive difficulty was intended to enhance performance. An additional justification for task order was the concern that a random ordering of MCs within trial blocks would cause confusion, degrading performance and increasing inter-trial variability. The MC order was 2 Hz (easiest), followed by FAP, then two conditions unrelated to the present study, then the 3 Hz condition, followed by two more tasks unrelated to the present study. In all, trials for 7-9 different MCs were performed over a period of 60-75 minutes. Approximately half way through the session, subjects were allowed a sitting rest break for about 5 minutes.

4.2.3 Kinematics

Kinematics were recorded using a Vicon Motion Systems Ltd.© (UK) 6-camera setup and the standard Plug-in Gait (PiG) full body reflective marker set including upper body and arms. Kinematic data were sampled at 200 Hz. To define specific rotations of the trunk at different spinal levels, which the standard PiG marker set cannot capture, two custom marker frames were constructed, each with 3 reflective markers defining a plane and placed at approximately the first

(TH1) and twelfth (TH12) thoracic levels (Fig. 4.1A). These were molded to fit each subject and affixed to the body with double-sided tape. The pelvic segment (PELV) was defined using the four PiG pelvic markers placed on the anterior and posterior superior iliac spines. The subject was oriented such that lateral displacement to the right was in the positive x direction, forward sagittal displacement was in the positive y direction, and upward vertical displacement was in the positive z direction. Subjects were instructed to keep the head level, facing forward, with arms held slightly out to the sides during trials.

FIGURE 4.1

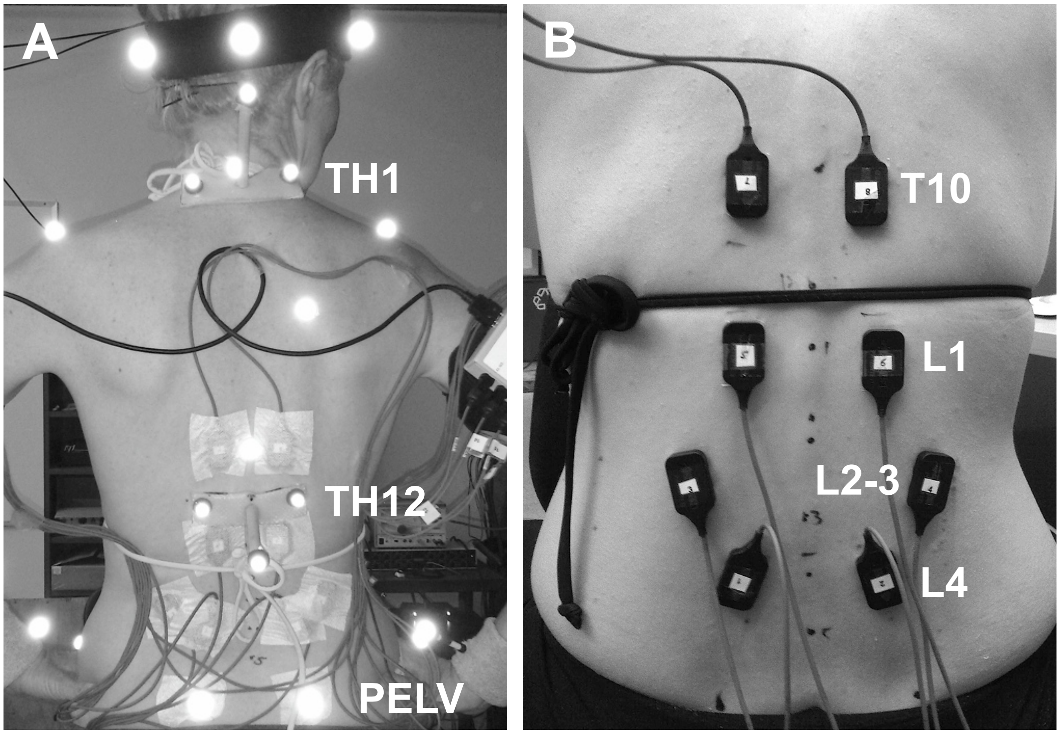

FIG. 4.1. Placements for EMG electrodes and kinematic markers. (A) In addition to the standard VICON full-body marker set from which the pelvic segment (PELV) was derived, subjects were fitted with marker frames at the first thoracic (TH1) and twelfth thoracic (TH12) segments. Three reflective markers on each frame and three of the pelvic markers defined the three planes for calculating relative segmental rotation angles. (B) EMG recording sites for ES muscles, bilaterally from longissiumus thoracis at T10, L1 and L4 and from the iliocostalis lumborum mid-way between L2 and L3. Photos by permission, Marilee Nugent.

4.2.4 Electromyography

Muscle activity was recorded using the Delsys Bagnoli™ (Massachusetts, USA) 16-channel sEMG system integrated with Vicon for synchronization with kinematics. Electrodes are bipolar with a 10 mm inter-electrode distance. EMG was collected bilaterally from the trunk and unilaterally from the right leg, at sixteen muscle sites sampled at 2 kHz. The EMG of eight of these muscle sites was analyzed in this study.

In a previous study on compartmental specificity in slow, medium amplitude belly dance movements (Nugent et al. 2012), erector spinae (ES) activity was recorded unilaterally from 8 electrodes spanning the right lumbar region (rostro-caudally from the first (L1) to the fifth (L5) lumbar vertebral levels and medio-laterally from multifidus to iliocostalis lumborum) following the electrode placement grid of Macintosh and Bogduk (1987). Because no difference in timing was found within each grouping of four electrode sites above and below the level of L3, a subset of these sites was chosen for the present study. Electrodes were placed bilaterally on the ES: longissimus thoracis (LT) at L1 and L4 levels and over the iliocostalis lumborum (IL) approximately midway between the L2 and L3 levels (Fig. 4.1B). To determine whether recording across a wider range of vertebral levels during the shimmy would reveal even greater segmental specificity, as in the traveling wave found by de Seze et al. (2008), two more electrodes were placed bilaterally on LT at the level of the tenth thoracic vertebra (T10). At this vertebral level, the LT is covered only by aponeurosis as opposed to the fibers of the trapezius (de Seze and Cazalets 2008). Other researchers have similarly recorded from the ES at levels spanning T9-T12 during locomotion (Cappellini et al. 2006; Ceccato et al. 2009; de Seze et al. 2008; Ivanenko et al. 2006).

4.2.5 Data processing

After pre-processing of kinematic data with NEXUS software, all EMG and kinematic data were processed using custom MATLAB script (The MathWorks, Inc., R2010b©, Massachusetts, USA). Motion data were low-pass filtered at 8 Hz. Rotation angles were calculated for each trunk segment (TH1, TH12 and PELV) around each rotational axis (x-sagittal rotation, y-frontal rotation, z-transverse rotation) relative to the initial stationary position of the subject. For each trial, mean cycle period (T) was calculated by first applying the MATLAB function 'findpeaks' to the pelvic frame angle PELVy, to identify frontal plane rotation maxima, after which the time intervals between peaks in the trial were averaged. Mean frequency for each MC for each subject was calculated as 1/T.

Raw EMG data for all shimmy trials were demeaned and plotted for visual inspection. Start and end points of each trial were manually determined to include only activity representing consistent performance of task relevant motion. In the majority of trials, this amounted to 0.5 to 2 s less than the trial length. Full-wave rectified EMG was low-pass filtered at 8 Hz using a digital third order Butterworth filter. The MATLAB function 'filtfilt' was used to avoid introducing time lags. Relative timing of peak activation between muscle sites was derived separately for each subject in each MC. For each subject-by-MC, the electrode channel corresponding to the ES signal with the best signal quality was selected as the reference for cross-correlation with each of the other 7 EMG channels using the MATLAB function 'xcorr'. Cross-correlations between EMG signals were performed for each given trial of 10-25 s duration, and then the mean lag and standard deviation of each were averaged across the trials. The number of trials per subject and per condition included in the analyses are listed in Table 4.1.

Outliers were identified as lag values smaller or larger than two standard deviations from the mean. These amounted to 6% of the total number of right side ES lag values. The rhythmic nature of the movements constrained lags to be less than one cycle period, which explains why the criterion for outliers was two rather than the usual three SDs.

The relative latency between the EMG recorded by the reference electrode and each of the other electrodes was defined as the lag at the peak of the cross-correlation function. The set of relative latencies for each trial was then normalized to percentages of the mean movement cycle period (%T) of the trial. Lag%T for each muscle was represented as % of mean cycle period relative to rL4 by subtracting Lag%T for rL4 from all others. Thus Lag%T for rL4 was always 0%. Positive values corresponded to activation preceding that at rL4 (lead), and negative values, activation following rL4 (lag). The Lag%T values for each electrode site were then averaged across trials by condition and subject. Mean lags for each signal were calculated from not fewer than 6 trials per subject. For simplicity in determining the intersegmental coordination patterns of ES compartments, only right side values for Lag%T were used in the analyses, since muscle activation was symmetrical on the right and left sides, differing by one half cycle.

TABLE 4.1 Subject information

ID	Age (yrs)	Age at start of training	Training (yrs)	Height (cm)	Weight (kg)	BMI (kg/m^2)	No. of Useable trials / Actual Mean FREQ (Hz)					
							2Hz *n = 12*		**3Hz** *n = 12*		**FAP** *n = 11*	
T1	39	*28*	11	172.0	52.6	17.8	*9*	2.07	*10*	2.55	*8*	5.49
T2	37	*31*	6	157.5	53.5	21.6	*10*	2.01	*9*	2.82	*10*	5.38
T3	28	*24*	3.5	156.0	53.9	22.1	*9*	2.00	*10*	2.99	*10*	5.37
T4	41	*33*	8	158.5	55.2	22.0	*10*	2.03	*10*	2.65	*10*	3.94
T6	36	*30*	6.5	173.0	66.5	22.2	*9*	2.00	*10*	3.50	*10*	4.06
T8	50	*17*	30	166.0	56.0	20.3	*10*	2.01	*10*	3.42	*10*	6.31
T9	41	*27*	14	168.5	65.4	23.0	*10*	2.01	*10*	3.14	*10*	4.65
T10	41	*30*	11	175.5	64.0	20.8	*10*	2.01	*10*	3.12	*10*	5.17
T11	29	*24*	5	168.5	52.9	18.6	*10*	2.00	*10*	3.18	*10*	3.60
T13	38	*27*	11	164.5	54.0	20.0	*10*	2.00	*10*	2.97	*10*	5.37
T14	57	*25*	32	164.6	61.5	22.7	*7*	2.34	*10*	2.81	*9*	4.94
T16	27	*16*	11	147.3	40.8	18.8	*10*	2.00	*10*	3.02	*10*	5.38
Mean	*38.7*	*26.0*	*12.4*	*164.3*	*56.4*	*20.8*		*2.0*		*3.0*		*5.0*
SD	*8.71*	*5.24*	*9.21*	*8.18*	*7.13*	*1.74*		*0.10*		*0.29*		*0.78*

ID	Age (yrs)	Training (yrs)	Height (cm)	Weight (kg)	BMI (kg/m^2)	No. of Useable trials / Actual Mean FREQ (Hz)					
						2Hz *n = 12*		**3Hz** *n = 12*		**FAP** *n = 12*	
N2*	32	0	173.0	56.7	18.9	*6*	1.99	*6*	2.69	*6*	3.48
N3	29	0	166.4	64.2	23.2	*10*	2.04	*10*	2.64	*10*	4.12
N4	29	0	175.5	62.5	20.3	*10*	2.02	*10*	4.16	*10*	4.79
N5	24	0	174.5	64.4	21.1	*10*	1.96	*10*	2.99	*10*	3.35
N7	20	0	160.0	55.7	21.8	*10*	2.00	*10*	3.15	*10*	4.15
N8	30	0	168.3	49.6	17.5	*9*	1.93	*9*	3.09	*10*	3.26
N9	24	0	170.0	52.3	18.1	*10*	1.99	*10*	3.01	*10*	4.00
N10	26	0	172.7	59.0	19.8	*10*	2.02	*10*	3.12	*10*	3.95
N11	18	0	156.5	45.0	18.4	*10*	2.31	*10*	2.89	*10*	3.68
N12	19	0	156.5	45.5	18.6	*10*	2.01	*10*	3.03	*10*	3.96
N13	18	0	159.0	51.6	20.4	*10*	2.00	*10*	3.16	*10*	3.41
N14	31	0.2	165.1	50.8	18.6	*10*	2.20	*10*	3.19	*10*	4.19
Mean	*25.0*	*0*	*166.5*	*54.8*	*19.7*		*2.0*		*3.1*		*3.9*
SD	*5.26*		*7.02*	*6.77*	*1.69*		*0.11*		*0.38*		*0.44*

TABLE 4.1 Subject demographics and trial information. Column 1 provides the subject identification numbers (ID): Columns 2-6 list demographic information. The last six columns list the mean movement frequencies and the number of trials used in statistical analyses for each MC by subject. *Only 6 trials of each condition were collected for subject N2. T, trained, N, novice subjects, BMI, body mass index.

4.2.6 Statistical analyses

All statistical analyses were performed using MATLAB or SPSS. All confidence limits were set at 95% ($p < 0.05$). Subject means for each electrode site were first calculated across the trials for each MC before determining pooled means and standard deviations across subjects. To test the hypothesis that pattern changes with frequency (first hypothesis), the 2 Hz pattern was compared with the 3 Hz pattern and the 3 Hz pattern was compared with the FAP pattern. We calculated the Euclidean distance between Lag%T values (square root of the sum of squared differences) at corresponding ES locations (excluding rL4 which was always 0%) for each subject for 2 Hz and 3 Hz and for 3 Hz and FAP. Thus, for each comparison, there was a set of 24 values, corresponding to the Euclidean difference between two MCs for each of the 24 subjects. Each set of differences was tested for significance with respect to a selected median value of 13%T using a Wilcoxon signed-rank test. The test median was based on the following rationale. A difference of 25%T in the Lag%T value (a quarter cycle) at any electrode location would represent a substantial shift in the relative timing because it is equivalent to the relative time difference between minimum and maximum rate of shortening during muscle contraction in a rhythmic movement. We reasoned that a shift of even half this magnitude or a 13%T overall difference in the Euclidean distance between groups would be functionally significant.

To test for a difference in timing patterns between TRG groups (second hypothesis), each NOV subject was paired with every TRD subject and the Euclidean distance between Lag%T values at corresponding ES locations was calculated for each of the three MCs. This generated a set of 432 distances (12 NOV x 12 TRD x 3 MCs). The hypothesized median Lag%T value of 13%T was used as the test statistic.

In classifying activation patterns we considered timing differences observed in lateral shifting movements of the pelvis (belly dance hip slide) where we found a timing difference of 50%T - a diagonal pattern synergy pattern during opposing lateral motion in upper and lower trunk segments. Also, in our previous study (Nugent et al. 2012), a difference of 22-28%T was found between L1 and L5 in pelvic isolation movements in the majority of the subjects, although some subjects produced simultaneous activation. Thus, we expected ES latencies to vary between ~ 0%T (simultaneous) and ~50%T (diagonal). The findings of Ceccato et al. (2009) and de Seze et al. (2008) also suggested that an intermediate phase-shifted pattern could be expected.

To investigate both the degree of segmental control specificity in the ES muscles during rhythmic lateral spine undulations at different tempos, and to more comprehensively characterize differences among activation patterns, we performed non-parametric Friedman's two-way ANOVA by ranks on T10-L4%T for each classified pattern separately, with TRG pooled. The values for each right side ES electrode position (rL4, rL2/3, rL1, rT10) were evaluated as repeated measures with stepwise post hoc comparisons between electrodes/segmental levels. Significance was adjusted for multiple post-hoc comparisons. Any missing %T values were filled with column means. These amounted to 11 out of 272 data points (subject means by electrode/ MC), or 4% of the total right side ES inter-electrode latency values, none of which were rT10 or rL4 values, being either rL2/3 or rL1.

4.3 RESULTS

The activity in the ES showed clear bilateral anti-phasic patterns with peak activation at each segmental level occurring at one half cycle delays between opposite sides the spine. Bursting at each electrode location occurred at the same frequency as the movement frequency. Figure 4.2 shows the muscle activation pattern (bottom eight traces) for both right and left side ES at all segmental levels and the associated segmental rotations for the FAP MC (one trained subject, one trial, ~4.5 movement cycles). At the right of each EMG trace the relative peak activation timing as a percentage of the movement cycle is shown, ordered relative to rT10 peak activity as defining the beginning of the cycle. These data show a clearly sequentially phase-shifted pattern of activity ipsilaterally from T10 to L4 levels with left-right 50%T difference at each segmental level. The top three traces show that the rotation amplitudes in the frontal plane for the three segments are similarly phase shifted.

Figure 4.3 compares the relative timing across right ES segmental levels for NOV and TRD by MC. Relative timing appears to differ both by training group and MC**.** The relative timing above and below L2 tends to be greater in the TRD group and greater with decreasing movement frequency. Figure 4.4 provides a similar depiction of ES timing by MC, separately for each subject (Fig. 4.4A - NOV subjects, Fig. 4.4B - TRD subjects). Comparing these two figures, we see that the large variance in the mean latency values of pooled data is due primarily to the between-subjects range and variability of pattern selection.

FIGURE 4.2

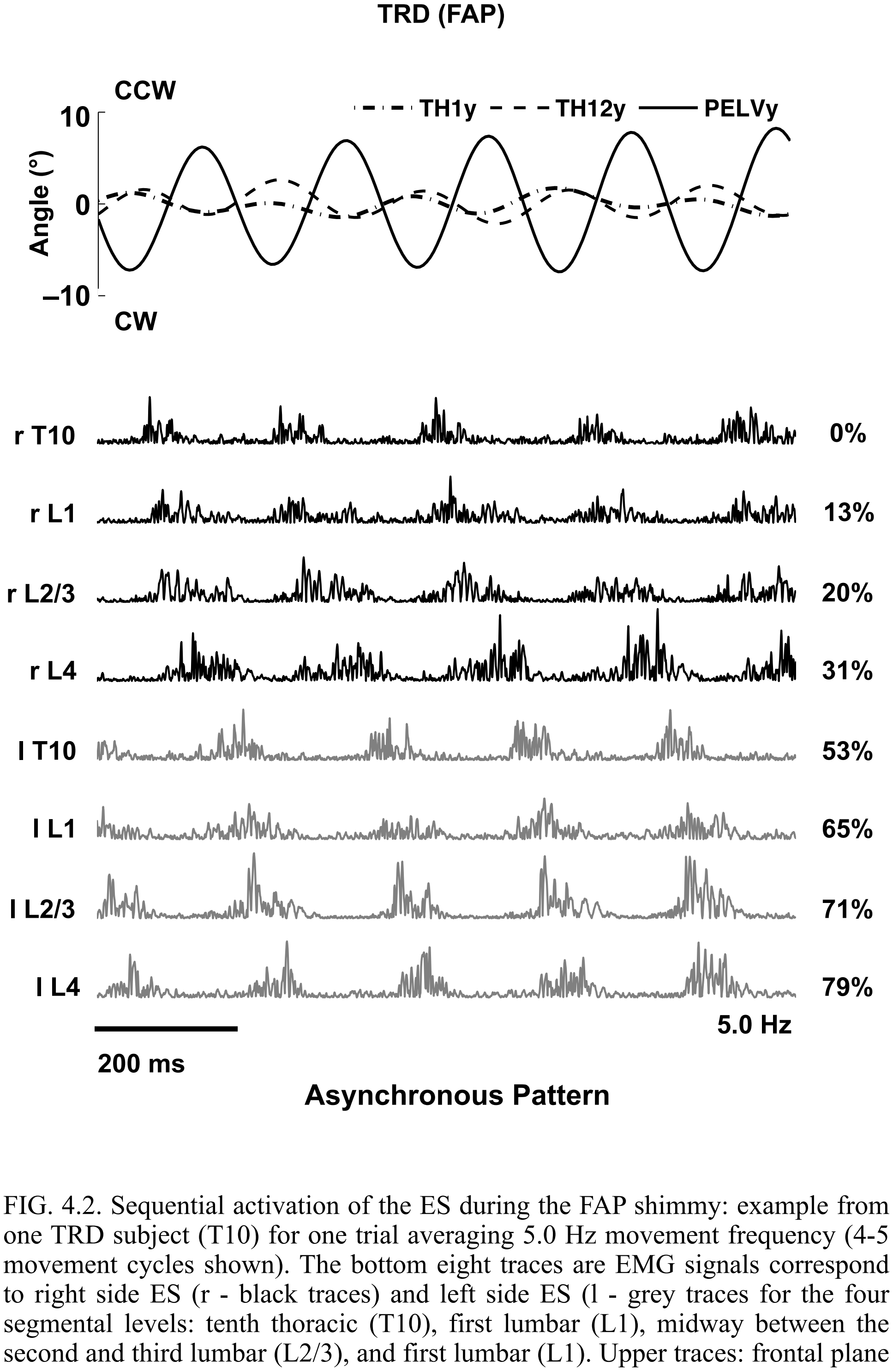

FIG. 4.2. Sequential activation of the ES during the FAP shimmy: example from one TRD subject (T10) for one trial averaging 5.0 Hz movement frequency (4-5 movement cycles shown). The bottom eight traces are EMG signals correspond to right side ES (r - black traces) and left side ES (l - grey traces for the four segmental levels: tenth thoracic (T10), first lumbar (L1), midway between the second and third lumbar (L2/3), and first lumbar (L1). Upper traces: frontal plane rotation angles for PELV, TH12 and TH1 segments.

FIGURE 4.3

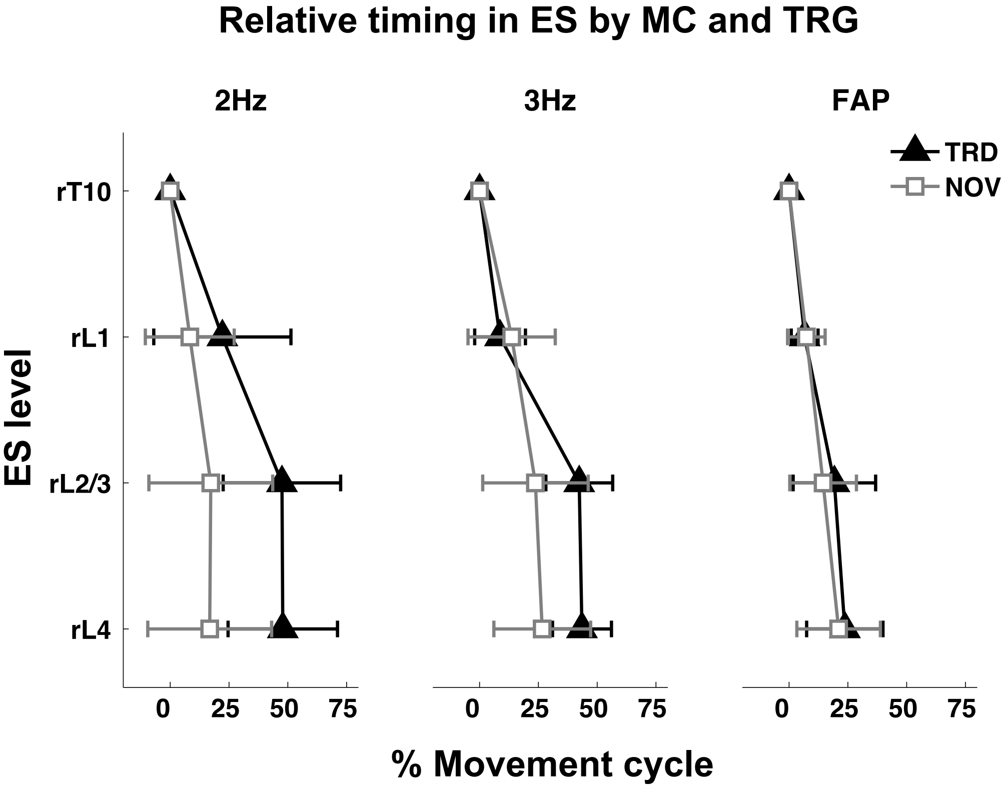

FIG. 4.3. Relative timing in the ES comparing the effects of MC and TRG. Mean lags have been shifted on the x-axis such that rT10 peak activity occurs at 0% of the movement cycle. Error bars equal 1 SD for each electrode mean, representing the between-subject/within group variability. Where no bars are visible, 1 SD is smaller than the width of the data symbol. *N* =12 for each TRG group for each MC.

4.3.1 Effect of movement frequency on ES pattern

Hypothesis 1 predicts that the CNS modifies the relative timing of ES muscle activation at different segmental levels as it increases the frequency of a rhythmic spinal movement. Table 4.2 lists the means and standard deviations for T10-L4 timing latencies by TRG group and MC. For the TRD group, the mean timing difference between ipsilateral rostral and caudal electrode locations in both the 2 Hz and 3Hz MC is about one half the cycle period. The 3 Hz pattern shows greater variability in timing (*SD* = 12.5%T) compared to the 2 Hz condition (*SD* = 5.0%T) and thus might represent a threshold between two timing patterns, since increasing variability with increasing movement frequency has been found to precede spontaneous gait and multi limb pattern changes (Jeka et al. 1993). The mean for the FAP condition is less than 30%T. Like the 3 Hz condition, this pattern has a large variance (*SD* = 16.2%T).

TABLE 4.2 Mean T10-L4%T by MC and TRG

	TRD					NOV				
MC	*n*	*Mean*	*SD*	*Mean -SD*	*Mean +SD*	*n*	*Mean*	*SD*	*Mean -SD*	*Mean +SD*
2Hz	12	57.6*	5.0	52.6	62.6	12	16.8	26.3	-9.6	43.1
3Hz	12	43.5	12.5	31.0	56.0	12	26.6	20.6	6.0	47.2
FAP	12	23.7	16.2	7.5	39.9	12	26.6	20.6	6.0	47.2

*Outliers removed: -2.17, 0.23

TABLE 4.2 Mean T10-L4%T by MC and TRG. Descriptives of T10-L4%T for each movement frequency condition (MC) include n, mean and standard deviation (SD) as well as the mean plus/minus one SD, by training (TRG) group to show the difference in specificity between the two.

Results from the Wilcoxon signed-rank test for differences in timing patterns, represented as the Euclidean distance between MCs, showed that the Euclidian distance across ES levels was not significantly different between 2 Hz and 3 Hz movement conditions since it was less than the hypothesized median of 13%T: *Mdn* = 13%T (p = 0.157, one-tailed, N = 24). However, the Euclidian distance across ES levels was different for 3 Hz and FAP movement conditions: *Mdn* = 17%T (p = .034, one-tailed, N = 24). Thus, for pooled TRG groups, there was no clear change in pattern between the 2 Hz and 3 Hz movement frequencies but the effect of frequency on pattern was confirmed in the comparison between the 3 Hz and FAP conditions.

FIGURE 4.4

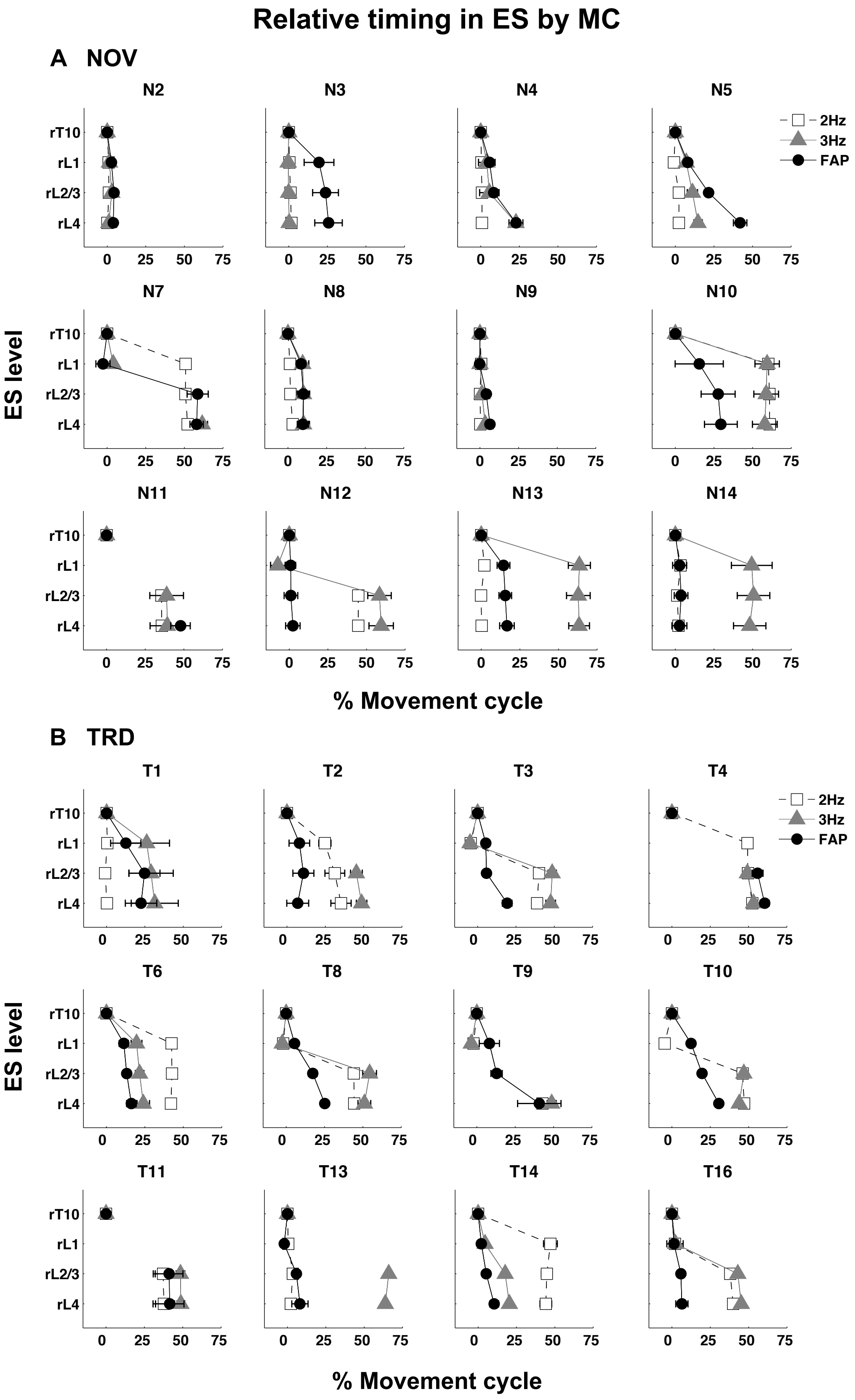
Relative timing in ES by MC
A NOV
N2
N3
N4
N5
N7
N8
N9
N10
N11
N12
N13
N14
2Hz
3Hz
FAP
rT10
rL1
rL2/3
rL4
0
25
50
75
ES level
% Movement cycle
B TRD
T1
T2
T3
T4
T6
T8
T9
T10
T11
T13
T14
T16
2Hz
3Hz
FAP
rT10
rL1
rL2/3
rL4
0
25
50
75
ES level
% Movement cycle

FIG. 4.4. (previous page) Relative timing in the ES comparing the effect of MC for each subject individually. (A) NOV group, (B) TRD group. Mean lags have been shifted on x-axis such that rT10 peak activity occurs at 0% of the movement cycle. Error bars equal 1 SD for each electrode mean, representing the within-subject variability. Where no bars are visible, 1 SD is smaller than the size of the data symbol. Missing data points resulted from technical problems with the signal or lack of phasic bursting at the site recorded.

FIGURE 4.5

FIG. 4.5. Descriptive plots of activation timing differences between ipsilateral ES recording locations. (A) Mean T10-L4%T values by MC and TRG group. Box edges denote 25th and 75th percentiles. Horizontal lines inside denote medians. Whiskers denote extreme values, crosses, denote outliers. (B) Differences between NOV and TRD in the distribution of T10-L4%T values (MCs pooled). (C) Overall effect of TRG on means for each right ES segment (MCs pooled).

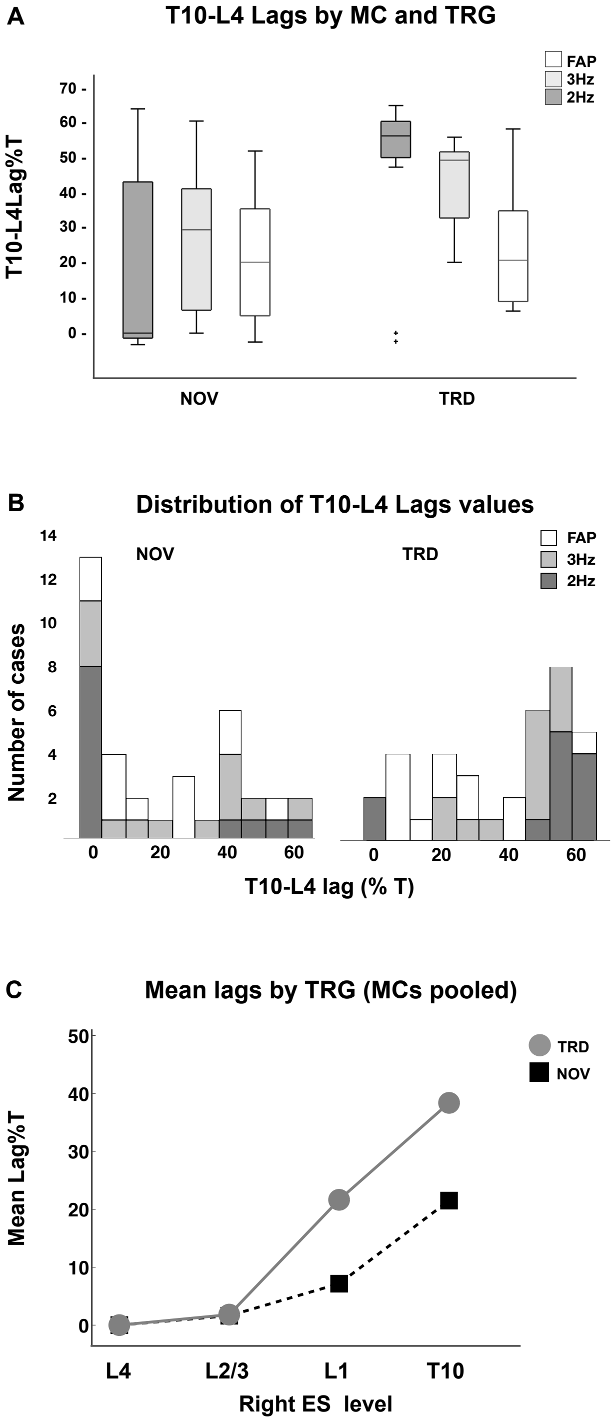

Figure 4.5A shows box plots of T10-L4 Lag%T by MC and TRG groups. While the TRD group shows a clear trend of decreasing relative timing of ES activation with increasing frequency, the picture is less clear for the NOV group whose T10-L4 timing differences range from zero to one-half of the cycle period for every MC. This is consistent with expectations that new learners employ a wider range of strategies in performance attempts, whereas experts show both high within and between subject consistency in the performance of skilled movement. What is noteworthy, is that each subject maintained a consistent pattern within each MC across the 10 trials. That is, for a given MC and subject, there was no pattern switching across trials. This is indicated by the small within-subject variance at each ES level, as depicted in Fig. 4.4.

4.3.2 Effect of training on ES pattern

Hypothesis 2 predicts that the preferred timing pattern will depend on the amount of training such that patterns requiring more specific control will be observed more frequently for TRD than NOV. Results from the Wilcoxon signed-rank test for differences in pattern between TRG groups showed the pattern of relative timing across ES levels was not the same for TRD and NOV subjects. The Euclidean distance between the two groups was greater than the test median of 13%T: *Mdn* = 31%T ($p < .0005$, one-tailed, $N = 432$). Fig. 4.5B shows the frequency distributions of T10-L4 Lag%T values for NOV and TRD. Note the multimodal characteristic which reflects the separation of T10-L4 relative timing between simultaneous and non-synchronous ipsilateral activity. The NOV group shows a greater tendency towards ipsilateral simultaneous ES activation than the TRD group, with values around 0% occurring most frequently. Asynchronous timing dominates in the TRD group with most lags in the 45-65%

range. Figure 4.5C illustrates the overall lower lag values for NOV compared to TRD**.** The asynchronous relative timing requires more specificity of control than the simultaneous activation of muscles at different segmental levels suggesting that highly trained performers employ muscle activation patterns that require specific control more often than novices.

FIGURE 4.6

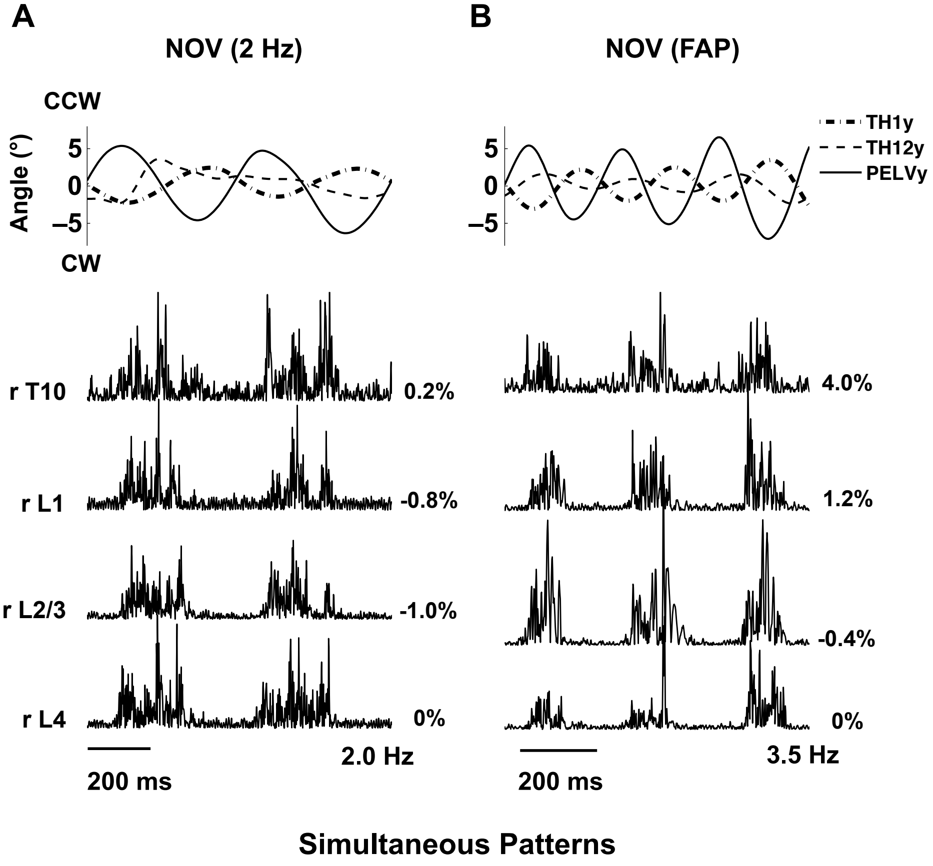

FIG. 4.6. EMG and segment kinematics for the simultaneous (S) pattern for single trials of one novice subject (N2) for the 2 Hz MC (A) and the FAP MC (B). Lower 4 traces: EMG for right ES. Upper traces: frontal plane rotation angles for PELV, TH12 and TH1 segments. Clockwise (CW) rotation corresponds to right hip elevation, left shoulder depression; counterclockwise (CCW) rotation corresponds to left hip elevation, right shoulder depression.

4.3.3 Timing patterns by MC and classification of activation patterns

From visual examination of EMG there appeared to be three distinct rostro-caudal timing patterns. Fig. 4.6 shows two sets of EMG traces recorded from NOV subject N2, depicting typical examples of the simultaneous (S) bursting pattern across ipsilateral ES levels in two different shimmy frequency conditions: 2 Hz and FAP (mean frequency 3.5 Hz). The respective Lag%T values are given to the right of each EMG trace. For the 2 Hz MC, the S pattern was seen in 8 of 12 NOV subjects but in only 2 of 12 TRD subjects. In contrast, the majority of the TRD subjects (10) showed a strict anti-phasic pattern between ipsilateral ES T10 and ES L4. Examples from two TRD subjects (T10, T8) performing the 2Hz and 3Hz MCs, respectively, are shown in Fig. 4.7. In this pattern, ES activity at more rostral levels is anti-phasic (antagonistic) to ipsilateral activity at more caudal levels. By virtue of the half cycle anti-phasic activity occurring at each vertebral level, taking right and left side ES together, this ipsilateral anti-phasic coordination represents a diagonal (D) synergy between contralateral ES T10 and L4. Only 4 of the 12 NOV subjects showed this D pattern for the 2 Hz MC. Both the S and D bursting patterns were also seen in the 3 Hz and FAP MCs, however, a third, asynchronous pattern emerged as the dominant one in the FAP condition. Examples from one NOV and one TRD subject in Fig. 4.8 (see also Fig. 4.2) clearly show incremental phase-shifts in burst activity along a rostral-caudal direction in ipsilateral segments of the ES. This asynchronous (A) pattern also occurred in the 3 Hz condition but never in the 2 Hz MC. The frontal plane rotation amplitudes for segments TH1, TH12 and PELV are shown for each of the EMG examples in Figs. 4.6 through 8. Strictly anti-phasic rotation between TH1 and PELV seen for the S pattern (Fig. 4.6, top) would suggest that the spine describes one continuous c-curve between these vertebral levels consistent with the idea of simultaneous activation along spine lateral flexors from ES T10 to L4.

FIGURE 4.7

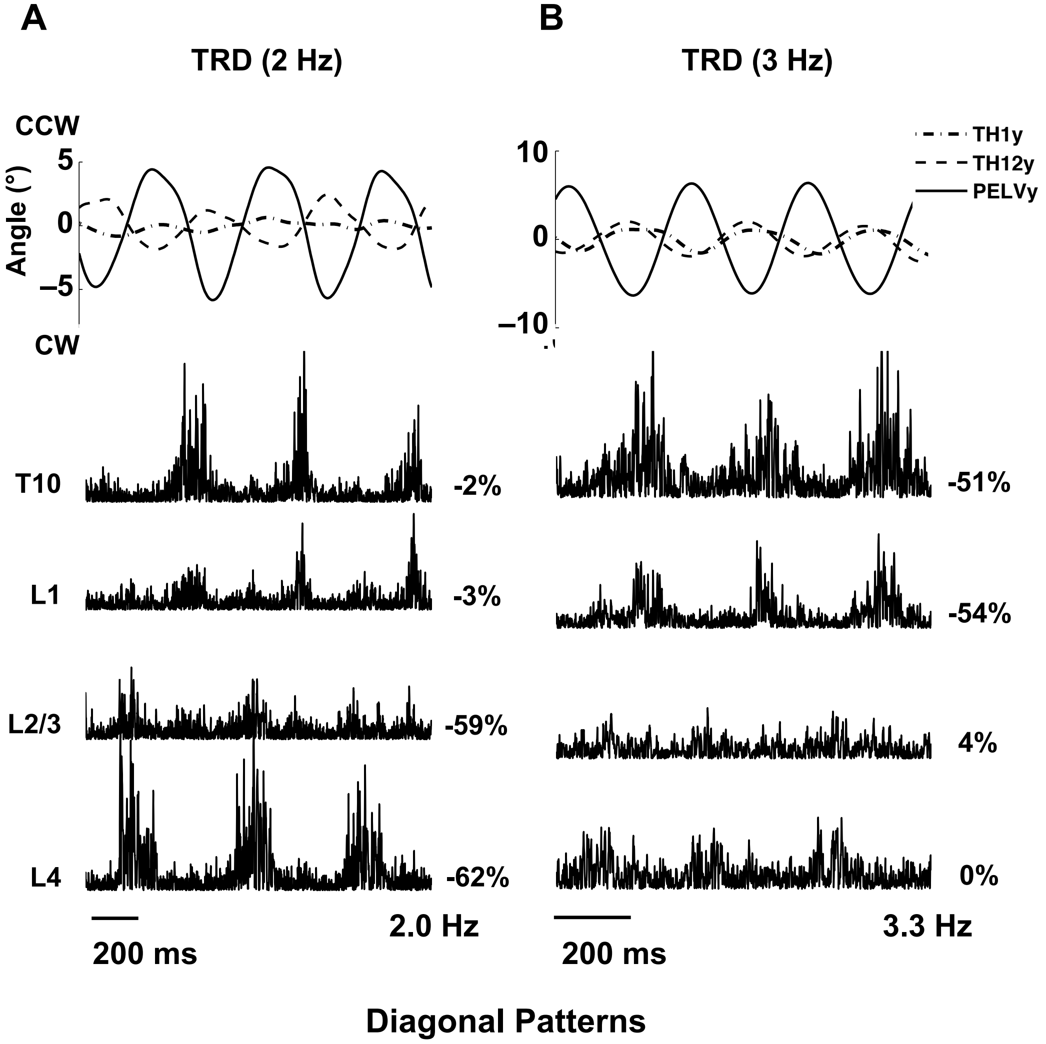

FIG. 4.7. EMG and segment kinematics for the diagonal (D) pattern for single trials of two TRD subjects: subject T10, 2 Hz MC, left side ES (A) and subject T8, 3 Hz MC (actual frequency 3.3 Hz), right side ES (B). Lower 4 traces: EMG for each ES level. Upper traces: frontal plane rotation angles for PELV, TH12 and TH1 segments. Clockwise (CW) rotation corresponds to right hip elevation, left shoulder depression; counterclockwise (CCW) rotation corresponds to left hip elevation, right shoulder depression.

FIGURE 4.8

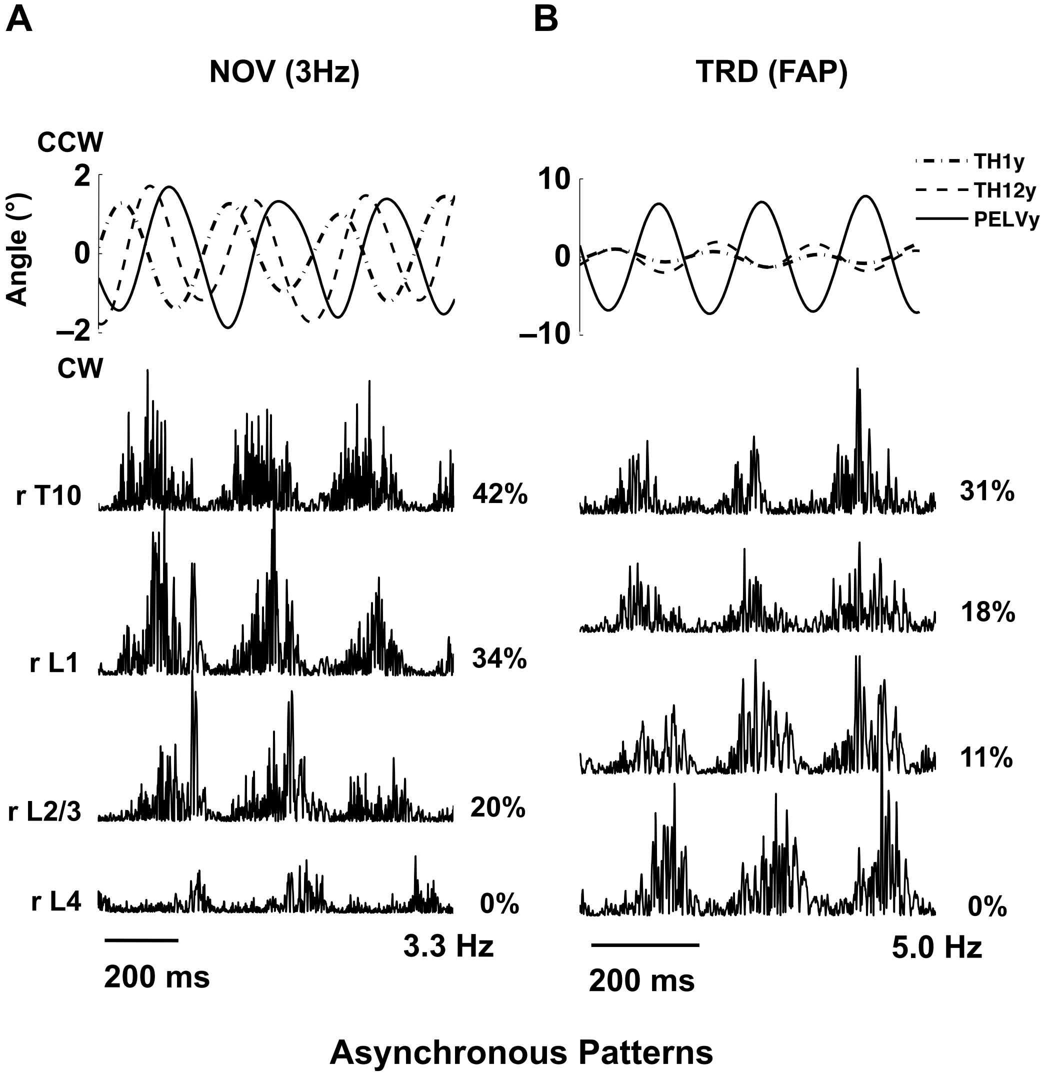

FIG. 4.8. EMG and segment kinematics for the asynchronous (A) pattern for single trials of the FAP MC for novice subject N5 at 3.3 Hz (A) and TRD subject T10 at 5.0 Hz (B). Upper traces: frontal plane rotation angles for PELV, TH12 and TH1 segments. Lower 4 traces: EMG for right ES. Clockwise (CW) rotation corresponds to right hip elevation, left shoulder depression; counterclockwise (CCW) rotation corresponds to left hip elevation, right shoulder depression.

Reduced amplitude of TH1 motion with no particular phase relationship to PELV (Fig. 4.7A, top), or clear anti-phasic relationship between TH12 and PELV (greater angle between these two segments - Fig. 4.7B, top) appeared to correspond to the D pattern. The ES T10 activation synchronized with the contralateral L4 burst likely provides the counter moment needed to stabilize the shoulder girdle/upper spine and prevent ipsilateral thoracic lateral flexion, possibly creating an additional curve inflection point for an s-shaped spinal curvature to produce the segmental motion. The kinematics corresponding to the A pattern (Fig. 4.8, top), illustrate a clear phase shift in the rotational movement between segments in a rostral-caudal sequence.

With confirmation of a change in pattern with movement frequency from the comparisons between MCs, and the indication of pattern differences coming largely from the TRD group, the descriptive statistics for the mean T10-L4%T lags by MC for the TRD group were used to reclassify all subject x condition latency sets as simultaneous (S), diagonal (D) or asynchronous (A) patterns. Note that in the TRD 2 Hz condition there are two extreme outliers (Fig. 4.5A), with values around zero, which were not included in the calculation of the mean and standard deviation. The ipsilateral pattern of activation was considered simultaneous if T10-L4%T was less than the TRD *Mean*-1 *SD* for the FAP condition, 8%T. The asynchronous pattern was defined as T10-L4%T being greater than 8%T but less than 31%T (*Mean*-1 *SD* for the 3 Hz condition). The right-left diagonal coordination pattern was identified where T10-L4%T was greater than 31%T *and* L2/3-L4%T < 8%T to meet the requirement that activation above and below L3 was one half cycle out of phase. There were two cases in which T10-L4% was greater than 31%T (N5: 42%T and T9: 41%T) but with L2/3%T values being extreme outliers (34%T for N5, 32%T for T9) compared to the *Mean*/*SD* for L2/3 (1.11/1.97). Consequently, these two cases were classified as A patterns. The D pattern was further subdivided into one group that showed synchrony of L1 with caudal (L4, L2/3), and one with more rostral (T10) ES levels, respectively: D-ros and D-cau.

FIGURE 4.9

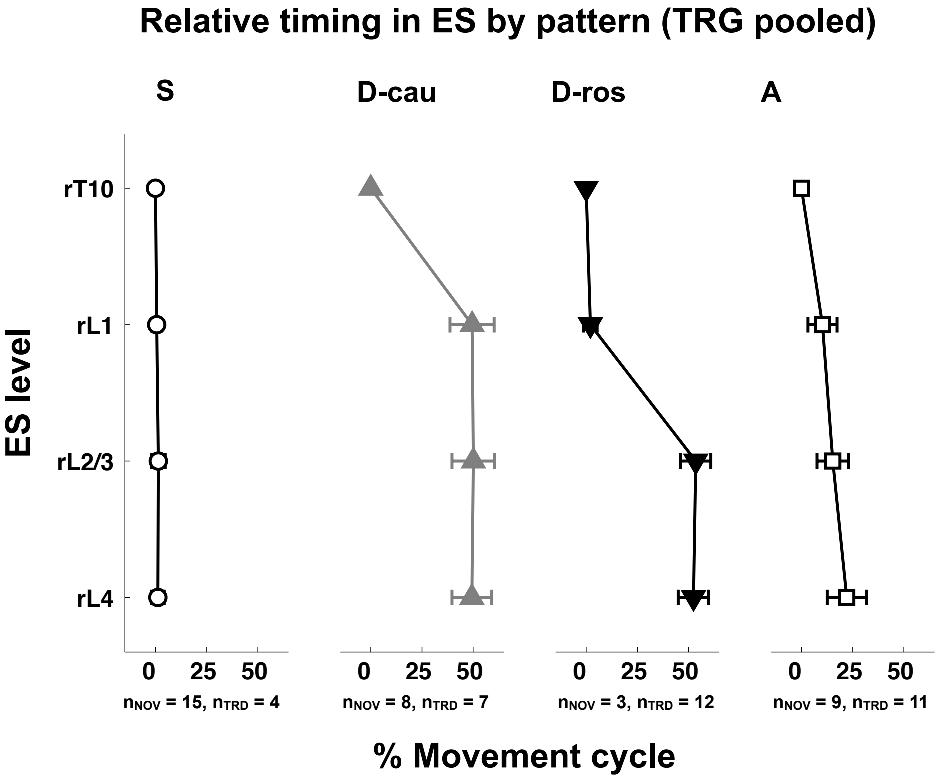

FIG. 4.9. Relative timing between right side ES segments for the simultaneous (S), diagonal (D), and asynchronous (A) patterns. Cases in the D pattern group were further subdivided dependent on whether rES L1 was synchronous with rostral (D-ros) versus caudal (D-cau) segments. Mean lags have been shifted on the x-axis such that rT10 peak activity occurs at 0% of the movement cycle. Error bars represent 1 SD. Where none are visible, 1 SD is smaller than the size of the data symbol.

Table 4.3 lists the means and standard deviations for T10-L4%T once all cases were reclassified by pattern type. Figure 4.9 depicts the relative timing at ES segmental levels for each pattern (TRG pooled), illustrating more clearly by MC than in Fig. 4.3, the different possible ES coordination patterns for producing the shimmy oscillations. Results from the Friedman's

ANOVA tests across right side ES levels by pattern illustrate the different characteristics of each pattern with regard to relative time between segmental levels of the ES. There was no difference in timing across the four vertebral levels in the S pattern, $\chi^2(3,19) = 0.778$, (4 TRD, 15 NOV), $p = .855$. Overall difference in peak activation timing of ipsilateral levels of the ES spanning T10-L4 was significantly different from zero for both diagonal patterns: D-cau pattern ($\chi^2(3,15) = 16.33$, (7 TRD, 8 NOV), $p=.000$); D-ros pattern ($\chi^2(3,15) = 22.47$, (12 TRD, 3 NOV), $p = .000$).

TABLE 4.3 Mean T10-L4%T by pattern

				Pattern Occurrence			2Hz	3Hz	FAP	FREQ (Hz)		
Pattern	Criteria	*Mean*	*SD*	*n*	*n* TRD	*n* NOV	TRD/NOV			*mean*	*min*	*max*
S	T10-L4%T < 8	1.2	3.1	19	4	15	2/**8**	0/3	2/4	2.9	2.0	5.4
D	T10-L4%T > 31 AND L2/3 < 8	50.7	8.4	33	21	12	**10**/4	**9**/**6**	2/2	2.7	2.0	4.2
A	8 ≤ T10-L4%T ≤ 31	21.9	11.1	20	11	9	0/0	3/3	**8**/**6**	4.2	2.6	6.3
N				72	36	36	24	24	24			

TABLE 4.3 Mean T10-L4%T by pattern. The criteria listed are the cutoff values for T10-L4%T from which cases were classified as S, D or A patterns. Means and standard deviations for each pattern are from pooled TRG groups, which results in standard deviations that are even smaller than those for the movement conditions (MCs) of the TRD group only. Summary of pattern occurrence by TRG and task condition highlight were the specific differences or similarities between TRG groups occurs. Most frequently occurring patterns by training and MC are highlighted in bold.

These findings are self-evident given that the two ipsilateral but antiphasic activation groupings in the D pattern correspond to functional specificity in opposite halves of the movement cycle. Overall timing difference across ES levels was also significantly different from zero in the A pattern, ($\chi^2(3,20) = 56.70$, (11 TRD, 9 NOV), $p = .000$).

The results of the multiple comparisons between rES levels by pattern are summarized in Table 4.4. For the two D patterns, these confirm the strict synergistic/antagonistic functional distinctions in ipsilateral ES at different segmental levels. For the two D patterns and the A pattern, T10 timing was significantly different from that at L4 ($p < .05$), which distinguishes these three from the S pattern. For the D-cau pattern, right rL4-rL2/3-rL1 formed one group with simultaneously activity, all having a significantly different latency from peak activation at rT10. In the D-ros pattern, the two groupings of activation were rL4-rL2/3 versus rL1-rT10. In the A pattern, rL1 timing was not different from rT10, and rL4 not different from rL2/3. However rL1 and rL2/3 peak activation timing was significantly different ($p < .05$). Thus the A pattern shows the same distribution of significant differences in timing across the ES levels as in the D-ros pattern, but with all of the activity occurring in the same half cycle, suggesting even greater segmental specificity. Overall, the results suggest a capacity for ipsilateral segmental specificity of activation timing in the ES at three levels spanning T10 and L4.

TABLE 4.4
Lag %T pairwise comparisons by pattern

	S	D-ros	D-cau	A
Overall *p*	0.855	.000†	.000†	.000†
	Sig	*Adj. Sig.*	*Adj. Sig.*	*Adj. Sig.*
T10-L4	-	.000†	.004	.000†
T10-L1	-	1.000	.000†	.165
T10-L2/3	-	.000†	.000†	.000†
L1-L2/3	-	.000†	1.000	.029*
L1-L4	-	.011*	1.000	.000†
L2/3-L4	-	1.000	1.000	.300
N	19	15	15	20

Significance at * $p < .05$, † $p < .001$

TABLE 4.4 Pairwise comparisons of Lag%T by pattern. Results of Friedman's ANOVA: overall timing difference between right side T10 and L4 by pattern and post-hoc tests between ES levels.

Table 4.3 also highlights the variation of patterns across the MCs for each TRG group. Once again we see that the S pattern dominated the 2 Hz MC for the NOV group (8 of 12) while the D pattern was the preferred coordination for the TRD group (10 of 12). For the 3 Hz condition, the D pattern was the most utilized activation pattern for both groups (TRD 9 of 12, NOV 6 of 12). The remaining 3 TRD subjects utilized the A pattern for 3 Hz, which suggests that this frequency may be a threshold for pattern change. Five subjects displayed no pattern changes with frequency/movement condition: N2 utilized the S pattern throughout conditions, and subjects N7, N11, T4, T11 utilized the D pattern throughout.

Maximum achievable movement frequency in the hip shimmy was significantly higher for the TRD group, the average being 1.09 Hz faster than that of the NOV group ($p < .0005$). Maximum frequency (*SD*) for the NOV group was 3.90 Hz (0.45), and ranged from 3.26 to 4.79 Hz. For the TRD group, maximum frequency was 4.95 Hz (0.77), and ranged from 3.60 to 6.31 Hz. Table 4.3 lists the means, minimum and maximum movement frequencies for each pattern. Pattern changes from S or D to A occurred anywhere from 2.6 Hz (minimum for A pattern) to 4.2 Hz (mean for A pattern and maximum for D pattern). At frequencies of 4 Hz and above, the D and S patterns were not observed, suggesting that at higher frequencies, the asynchronous pattern was the only possible one, and may be selected involuntarily.

Figure 4.10 shows the linear regressions for the relationship between right side T10-L4 latencies in ms plotted and movement frequency and grouped by pattern category. At 2 Hz there are two clusters of values around 0%T and 45-55%T, respectively, showing again that, at the lowest movement frequency, subjects selected one of two possible coordination patterns. An interaction between training and movement frequency can be seen. Two opposite trends in latency scaling occur with increasing spine oscillation frequency: T10-L4 timing difference for the simultaneous pattern increases slightly with frequency while that for the D pattern decreases sharply with decreasing T (increasing frequency), switching to an asynchronous pattern. Both trends converge around a 20-50 ms timing difference between ipsilateral T10 and L4 ES levels once oscillation frequency of the spine reaches approximately 4 Hz. Kruskal-Wallis tests confirmed that timing difference between ipsilateral T10 and L4 ES was not equivalent across patterns, $\chi^2(2,72) = 57.42$, $p = .000$. Results of post hoc pairwise comparisons for each combination of patterns were all significant. S versus A: $\chi^2(1,39) = -20.00$, $p = .002$. S versus D: $\chi^2(1,49) = -43.66$, $p = .000$. A versus D: $\chi^2(1,50) = 23.66$, $p = .002$.

FIGURE 4.10

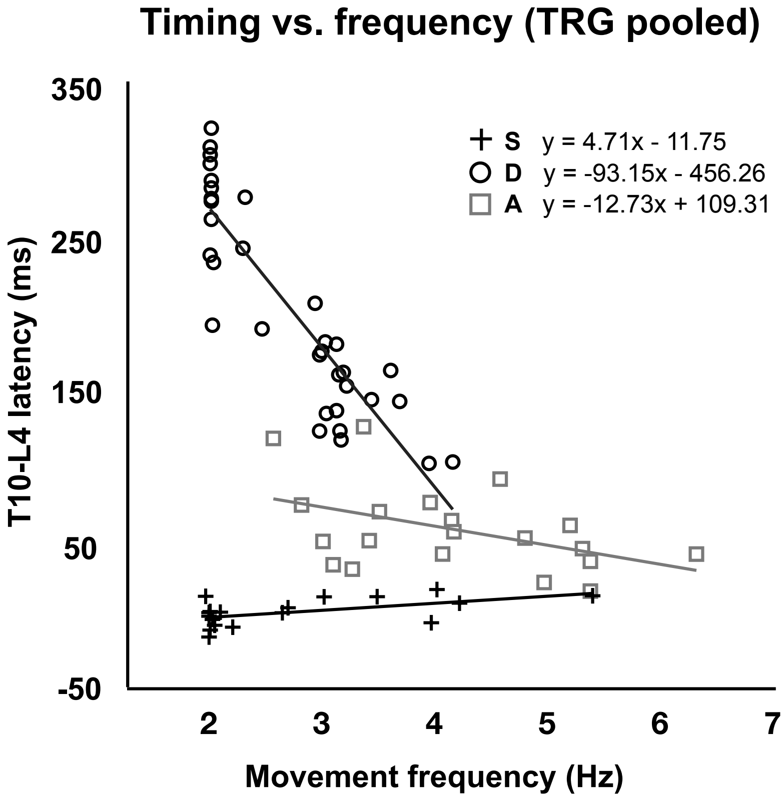

FIG. 4.10. Relationship between ipsilateral T10-L4 relative timing (in ms) and movement frequency with TRG groups pooled. Each data point corresponds to an MC mean for one subject (three data points per subject). Simultaneous pattern (S) denoted by crosses, diagonal (D) by circles and, and asynchronous (A) by squares.

4.4 DISCUSSION

The present study used voluntary segmentally specific trunk oscillations from belly dance to explore coordination and control of spine extensor muscles in rhythmic lateral spine undulations. Different patterns were identified by differences in the relative timing of ES muscle activation across four vertebral levels spanning T10 to L4. Changes in erector spinae activation timing patterns with increasing frequency confirmed the hypothesis that different control mechanisms underlie rhythmic undulating spine motion at different tempos in humans. Differences between novices and trained performers in the likelihood of engaging a particular activation timing pattern occurred at the lower frequencies, supporting the hypothesis that these mechanisms are modifiable by training.

Three distinct muscle activation patterns were identified: ipsilateral simultaneous bursting across segmental levels of erector spinae, with alternation between right and left sides every half cycle (S pattern); a diagonal synergy seen as simultaneous contralateral activation of the ES at T10 and L4 levels, alternating with the opposite diagonal synergy every half cycle (D pattern); and non-synchronous, sequential activation in a rostral-caudal direction along ipsilateral ES segments (A pattern). The S and D patterns are analogous to standing waves of activation, while the A pattern resembles a metachronal traveling wave of activation. There was a general trend for the activation pattern to change with movement frequency, as well as an interaction between the amount of training and the pattern most frequently adopted.

Pattern A, which involved the greatest degree of compartmental specificity, seen as incrementally phase shifted activation along segments, emerged between 3 and 4 Hz. At the lowest shimmy frequency (2 Hz) the S and D patterns were equally likely, but there was an influence of training on pattern selection, with S being more likely for NOV and D occurring more frequently in TRD. As movement frequency increased the T10-L4 Lag%T increased for the S pattern but decreased for the D pattern as both converged towards the A pattern. At the higher frequencies, the effect of training was manifested as differences in maximum movement frequency, with TRD achieving faster tempos.

The A and S patterns closely resembled those described by de Seze, et al. (2008) in their investigation of axial muscle patterning in humans during various forms of locomotion. From recordings at four spinal levels of the ES (C7, T3, T12, L4) they observed a traveling descending wave during forward walking, backward walking and crawling on hands and knees. In forward and backward walking the phase shift in burst onset increased linearly with distance between electrode sites (ES muscles) in a rostro-caudal direction. The increasing phase shift in peak burst activation that we found in our A pattern mirrors this finding. In contrast, when de Seze et al. (2008) recorded activity in amble walking (homolateral arm/leg moving in the same direction), ES activation showed no significant change in burst onset timing across ES levels, similar to our finding in the S pattern of no difference in peak activation timing across the ipsilateral ES segmental levels. De Seze, et al. (2008) compared their findings to the gait-dependent patterns in salamanders (Delvolve et al. 1997). Trotting over land involves ipsilateral simultaneous activation of axial muscles along segments between the fore and hind limb girdles - a right-left anti-phasic standing wave of activation analogous to the S pattern. In swimming, axial muscle activation switches to a rostral-caudal sequential wave analogous to the A pattern. The S and A spine extensor patterns observed in the present study may involve pattern generators that produce an analogous phase shift between gaits.

In the lamprey (Grillner 1985), the capacity for rhythmic motor output is distributed along the cord, with each segment activating a particular motoneuron pool. Intersegmental coordination is achieved via mutual excitation of serially coupled networks. This segment-to-segment excitation occurs at a constant phase lag. Left-right coordination of anti-phasic activity is afforded through reciprocal inhibitory connections between corresponding units at each segmental level. This functional arrangement allows for the type of propagating sequential wave of paraspinal muscle activation along the spine that we observed in the A pattern at the higher shimmy frequencies.

This same overall organization is presumed to exist in the salamander, however, with additional circuitry for controlling the legs and coordinating their motion with that of the trunk. Ijspeert (2001) used simulations and robotic salamanders to show that tonic drive to the spinal oscillators produces the swimming pattern, with increased level of drive producing faster swimming. If the drive to the leg oscillators dominates that of the spinal oscillators the spinal pattern is entrained to the leg pattern, which results in the characteristic side-bending pattern of the trunk (ipsilateral synchronous activation in axial muscles between limb girdles). Ijspeert noted that during very fast trotting the spinal activation pattern of salamanders returns to the undulatory pattern of swimming. This is similar to the switch we observed from the S to the A pattern once spine oscillations reached 3-4 Hz.

Using localized NMDA excitation to stimulate fictive locomotor patterns in *in vitro* lamprey spinal cord preparations, Matsushima and Grillner (1992) showed that increasing a segment's excitability causes it to become the leading segment, which also determines the cycle duration. Adjacent segments are entrained by the one with the higher excitability at a fixed phase lag. Furthermore, the magnitude of the phase lag between segments is determined by the difference in excitability between the leading segment and adjacent ones: the greater the difference in excitability, the greater the phase lag between segments.

Recent studies using in vitro spinal preparations from neo-natal rats suggest that similar central mechanisms may underlie the generation of rhythmic axial muscle patterns in mammals (Falgairolle and Cazalets 2007) (Beliez et al. 2015). These researchers recorded from the ventral roots at 6 segmental levels (T4, T6, T10, T12, L2, L5) during fictive locomotion. They identified three spinal regions capable of independent generation of bilateral alternating motoneuron activity: thoracic (axial muscles), lumbar (axial and hindlimb muscles), and sacral (tail). In addition, activity was metachronal, traveling caudo-rostrally with a constant intersegmental phase lag. The authors suggest that the neuronal networks that produce sequential activation patterns in the axial muscles of primitive vertebrates are highly conserved in mammalian locomotor circuits. These include both crossed connections and long and short propriospinal connections to produce the undulating spine movements that allow coordination between trunk and limbs during locomotion.

There is some evidence that trunk muscle activation patterns similar to those which we observed may be innate. Felt et al. (2012) describe slow, cyclic sideways bending movements recorded in human embryos. This simple and stereotyped motion is the only movement pattern from weeks 5.5 to 7 of development. The authors propose that these patterns reflect the earliest developmental features of neural networks. Similar findings in a variety of animal species suggest their evolutionary conservation. Dominici et al. (2011) hypothesize a developmental trajectory for locomotion that begins with motor primitive patterns are that retained and modified through experience: during the first few months, basic motor patterns emerge via additions to existing circuitry and tuning through the increasing influence of descending and sensory signals. These researchers elicited stepping response in newborns, recording kinematics and EMG of leg and trunk muscles including ES at the L2 level. Their results show striking similarities between neonatal humans and rats, and among toddlers, monkeys, cats, rats and guineafowl. Their findings are presented as evidence for the phylogenetic conservation of locomotor patterns across vertebrates as inborn motor primitives that are modified and augmented rather than discarded and replaced. In light of these findings, it may be plausible that the belly dance shimmy involves exploitation of such patterns, possibly in the form of learning to selectively activate them instead of more dominant patterns.

Pattern selection in axial muscles during human rhythmic spine motion is related to training and movement frequency. At lower frequencies training and experience influence pattern selection. The S pattern does not appear to require independent control of trunk muscles, unlike the D pattern which may require learning to disrupt innate global trunk lateral flexor patterns to create a new pattern where muscles and/or muscle compartments at different segmental levels can be specifically controlled. The undulatory locomotor patterns of the lamprey are modifiable for different behaviors such as burrowing or mating (Grillner, 1985), which require different relative timing of muscle activation. The independent control of parts of the neural network of the lamprey spinal cord that produce such timing differences may provide insight into human control of trunk muscles.

Training appears to be indispensable in achieving the highest movement frequency where experience is related to the ability of trained dancers to modulate muscle bursts at higher frequencies in order to achieve higher hip shimmy frequencies than novices. Acquired skill may also include learning to inhibit unwanted activation such as concomitant increased drive to limbs which may interfere with or overshadow the emergence of primal axial pattern generation.

Acknowledgements

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Chapter 5

Simultaneous control of cortical and spinal pattern generators in a polyrhythmic, segmentally specific trunk motor skill

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Preface to the third article

Drawing near the end of my PhD, I had thoughts of addressing a simpler question for the final chapter - one based more on biomechanics and muscle function. I am glad that instead, I went back to the original interesting hypothesis of two separate control signals operating in the superposition of polyrhythmic patterns within the same muscles, during the performance belly dance “layered” movements. These involve the simultaneous performance of the fast hip shimmy oscillation overlaid on any type of low frequency motion, and represent the highest levels of skill in the dance, requiring extensive practice.

Having previously concluded that slow versus fast pelvic isolation movements, both involving lateral spine undulations, are under voluntary versus automatic control, respectively, the next question was, what can comparisons of these movements in isolation and combination tell us about the hierarchical control of complex voluntary trunk movement? Here we expected to find very striking differences between naive and expert performers in the performance of the combination movement. The predicted breakdown in patterns for novices with superposition of the two movement frequencies was expected to provide the means for assessing which hierarchical levels of the CNS generate control signals for which movement components. Additionally, from these comparisons we expected to be able to infer the likely locus of successful integration of signals, and of signal interference. The findings provide very interesting insights on 1) mechanisms for generating voluntary rhythmic spine motion in humans, 2) the phylogenetic conservation of locomotor neural circuitry - rhythmic pattern generators - in humans, and 3) the capacity of the CNS for generating novel rhythmic trunk movements through the interaction of descending input, spinal pattern generators and sensory feedback for long-term adaptation and reorganization of spinal circuitry.

ABSTRACT

We investigated the interaction between cortical and spinal pattern generators simultaneously controlling rhythmic oscillations of segmentally specific trunk muscle compartments at two disparate frequencies. Expert and novice subjects performed a belly dance skill in which a high frequency trunk oscillation previously shown to be controlled by a spinal pattern generator is superposed on a low frequency voluntary movement under cortical control. Decomposed high and low frequency elements of the polyrhythmic movement were compared to the same motion elements performed separately to assess mutual modulation between patterns. Relative muscle timing at 4 erector spinae vertebral levels and trunk motion were analyzed. By identifying invariances and alterations in timing patterns we determined that expert dancers can generate two simultaneous but independent neural control signals which are summed at the spinal level to generate a dual frequency pattern in the same effector. By contrast, when novices attempt this composite skill, the two movement plans are conflated centrally, with the resulting pattern resembling a hybrid of the two, without preservation of the separate rhythmic motions. Control of complex polyrhythmic trunk undulation requires a learned ability to integrate cortical control signals for large amplitude slow rhythmic motion with small amplitude high frequency oscillations controlled by a spinal pattern generator. This integration likely involves learned gating of innate neural oscillators. Naive attempts are characterized by mutual modulation between patterns resulting in a simplified spatiotemporal pattern of erector spinae activity and/or loss of one of the frequency patterns suggesting adoption of a single, voluntary control signal.

5.1 INTRODUCTION

Rhythmic trunk movements from belly dance were used to investigate the neural integration mechanism to coordinate multi-frequency segmental spine motion. Belly Dance was used previously as a paradigm for investigating the production of segmentally specific rhythmic trunk movements at low frequencies (0.5 and 1 Hz). Using a range of different lateral undulating spine motions (vertical figure 8s, horizontal hip slide, slow and fast hip shimmies) across a range of tempos (0.5 Hz to 6 Hz) we identified four task, tempo and training-specific muscle activation patterns including standing waves of 1) ipsilateral simultaneous and 2) contralateral rostral-caudal synergies, as well as metachronal traveling waves in 3) descending and 4) ascending directions (Nugent and Milner in press; Nugent et al. 2012). These patterns bear striking resemblance to axial muscle locomotor patterns observed in lower vertebrates, other mammals, and humans, suggesting both the phylogenetic conservation of the neural circuitry responsible for rhythmic pattern generation in paraspinal muscles and the exploitation of locomotor pattern generators to produce novel movements.

We proposed that these movements, when performed at slower tempos, are under voluntary, descending control, whereas at higher frequencies, central pattern generators are likely activated. The ability of trained belly dancers to simultaneously combine movements that follow different trajectories and rhythms allows exploration of how the nervous system controls complex movements. We predicted that novices would not be able to integrate patterns at two very different frequencies, even if they could produce the individual patterns separately. We expected that the forms of pattern breakdown and degree to which each pattern would modulate the other, would provide insights into how the nervous system organizes composite movements by parsing out which movement elements are likely to be under descending control and which are centrally generated and modified by reflex interaction.

Perhaps the closest analogy from animal research to the kinds of polyrhythmic combined actions performed by belly dancers is the paw shake during locomotion in the cat. In normal cats, the higher frequency paw shake is superimposed on the swing trajectory and increases swing duration as well as stance duration in support limbs. Another animal analogy is the non-periodic unilateral increase in activation of axial muscles superimposing steering control on oscillatory trunk locomotor patterns as seen in the salamander (Crespi et al. 2013). It has been shown that humans can coordinate rhythmic motion of opposing limbs at two different frequencies, for example, with the arms in the performance of a novel bimanual task (Park and Sternad 2015; Peper et al. 1995) or with the legs while walking on a split-belt treadmill moving at different speeds (Dietz et al. 1994). An example from human locomotion is the trunk segmental movements in the sagittal plane and accompanying muscle activation patterns at twice the frequency of the walking cycle in humans (Anders et al. 2007; Carlson et al. 1988; Thorstensson et al. 1982; Winter and Yack 1987). Adamovich et al. (1994) and Sternad et al. (2000) investigated movement superposition using tasks combining rhythmic oscillation of the elbow joint with reaching in the horizontal plane to assess the interaction between superimposed rhythmic and discrete movements. However, none of the studies in humans have focused on polyrhythmic movements with components of markedly different frequencies performed by the same actuators in multi-segmental coordination. To our knowledge, the interaction between rhythms in composite, highly skilled trunk movements has never been studied. Using three rhythmic belly dance movements - a slow (0.5 Hz) medio-lateral pelvic translation, a fast (3-6 Hz) hip shimmy and simultaneous combination of the two movements, we tested the following hypotheses:

Hypothesis 1: The high and low frequency patterns are each controlled independently by different mechanisms;

Hypothesis 2: The composite task is a highly skilled movement that requires extensive training for superposition of two independent control signals (generated by different control mechanisms).

5.2 MATERIALS & METHODS

5.2.1 Subjects

Fourteen novice (NOV) subjects and sixteen trained (TRD) subjects were recruited. All subjects were female. TRD were defined as those having engaged in belly dance training and practice regularly for 3 or more years. NOV had no prior belly dance training and were selected such that their ages at the time of data collection were matched to the ages at which TRD subjects had begun their belly dance training. Care was taken to select participants with a low-to-normal body mass index (BMI) to maximize signals recorded with surface electromyography (sEMG) (De la Barrera and Milner 1994). Subjects were included in the analysis if there were complete data sets for each of the 3 movement conditions. After exclusions, 12 trained (TRD) and 9 novice (NOV) subjects remained. Subject demographic information is provided in Table 5.1. NOV age range was 18 to 32 years (23 ± 5 years), TRD range was 27 to 57 years (39 ± 9 years), with age at start of training ranging from 16 to 33 years (26 ± 5 years). For the TRD group, amount of training ranged from 3.5 to 32 years (12.4 ± 9.2) years. The first author was a professional belly dancer and one of the subjects. All subjects were free from injuries or medical conditions that might impair physical performance. The study was approved by the McGill Research Ethics Board and all participants gave written informed consent.

TABLE 5.1 Subject information and EMG data trials

TRD							**HIPSLD**			**FAP**			**COMBO**						
ID	*Age* (yrs)	*Age init.* (yrs)	*Trg* (yrs)	*Ht* (cm)	*Wt* (kg)	*BMI*	n. Trls	Pat	*f* (Hz)	n. Trls	Pat	*f* (Hz)	n. Trls	*Lf* Pat	*Lf* (Hz)	n. Trls	*Hf* Pat	*Hf* (Hz)	Pats chgd
T1	39	28	11	172.0	52.6	17.8	6	D	0.50	8	A	5.49	10	D	0.52	10	S	5.60	HF
T2	37	31	6	157.5	53.5	21.6	6	D	0.50	10	S	5.38	10	D	0.51	10	A	6.12	HF
T3	28	24	3.5	156.0	53.9	22.1	6	D	0.50	10	A	5.37	10	D	0.51	10	A	5.98	N
T4	41	33	8	158.5	55.2	22.0	6	D	0.52	10	D	3.94	10	D	0.50	10	S	5.29	HF
T6	36	30	6.5	173.0	66.5	22.2	6	D	0.50	10	A	4.06	8	D	0.51	10	A	6.04	N
T8	50	17	30	166.0	56.0	20.3	6	D	0.50	10	A	6.31	10	D	0.50	10	A	5.52	N
T9	41	27	14	168.5	65.4	23.0	6	D	0.50	10	A	4.65	10	D	0.50	10	D	3.96	HF
T10	41	30	11	175.5	64.0	20.8	6	D	0.50	10	A	5.17	10	D	0.50	10	A	5.58	N
T11	29	24	5	168.5	52.9	18.6	6	D	0.50	10	D	3.60	10	D	0.50	10	D	4.34	N
T13	38	27	11	164.5	54.0	20.0	6	S	0.50	10	A	5.37	10	S	0.50	10	A	4.99	N
T14	57	25	32	164.6	61.5	22.7	6	S	0.50	9	A	4.94	10	S	0.50	10	S	5.73	HF
T16	27	16	11	147.3	40.8	18.8	6	S	0.51	10	S	5.38	10	D	0.51	10	A	5.56	HF
Mean	38.7	26.0	12.4	164.3	56.4	20.8			0.50			4.97			0.51			5.39	
SD	8.71	5.21	9.21	8.18	7.13	1.74			0.00			0.78			0.01			0.66	
n = 12											*min*	3.60					*min*	3.96	
											max	6.31					*max*	6.12	

NOV							**HIPSLD**			**FAP**			**COMBO**						
ID	*Age* (yrs)		*Trg* (yrs)	*Ht* (cm)	*Wt* (kg)	*BMI*	n. Trls	Pat	*f* (Hz)	n. Trls	Pat	*f* (Hz)	n. Trls	*Lf* Pat	*Lf* (Hz)	n. Trls	*Hf* Pat	*Hf* (Hz)	Pats chgd
N2	32		0	173.0	56.7	18.9	6	D	0.50	6	S	3.48	6	S	0.51	6	A	3.78	B
N3	29		0	166.4	64.2	23.2	6	D	0.50	10	A	4.12	0(10)	id	0.49	10	A	4.62	LF-
N5	24		0	174.5	64.4	21.1	6	D	0.51	10	A	3.35	10	S	0.49	10	A	3.75	B
N8	30		0	168.3	49.6	17.5	6	D	0.52	10	A	3.26	5	S	0.66	0(5)	nd	-	LF, HF-
N9	24		0	170.0	52.3	18.1	6	S	0.50	10	S	4.00	10	S	0.50	0(10)	nd	3.95	HF-
N10	26		0	172.7	59.0	19.8	6	D	0.50	10	A	3.95	10	D	0.51	10	D	4.03	HF
N11	18		0	156.5	45.0	18.4	6	S	0.50	10	D	3.68	0(10)	id	0.51	10	D	4.19	LF-, HF
N13	18		0	159.0	51.6	20.4	6	D	0.50	10	A	3.41	10	S	0.50	10	D	3.55	B
N14	31		10w	165.1	50.8	18.6	6	D	0.50	10	S	4.19	5	S	0.49	5	A	4.22	B
Mean	23.2		0	150.5	49.4	17.6			0.50			3.72			0.52			4.01	
SD	5.26			6.26	6.68	1.78			0.01			0.36			0.05			0.33	
n = 9											*min*	3.26					*min*	3.55	
											max	4.19					*max*	4.62	

T, trained, N, novice, w, weeks, ID, subject identification, *Age init.*, age at which training was initiated, *TRG*, training, *Ht*, height, *Wt*, weight, *BMI*, Body Mass Index, n. Trls, number of trials, Pat, pattern, *f*, frequency, *Lf*, low frequency, *Hf*, high frequency, id, insufficient data, nd, no data, Pats chgd, patterns changed. Minus - indicates pattern disappeared.

5.2.2 Procedure

To test the hypothesis of two independent control signals activating the same trunk muscles, we compared the trunk kinematics and patterns of trunk muscle activation for the two training (TRG) groups and three movement conditions (MCs). Three-dimensional motion capture videos of these movements can be viewed in online at www.facebook.com/Shimmylab. All subjects performed three rhythmic segmental spine movements from the belly dance repertoire: a low frequency (0.5 Hz), horizontal medio-lateral hip translation (HIPSLD), the hip shimmy (SHIM) performed as fast as possible (3.6 to 6.3 Hz depending on individual ability), reported in our previous study (Nugent and Milner, in press), and the combination of the two movements performed simultaneously (COMBO). The shimmy is performed by bending the knees to effect a slightly lowered baseline stance and then alternating right and left leg extension/ flexion and lumbar spine lateral flexion to produce a rhythmic rotation of the pelvis in the frontal plane (alternating pelvic obliquity). Leg extensor muscles are synergists with ipsilateral abdominals and spine extensors to produce hip elevation and thus pelvic rotation. Extension of the knees also produces some transverse rotation of the pelvis and spine. Vertical bouncing is kept to a minimum so that, from an observational standpoint, motion is isolated to the pelvis. In the HIPSLD, the head is kept over the feet while the pelvis is shifted sideways outside of the base of support, alternating from side to side for near maximum range of motion in the hips. Thus the spine tilts with respect to vertical and weight transfers almost completely to one foot with each sideways movement while the head and shoulders are kept as level as possible. During performance of the HIPSLD, subjects were instructed to match the maximum lateral displacements of the pelvis to each beat of a digital metronome set at 1 Hz, making each cycle period equal to 2 s. Subjects were instructed to avoid making a hard stop at each lateral maximum, aiming for smooth transition through the lateral excursions and direction changes.

The COMBO was also performed to the 1 Hz metronome beat to standardize the low frequency motion element. Subjects were told to perform the fast shimmy simultaneously, with the aim to superimpose both movement frequencies in a continuous poly-rhythmic movement without interruption. Because the HIPSLD can be performed with straight knees, whereas the frontal plane rotation of the pelvis in the hip shimmy requires some “play” in the knee joints (typically performed in a slightly lowered stance as described above), NOV subjects were advised to keep the knees slightly flexed. Although experts are used to performing more intricate low frequency figures in combination with the fast hip shimmy, the hip slide was chosen because the amplitude of out-of-plane of motion is less than for more intricate figures making for easier kinematic analysis. Specification of this movement variation was well within the experience and repertoire of the TRD group. A functional stance width for performing all three movement conditions was established for each subject and marked on the support surface with masking tape. Feet were aligned with the tape markings to standardize width of base of support across trials.

Subjects performed 3 practice trials while watching a videotaped demonstration recorded with the metronome for the HIPSLD and COMBO. No auditory cues accompanied the SHIM condition in either practice or data collection trials. Verbal cues and a brief demonstration on how to perform each MC were given before the practice trials and during rest periods between trials, as necessary. For the HIPSLD subjects performed 6 trials of 25 seconds duration each. For the SHIM, subjects performed 10 trials of 10s duration each. COMBO trials were performed 10 times for 15 s duration each, and were the most challenging condition, with regard to coordination and muscle fatigue. Between trials subjects had 15-20 s rest standing in place.

Data collection included several additional movement conditions that were not analyzed as part of this study. The MC order was designed to alternate more and less fatiguing tasks, and to follow a difficulty progression that would allow easier tasks to serve as practice/warmup for more difficult ones. Thus, data collection began with a lower frequency version of the hip shimmy (used in the previous study) followed by SHIM, HIPSLD and COMBO, then three conditions unrelated to the present study. In all, trials of 7 different MCs were performed over a period of 60-75 minutes. Approximately half way through the session, subjects were given a sitting rest break of about 5 minutes.

5.2.3 Kinematics

Kinematics were recorded using a 6-camera Vicon Motion Systems Ltd.$^{©}$ (UK) setup. Kinematic data were sampled at 200 Hz. Subjects were instrumented with the standard Plug-in Gait (PiG) full body reflective marker set including upper body and arms (Fig. 5.1A & B). Two custom marker frames were constructed, each with three reflective markers to define a plane, in order to capture specific rotations of the trunk at different vertebral levels, which was not possible with the standard PiG marker set alone. Each frame consisted of a wooden rod attached to a plastic base that could be reheated and molded for a custom fit to each subject. The frames were affixed to the body with double-sided tape at the approximate levels of the first (TH1) and twelfth (TH12) thoracic vertebrae. The pelvic segment (PELV) was defined using the four standard PiG pelvic markers at the anterior and posterior superior iliac spines (Fig. 5.1A & C). The subject was oriented with respect to the laboratory Vicon reference frame such that lateral displacement to the right was in the positive *x* direction, forward sagittal displacement was in the positive *y* direction, and upward vertical displacement was in the positive *z* direction (Fig. 5.1B). Frontal plane segment rotation (around the anterior-posterior, *y*-axis) was positive in the counterclockwise direction, viewed facing the subject. Subjects were instructed to keep the head level, facing forward, with arms held slightly out to the sides during trials.

5.2.4 Electromyography

Muscle activity was recorded using the Delsys Bagnoli™ (Massachusetts, USA) 16-channel system integrated with Vicon for synchronization of EMG and kinematics. EMG was recorded bilaterally from the trunk and unilaterally from the right leg, at sixteen muscle sites sampled at 2 kHz using bipolar surface EMG electrodes with a 10 mm inter-electrode distance. The EMG of eight muscle sites on the thoracic (T) and lumbar (L) posterior trunk was analyzed in this study. Erector spinae (ES) activity was recorded bilaterally from the following muscle compartments and vertebral levels: longissimus thoracis (LT) at T10, L1 and L4 and iliocostalis lumborum (IL) approximately midway between L2 and L3 (Fig. 5.1C). Rationale for these electrode placements is explained in detail in the previous studies (Nugent and Milner in press; Nugent et al. 2012). The EMG of the right and left external obliques (EO) was recorded with electrodes placed 1 cm medial to ASIS, 2 cm superior to the level of the navel. The following right lower limb muscles were recorded using the SENIAM guidelines for electrode placement (Hermens et al. 1999): gluteus medius (GM) placed slightly higher than stated in SENIAM to avoid thicker fat layers, tensor fascia latae (TFL), vastus medialis (VM), biceps femoris (BF), tibialis anterior (TA), and the medial soleus (SM).

FIGURE 5.1 Instrumentation of subjects for data collection.

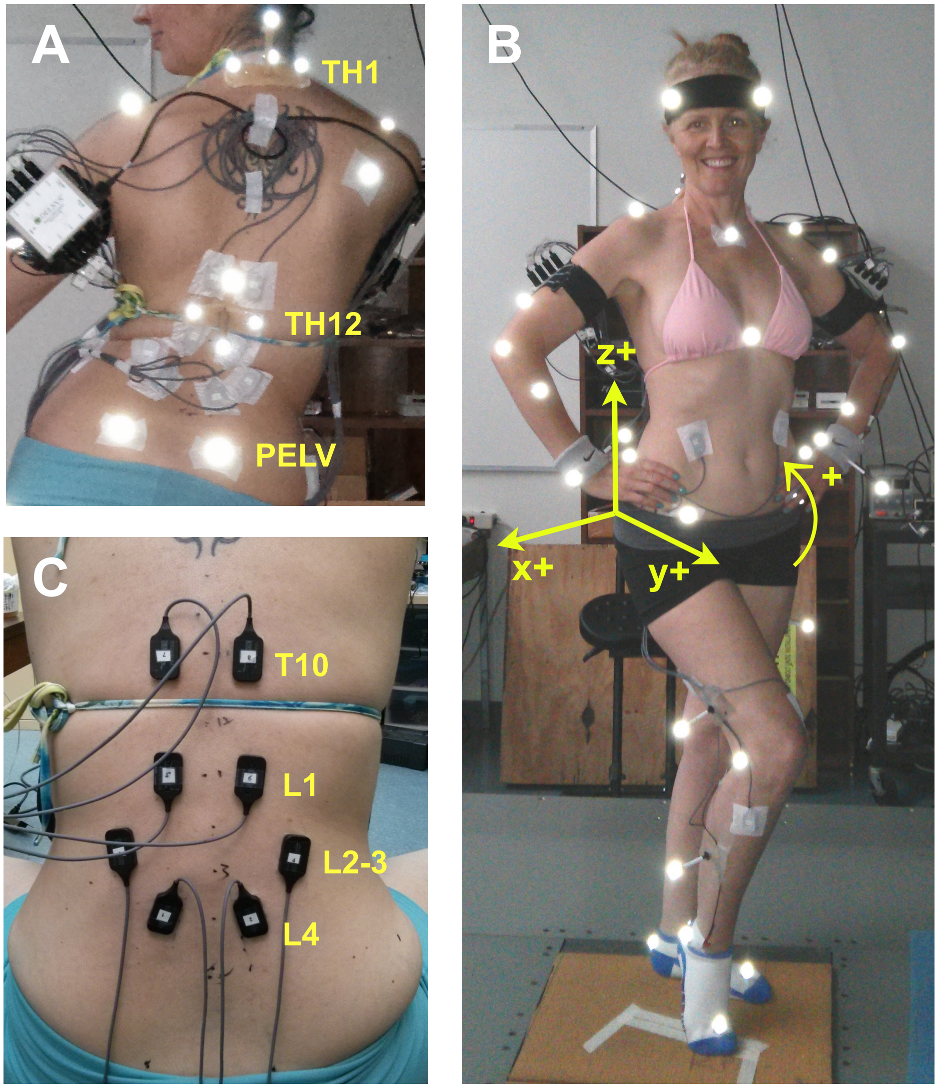

FIG. 5.1 (A) Marker frames defining segmental planes. Note: individual reflective markers at 7th cervical and T10 vertebrae are not parts of the marker frames. (B) PiG marker set and laboratory reference frame for kinematics (axes pictured are with respect to subject when facing forward in the Vicon collection volume, not as the subject is facing in the photo). Curved arrow indicates that counter clockwise rotation of segments is designated as the positive direction (viewed from the front, e.g. when left leg extends and left hip rises, pelvic rotation is positive). (C) Placement of electrodes to record from different regions of the ES muscles. Photo by permission: Marilee Nugent (photographer and model in B, Diane LaBelle (model in A, C).

5.2.5 Data processing

After pre-processing of kinematic data with NEXUS software, all EMG and kinematic data were processed using custom MATLAB scripts (The MathWorks, Inc., R2010b©, Massachusetts, USA). All kinematic data were low-pass pre-filtered at 8 Hz with a second order Butterworth digital filter using the Matlab function 'filtfilt'. For certain analyses of the COMBO, trunk segmental data were additionally filtered with a band-pass filter between 0.15 and 1 Hz to extract the low frequency hip slide component or a high-pass filter with a 3 Hz cutoff to extract the shimmy component. The resulting filtered kinematics could then be compared to the corresponding HIPSLD and SHIM data to determine if and in what way these patterns influence each other when superimposed. Rotation angles were calculated for each trunk segment (TH1, TH12 and PELV) around each rotational axis (x-sagittal rotation, y-frontal rotation, z-transverse rotation) relative to the initial stationary position of the subject (see Fig. 5.1B). For each trial, mean cycle period (T) was calculated by first applying the MATLAB function 'findpeaks' to the pelvic frame angle PELVy, to identify frontal plane rotation maxima, after which data in the time intervals between peaks, representing successive cycles, were averaged. Mean frequency for HIPSLD, SHIM and each COMBO frequency component for each subject was represented as 1/T.

Raw EMG data for all shimmy trials were demeaned and plotted for visual inspection. Start and end points for analysis of each trial were manually determined to include only activity representing consistent performance of task relevant motion. In the majority of trials, this meant that 0.5 to 2 s of data were excluded from the total trial length. For each subject, approximately 72 cycles (24 s x 0.5 Hz x 6 trials) of rhythmic movement were acquired for the HIPSLD, 70 cycles (14 s x 0.5 Hz x 10 trials) for the low frequency component of the COMBO, between 525 cycles (14 s x 3.5 Hz x 10 trials) and 840 cycles (14 s x 6 Hz x 10 trials) for the high frequency component of the COMBO and 324 cycles (9 s x 3.6 Hz x 10 trials) to 567 cycles (9 s x 6.3 Hz x 10 trials) for the SHIM, depending on the subject's performance.

Full-wave rectified EMG were low-pass filtered with a third order Butterworth digital filter using the Matlab function 'filtfilt'. Cutoffs for HIPSLD and SHIM EMG were 6 Hz and 12 Hz, respectively. The COMBO EMG were filtered twice, at 6 Hz and then at 12 Hz, in order to parse out the low frequency (COMBO-LF) and high frequency (COMBO-HF) components for comparison with the respective HIPSLD and SHIM patterns. Relative timing of EMG burst peaks at each electrode site was determined separately for each subject in each MC from cross-correlation analysis. For each subject and for HIPSLD, SHIM and COMBO-LF, the electrode channel corresponding to the ES EMG with the best signal quality was selected as the reference for cross-correlation with each of the other 7 EMG channels using the MATLAB function 'xcorr'. For the COMBO-HF, an ES signal was used as the reference for 2 TRD and 2 NOV subjects, but in the others, either VM (9 TRD, 4 NOV) or TFL (1 TRD, 1 NOV) was used, as these had the clearest high frequency burst patterns. The lag at the peak of the cross-correlation function represents the timing difference in ms between rhythmic burst peaks in the two signals. Cross-correlations between EMG signals were performed on the 10-25 s duration of each trial. For each trial, latencies were normalized as percentages of mean cycle duration and represented as Lag%T. Peak activity at ES sites was found to either coincide with or follow that at rT10, so for each subject, relative timing of each trial was standardized by subtracting the rT10 Lag%T from all values. Thus Lag%T for rT10 was always 0%. Positive values corresponded to activation preceding that at rT10 (lead), and negative values, activation following rT10 (lag). The Lag%T values for each electrode site were then averaged across trials by condition and subject. Mean lags for each signal were calculated from not fewer than five 10-25 s trials per subject. Two sets of lags were generated for the COMBO, corresponding to the high and low frequency components, respectively. While the EMG of all TRD subjects included both frequency patterns in their EMG, that was not the case for all of the NOV subjects. The number of trials per subject and per condition included in the analyses are listed in Table 5.1. Outliers were identified as lag values smaller or larger than two standard deviations from the mean. These amounted to 5.4% of the total number of right side ES lag values. The rhythmic nature of the movements constrained lags to be less than one cycle period, which explains why the criterion for outliers was two rather than the usual three SDs. The resulting sets of means for each subject were used in subsequent analyses.

Data were included in the analysis only if Lag%T values were available for both T10 and L4 ES levels to allow pattern classification and thus comparison between MCs. Lag%T values for each ES level were represented in data plots relative to the activity peak of rES T10 which was set as 0% of mean cycle duration. For simplicity in determining the intersegmental coordination patterns of ES compartments, only right side values for Lag%T were used in the analyses, since muscle activation was symmetrical on the right and left sides, differing by one half cycle.

5.2.6 Statistical analyses

We hypothesized that the high frequency and low frequency muscle activity patterns in the COMBO are independently controlled. The null hypothesis would predict the following: a) *the relative timing of muscle activity at different ES levels is the same for both frequency patterns when normalized to cycle time.* Therefore, we predicted (i) that timing patterns would be different for the HIPSLD and SHIM and (ii) that superimposing the movement frequencies should modify one or both of these muscle activation timing patterns as a result of the increased complexity in coordinating polyrhythmic movements. The null hypothesis also predicts that b) *superimposing the high frequency component should not distort the kinematics of the hip slide motion when performed in the COMBO compared to the isolated HIPSLD.* Therefore, we predicted (iii) that the low frequency kinematic pattern would be perturbed by superposition of the two components as the result of difficulty in performing a dual task with the same effector.

Our second hypothesis states that the difficulty of producing a combined movement from two separate control signals will be seen as an interference between patterns, which will be more pronounced for NOV subjects compared to TRD. We predicted a breakdown in either the low frequency or high frequency pattern, or both, when novices attempt the combined movement, but better preservation of separate patterns, when performed together, in the TRD group. The control complexity inherent in superimposing these two motor patterns may be seen as an inability to produce both patterns simultaneously, characterized by any or all of the following: loss of one pattern or the other (or both), increased variability in the kinematics, switching of muscle timing patterns (i.e. reversion to a simpler coordination strategy) in either or both the high and low frequency components of the COMBO, as compared with the HIPSLD and SHIM performed in isolation.

5.2.6.1 ES muscle timing patterns

Each set of ES data was classified as to pattern type using the criteria derived in the previous study (Nugent and Milner in press). The criteria were based on relative timing of peak burst activity between T10 and L4 ipsilaterally. Timing patterns were defined as either simultaneous (S), diagonal (D) or asynchronous (A) according to different T10-L4%T value ranges (Table 5.1). Mean Lag%T sets were classified as S if the T10-L4 activation timing difference was less than 8% of mean cycle duration. If this difference was greater than 31%, the pattern was classified as D, and the remaining patterns, i.e. T10-L4 difference less than 31% but greater than 8%, were classified as A. These criteria were applied in the present study to classify timing patterns of isolated HIPSLD and SHIM movements as well as the COMBO-HF and COMBO-LF components of the COMBO. A method for determining muscle timing pattern differences by MC or TRG was previously established by calculating the Euclidian distance (square root of the sum of squared differences) between corresponding sets of right side ES timing latencies (Lag%T values). This method was used in the present study to evaluate pattern differences (Hyp 1 (i)) and pattern changes between isolated and combined components (Hyp 1 (ii)), and between NOV and TRD groups (Hyp 2).

To test prediction (ii) that the low frequency timing pattern changes when the two movement frequencies are superimposed we calculated the Euclidean distance between Lag%T values for the HIPSLD and COMBO-LF. TRD and NOV were tested separately and the results compared to test the prediction of greater likelihood of pattern switching in NOV compared to TRD (Hyp 2). Similarly, we calculated the Euclidean distance between timing patterns for the to test the effect of superposing the low frequency pattern on the high frequency pattern, and compared the results for TRD and NOV. Each of these four sets of differences was tested individually for pattern change/difference using one-sample Wilcoxon signed rank tests with a threshold median value of 13%T. The threshold median was based on the following rationale. A difference of 25%T in the Lag%T value (a quarter cycle) at any electrode location would represent a substantial shift in the relative timing because it is equivalent to the relative time difference between minimum and maximum rate of shortening during muscle contraction in a rhythmic movement. We reasoned that a shift of even half this magnitude or a 13%T overall difference in the Euclidean distance between movement components or TRG groups would be functionally significant.

Our second hypothesis implies that there will be less of a difference between NOV and TRD in the isolated HIPSLD and SHIM compared to the corresponding components of the COMBO. To verify this assumption, additional comparisons were performed using Wilcoxon rank sum tests to test for differences in the isolated patterns due to training. The cases with D pattern in HIPSLD (HIPSLD-D) were used to compute Euclidean distance between muscle activation patterns in NOV vs. TRD. The same analysis was not performed for the high frequency components, since testing by pattern sample sizes were too small for robust statistical results.

Additionally, the effect of superposition on movement frequency was assessed using Wilcoxon rank sum tests for SHIM versus COMBO-HF, and for HIPSLD versus COMBO-HF, separately for each group. The same test was used to compare movement frequency between TRD and NOV in separate tests for SHIM and COMBO-HF.

5.2.6.2 Kinematics

To assess differences due to superposition (Hyp 1 (iii)) and training (Hyp 2) on the modulation of the low frequency motion by the high frequency component, we analyzed the trajectory of the right anterior superior iliac spine (RASIS), representing pelvic medio-lateral translation, in both HIPSLD and COMBO. Note that for these tests, the full COMBO signal containing both frequency components was used. First we calculated the direction of the instantaneous velocity vector using the x (mediolateral) and z (vertical) coordinates. This velocity vector represents the instantaneous direction of motion in the frontal plane. The Matlab function "var" was applied to the orientation angle of the velocity vector to obtain the variance of the direction of movement. Subject means were calculated for HIPSLD and COMBO separately by taking the mean variances across trials for these MCs. To test for overall pattern difference between HIPSLD and COMBO (Hyp 1 (iii)) a Wilcoxon rank-sum test was first performed on variances with TRG pooled. Next, Wilcoxon rank-sum tests were performed to compare movement variance between NOV and TRD groups to evaluate differences in variance due to training for the HIPSLD and COMBO separately.

To further test the hypothesis that the different movement patterns are mutually perturbing (Hyp 1 (iii)) and that the degree of modulation is affected by training (Hyp 2), Wilcoxon rank-sum tests were used to compare smoothness between HIPSLD and the low frequency component of the COMBO with TRG pooled. We also compared the smoothness of the low frequency COMBO component for NOV and TRD. Smoothness was evaluated by first low-pass filtering the x-velocity of the RASIS marker at 2 Hz to extract the low frequency component of the COMBO. The filtered velocity signal was then differentiated twice to obtain the jerk and the RMS jerk was calculated for the low-frequency component of pelvic medio-lateral motion (x-velocity) and normalized by the RMS x-velocity. This procedure was performed for each trial and the normalized RMS jerk was averaged across trials for each subject for the statistical analyses.

All statistical analyses were performed using Matlab or SPSS. All confidence limits were set at 95% ($p < 0.05$). All reported p-values correspond to one-tailed tests unless stated otherwise.

5.3. RESULTS

5.3.1 Observations of performance during data collection

A frequent observation amongst novices was that in trying to superimpose the two different movement frequencies one or the other would come to dominate, if not continuously, then intermittently. For example, lateral excursion amplitude was reduced and hip oscillation was emphasized, or hip oscillation dwindled away while lateral excursion amplitude was better maintained. In some cases, at the extremes of each HIPSLD cycle a sharp stop and exaggerated lateral pelvic tilt was produced instead of a smooth transition in direction change while maintaining a baseline horizontal orientation of the pelvis, as though the HIPSLD was being executed as a concatenated series of discrete movements rather than as a single continuous rhythmic movement. For one novice subject (N8) only 5 trials of the COMBO were recorded because the subject was unable to perform the composite movement even intermittently. Figure 5.2 shows kinematic patterns of the right hip for all three movement conditions by subject. We can see that in general, pelvic trajectory is similar between TRD (Fig. 5.2A) and NOV (Fig. 5.2B) for the HIPSLD and SHIM, but whereas the TRD appear to preserve both patterns well in the COMBO, with slight decreases in medio-lateral amplitude, in the NOV group this motion is markedly altered compared to the profiles for the TRD group. Subject N8 produced a completely different movement, akin to a 3-dimensional hip circle (video available online: www.facebook.com/Shimmylab) which is evident from the oval shape of the RASIS trajectory (Fig. 5.2B).

FIGURE 5.2 Pelvic trajectories in the three movement conditions.

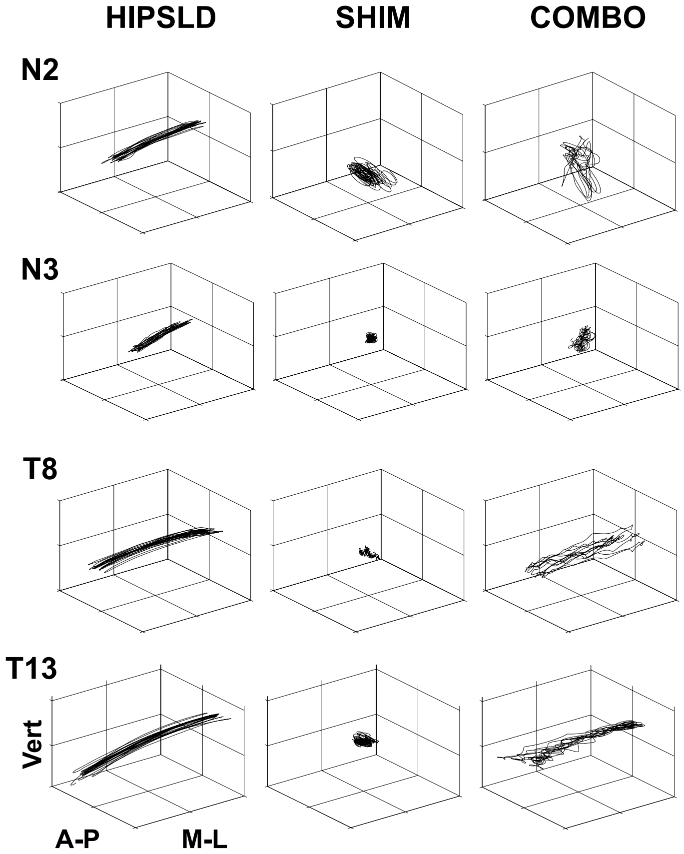

FIG. 5.2 Kinematics traces of the RASIS in each movement condition (buy column) for four representative subjects (by row): 2 novice (N2, N3) and 2 trained (T8, T13). A-P, antero-postural dimension, M-L, medio-lateral dimension, Vert, vertical dimension, with respect to the subject. Units are in cm. All axes represent 20 cm distances.

It was apparent that NOV subjects found the COMBO to be the most mentally and physically demanding of all the MCs. They needed more frequent and longer pauses between trials and tended to perspire more than the TRD group. Some NOV subjects expressed frustration about their inability to produce the movement. Some expressed concern that they could not produce the movement properly but were reassured that there was no expectation that they should be able to perform it perfectly, but rather, we were interested to see what happens in the attempt. One NOV subject remarked after the COMBO trials that she felt an improved ability to coordinate the SHIM with the HIPSLD when she mentally counted to 6 during each half cycle of the low frequency component (essentially counting a 6/8 time signature within a 3/4 timing for the HIPSLD) as a way to help produce and maintain the high frequency component (she had previous piano training). The best performances by NOV subjects involved maintenance of both movement patterns but with restricted HIPSLD amplitude. However, some did not perform either movement correctly, but performed an apparent hybrid of the two movement patterns - as though a fast shimmy was superimposed on a lower frequency shimmy, the low frequency motion becoming reduced in lateral amplitude with an increase in frontal plane rotation and hard stops before direction reversals).

5.3.2 General observations of EMG patterns

Figure 5.3 shows representative EMG patterns for the three MCs for one NOV subject and one TRD subject. For these two subjects, both high and low frequency patterns are clearly visible in the kinematics and EMG for the COMBO. All TRD subjects had sufficiently distinct high and low frequency modulation of the EMG to allow generation of reliable lag values for the majority of the ES muscles. In addition to the ES muscles, VM, BF and GM typically showed the high frequency pattern and sometimes the low frequency envelope as well (Fig. 5.4A, B, C, D). In contrast, not all NOV (Fig. 5.5) subjects had regular phasic muscle bursting at both frequencies at all ES levels. For some NOV subjects one or both frequencies would be evident at some ES levels but not at others. For example, only the high frequency pattern could be identified in the L4 ES compartments of subject N3 (Fig. 5.5A) so the low frequency pattern could not be classified by T10-L4 timing difference. In the case of N11 (Fig. 5.5B), there was no

FIGURE 5.3 EMG and kinematics for each movement condition.

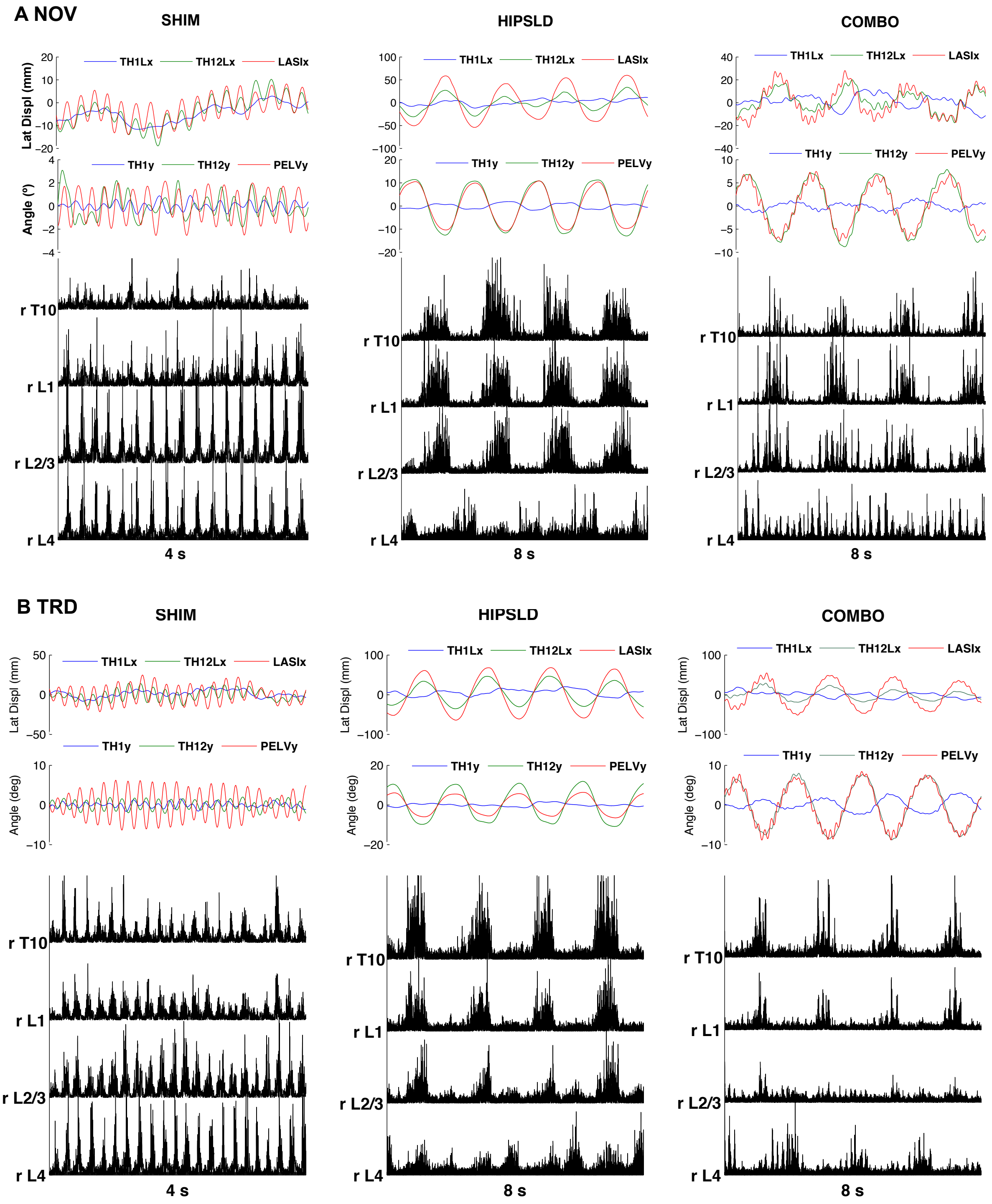

FIG. 5.3 Kinematic and muscle patterns from exemplary (A) NOV (N3) and (B) TRD (T10) subjects. The bottom four traces in each panel are the EMG patterns for ipsilateral ES at the four segmental levels. The top graphs in each panel show the kinematics for linear displacement in the x (lateral direction) for one marker from each segment frame. The second graph shows the rotation angles for each segment in the frontal plane (low frequency postural drift removed). The data segments pictured span 4 s of one trial for the SHIM conditions and 8 s of one trial for each of the HIPSLD and COMBO conditions. LASIx = left anterior superior iliac spine x-direction, Lat. Displ. = lateral displacement.

FIGURE 4.4 Raw EMG from 16 muscle during COMBO in TRD.

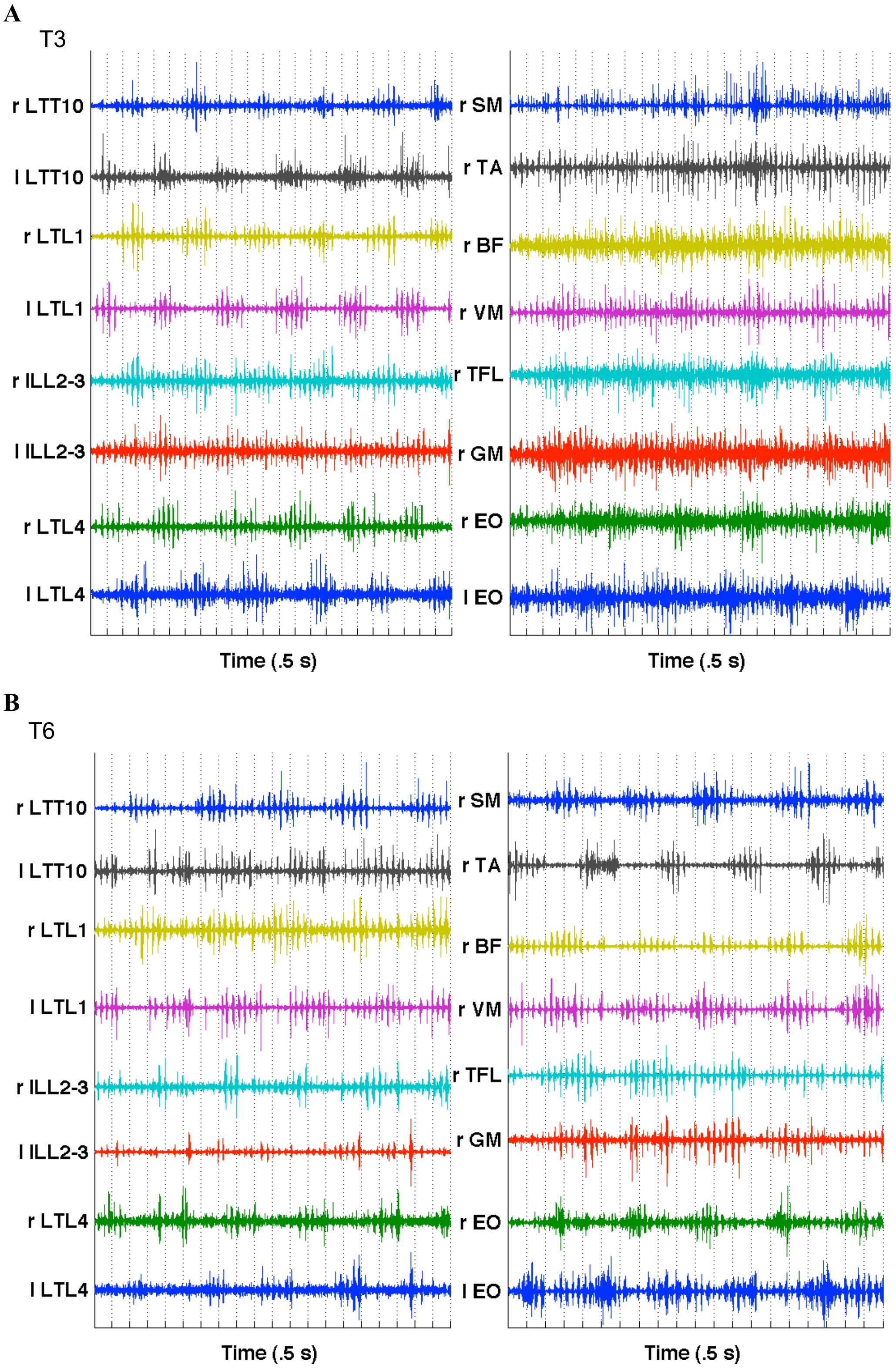

FIG. 5.4A, B Examples from single trials for TRD subjects. X-axes divisions are in 0.5 s intervals.

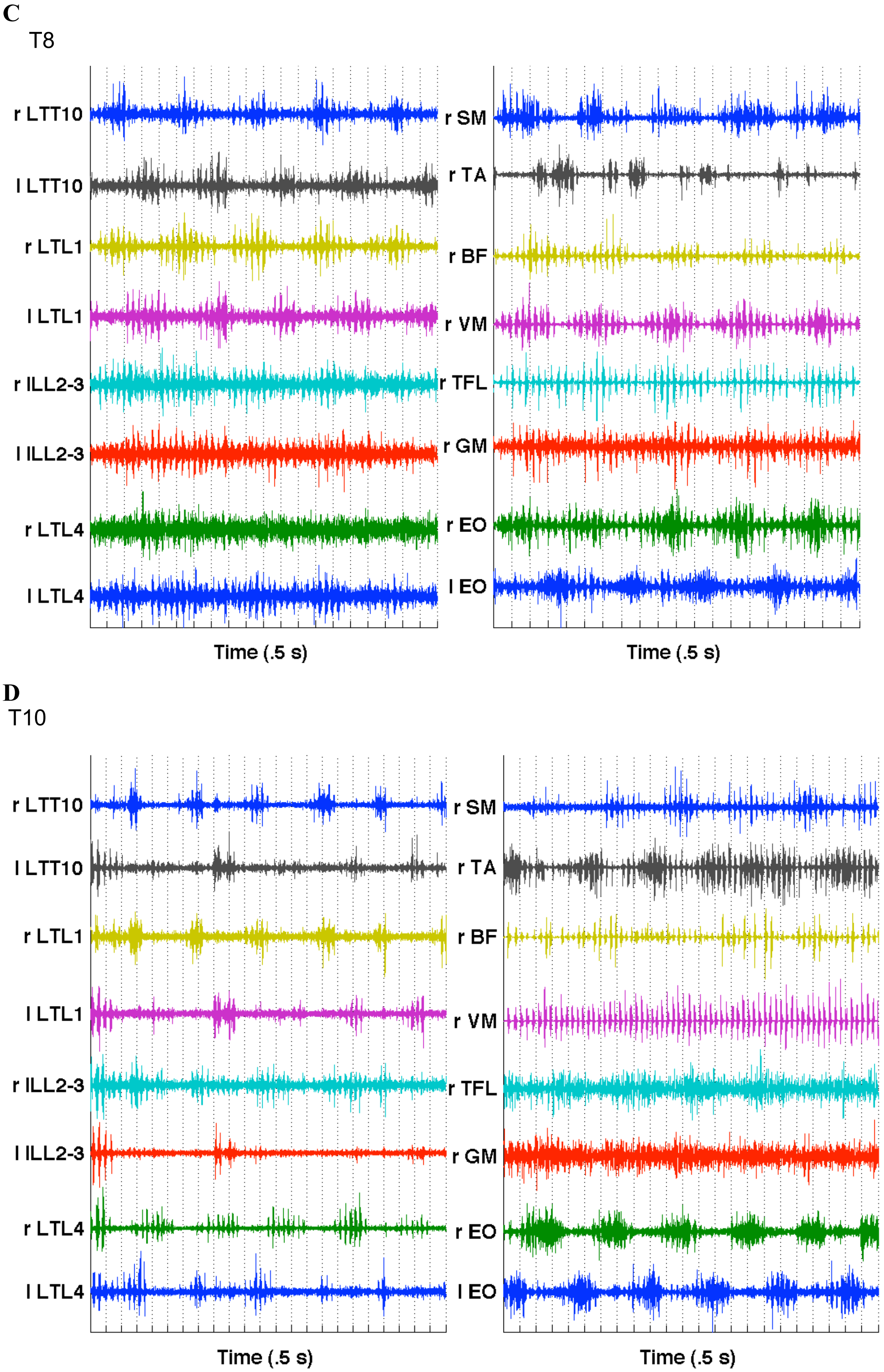

FIG. 5.4C, D Examples from single trials for TRD subjects. X-axes divisions are in 0.5 s intervals.

FIGURE 5.5 Raw EMG from 16 muscles during COMBO in NOV.

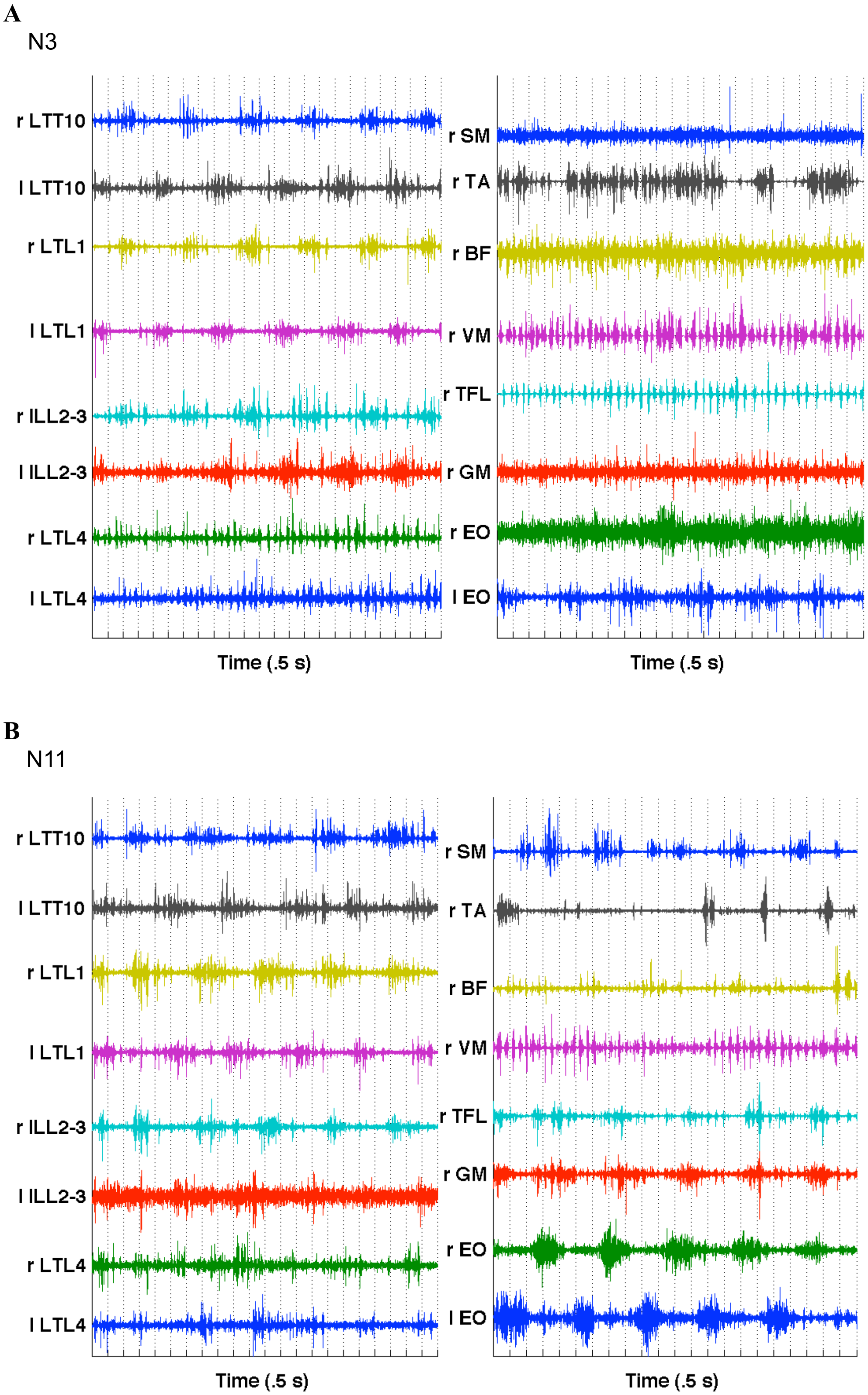

FIG. 5.5A, B Examples from single trials for NOV subjects. X-axes divisions are in 0.5 s intervals.

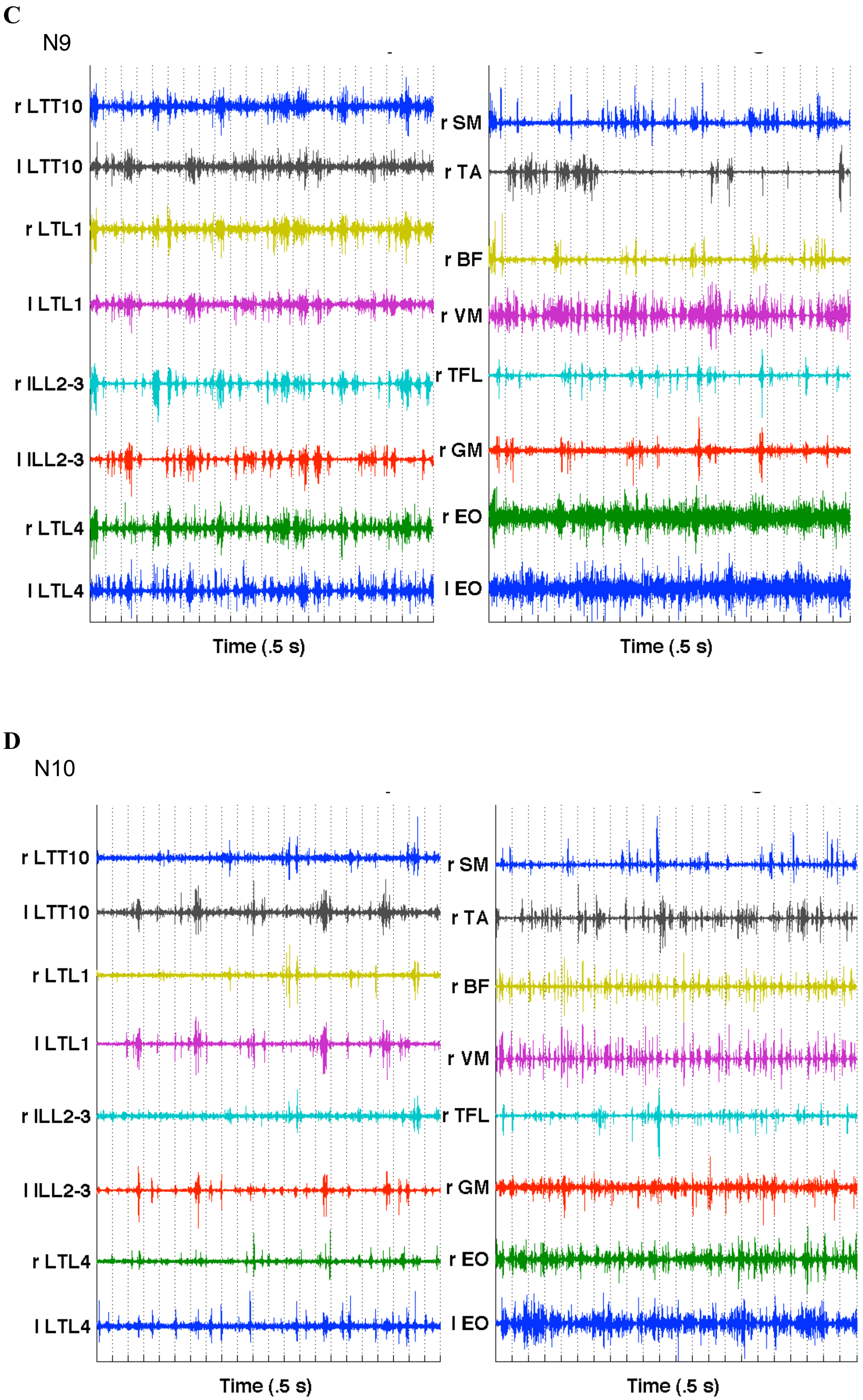

FIG. 5.5C, D Examples from single trials for NOV subjects. X-axes divisions are in 0.5 s intervals.

regular phasic low frequency muscle burst pattern in either left or right ES L4 during the COMBO, so the EMG pattern could not be classified. Consequently, neither N3 nor N11 were included in EMG pattern analyses of the low frequency component. A clear low frequency pattern was evident for subject N8 but the ES EMG was completely devoid of the high frequency pattern. Although there was evidence of both patterns in the EMG of subject N9 (Fig. 5.5C), there were not enough ES records with sufficiently distinct high frequency burst patterns to perform cross correlation. The EMG of subject N10 (Fig. 5.5D) illustrates very sporadic bursting, i.e. patterns of either frequency are sparsely represented. In summary, breakdown of the COMBO EMG patterns in the NOV group could represent failure in any one of the following forms: 1) one of the patterns was lost, 2) both patterns were evident, but one of the patterns dominated in some or all of the ES channels, 3) activation patterns were erratic and spikey, expression of one or both patterns was sporadic and indistinct.

5.3.3 Comparison of erector spinae timing patterns for SHIM, HIPSLD and COMBO

Figure 5.6 shows plots of ES Lag%T by pattern classification. One obvious difference between high and low frequency motions is that there appear to be fewer possible coordination patterns for producing the HIPSLD motion than for the SHIM, both in isolation and in the COMBO. For the HIPSLD, 9 of 11 NOV and 9 of 12 TRD subjects showed a diagonal pattern (D) of ES segmental muscle activation, defined as a timing difference between ipsilateral ES T10 and L4 of ~ 50% mean cycle duration. Thus, in this pattern, there is a diagonal synergy between the ES T10 and L4 on opposite sides of the spine. In our previous study we also found diagonal synergies in the SHIM across a range of frequencies (see Table 5.1). In that study we found two possible patterns of ipsilateral simultaneous versus antiphasic activation: T10 vs. L1-L2/3-L4

(L1 simultaneous with the more caudal levels), referred to as D-cau, and T10-L1 vs. L2/3-L4 (L1 simultaneous with the most rostral, T10), referred to as D-ros. However, in the present study, all low frequency instances of the D pattern involved a different timing segmentation with T10-L1-L2/3 grouped vs. L4. The remaining 2 NOV and 3 TRD subjects had simultaneous activation (~0% timing difference) of ipsilateral ES levels T10 to L4 (Fig. 5.6B).

FIGURE 5.6 Muscle activation patterns by timing pattern and frequency of movement

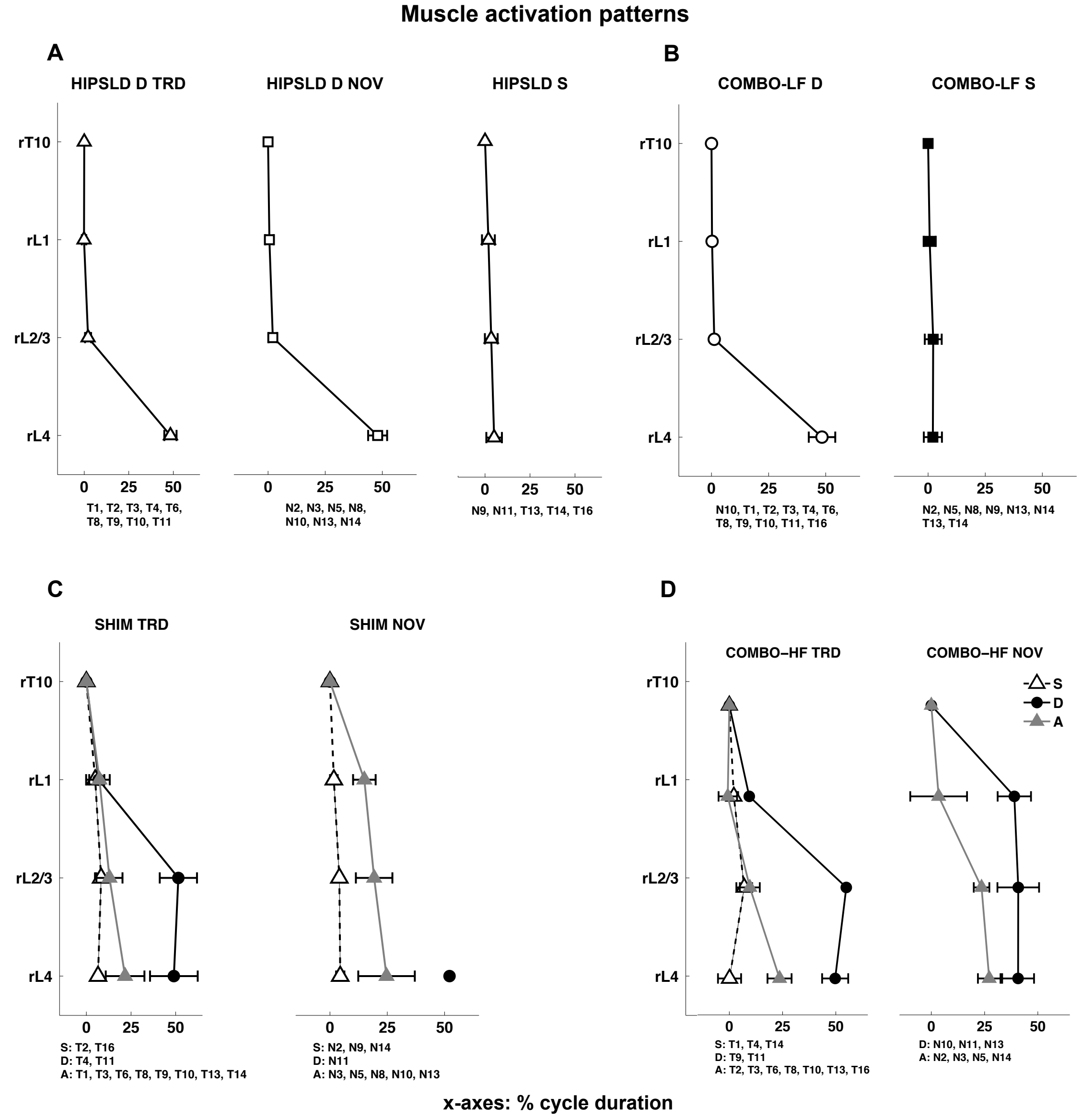

FIG. 5.6 (A) The two left panels include TRD and NOV subjects respectively, who showed the D pattern during the HIPSLD, while the third panel combines TRD and NOV subjects showing the S pattern. (B) NOV and TRD subjects are combined in the plots of the D and S patterns characterizing the low frequency motion of the COMBO. Timing patterns for the SHIM condition (C) and COMBO-HF (D) motion. Error bars represent 1 standard deviation (SD). Where none are visible, 1SD was less than the width of the data symbol.

Figure 5.7 shows the sets of lags for each MC and frequency component for each subject. This provides a picture of the distribution of specific patterns across subjects and movement conditions and indicates how the patterns changed when subjects attempted to superimpose movements of different frequencies. As mentioned previously, in the NOV group, 2 subjects lacked sufficient high frequency modulation in L4 ES and 2 lacked sufficient low frequency modulation for pattern determination. Table 5.2 shows the pattern classifications and pattern modifications for each subject by MC and frequency component. In superimposing the SHIM on the HIPSLD to create the COMBO, 11 TRD subjects retained the same low frequency pattern as in the HIPSLD (2 S, 9 D). One TRD subject switched from the S to the D pattern. Within the NOV group, 5 subjects adopted simpler timing, switching from the D pattern to the S pattern. Two retained the same pattern (1 S, 1 D). Two NOV subjects lost the low frequency pattern in the L4 ES muscles, so could not be classified for the COMBO-LF.

Superimposing the HIPSLD on the SHIM caused some subjects to increase ES segmental timing differences and some to decrease segmental timing differences for the high frequency component. Five TRD subjects maintained asynchrony across ES levels as in the isolated SHIM, as did two NOV subjects (N3, N5). One TRD subject (T11) produced the D pattern for all four movement patterns. Four TRD subjects reduced relative timing differences across ES levels resulting in a change in pattern (2 A to S, 1 D to S, 1 A to D) and 2 TRD subjects increased timing complexity (S to A). In the NOV group, 2 subjects lacked sufficient high frequency modulation in L4 ES for pattern determination. Two showed an increase in timing difference in the COMBO-HF compared to the SHIM (S to A) and 3 had no change in overall timing pattern between T10 and L4 (1 - D, 2 - A). According to our pattern classification criteria, 2 subjects (N10, N13) shifted timing pattern from A to D. However, from Figure 5.7B, it appears as though they retained the asynchronous pattern but the activity at the 3 lower ES sites was phase shifted to occur later in the movement cycle, rather than following a strict D pattern with some sites synchronous and others 50% out of phase.

TABLE 5.2 Pattern changes with movement condition

Subject ID	HIPSLD	COMBO *LF*
T13, T14 N9	S	S
T16 N2, N5, N8, N13, N14	D	S
T1, T2, T3, T4, T6, T8, T9, T10, T11 N10	D	D
N11	S	-
N3	D	-

Subject ID	SHIM	COMBO *HF*
T2, T16 N2, N14	S	A
T4	D	S
T11 N11	D	D
T3, T6, T8, T10, T13 N3, N5	A	A
T1, T14	A	S
T9 N10, N13	A	D
N8	A	-
N9	S	-

Table 5.2 T, trained, N, novice, ID, identification code, *LF*, low frequency, *HF*, high frequency. Patterns: S, simultaneous, D, diagonal, A, asynchronous.

FIGURE 5.7 ES timing patterns by subject and movement condition/frequency

A

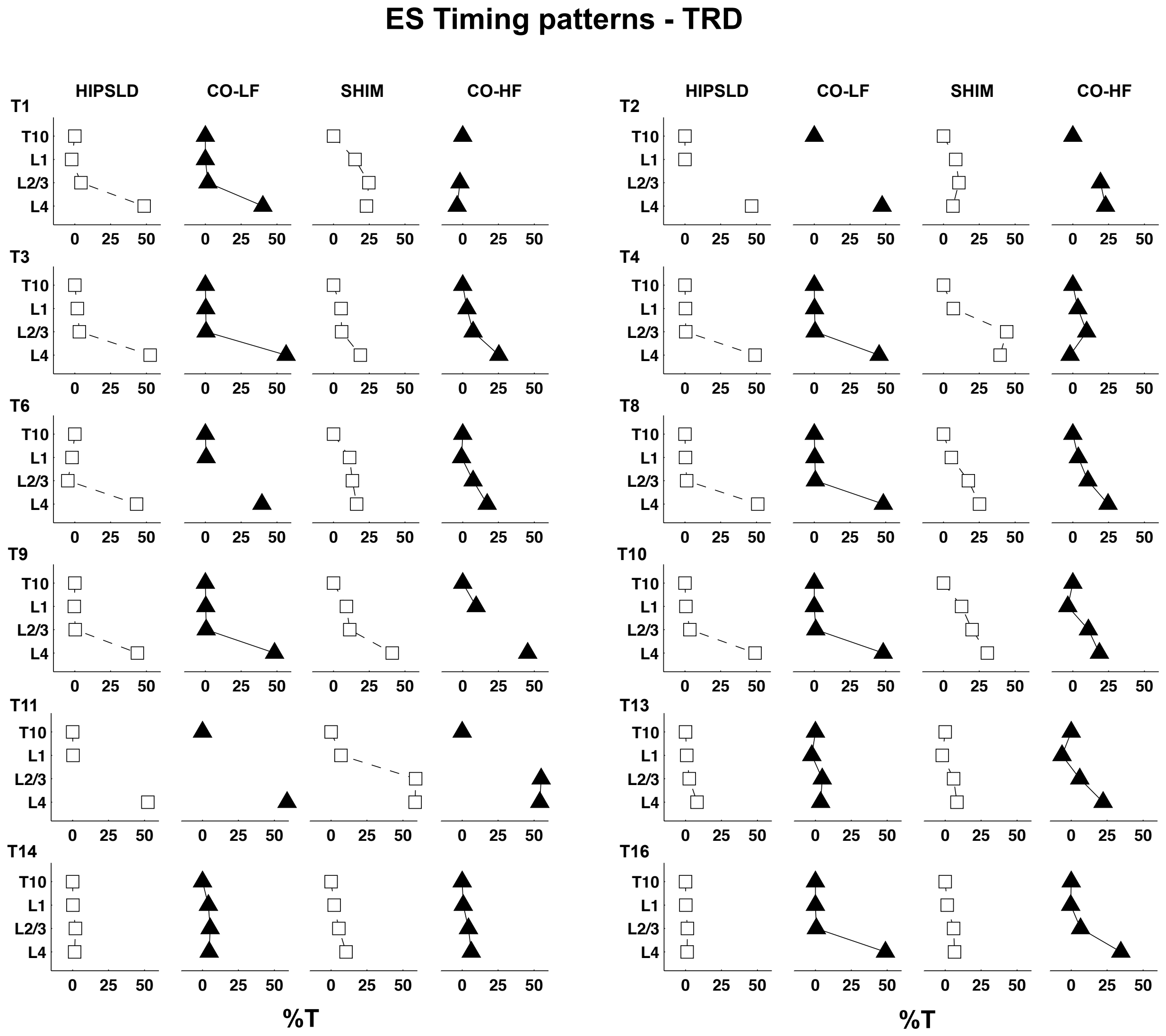

FIG. 5.7A Each group of 4 graphs represents mean lags for each TRD subject by movement condition and extracted motion frequencies. CO-LF = low frequency motion of the COMBO, CO-HF = high frequency motion of the COMBO. Vertical axes show the vertebral levels for right side ES electrode placements. Horizontal axes show relative timing as percentage of mean cycle duration.

FIGURE 5.7

B

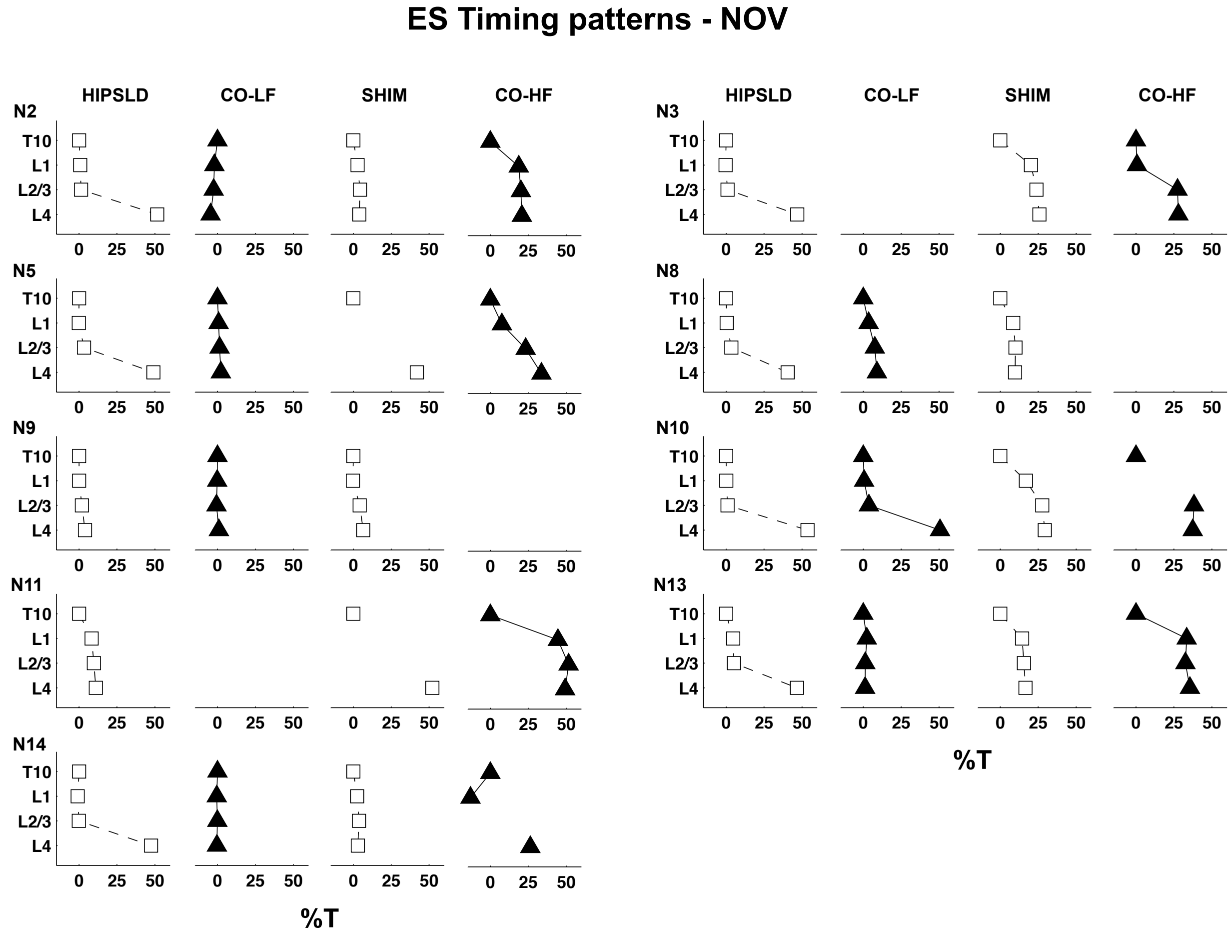

FIG. 5.7B Each group of 4 graphs represents mean lags for each NOV subject by movement condition and extracted motion frequencies. CO-LF = low frequency motion of the COMBO, CO-HF = high frequency motion of the COMBO. Vertical axes indicate the vertebral levels for right side ES electrode placements. Horizontal axes indicate relative timing as percentage of mean cycle duration. Empty axes indicate insufficient high frequency modulation in L4 ES for timing determination.

The last column of Table 5.1 summarizes whether pattern changes occurred in the low frequency component (LF), high frequency component (HF), both (B) or neither (N). A minus sign indicates that the component disappeared at ES L4 and in some cases at additional ES levels. Half of the TRD group showed no pattern change in either low or high frequency EMG timing patterns in the COMBO compared to HIPSLD and SHIM. The remaining 6 TRD subjects showed a change in pattern only for the COMBO-HF with the COMBO-LF remaining the same as in the HIPSLD. The picture was quite different for the NOV group in which 4 subjects changed their pattern for both components, 3 changed their pattern for one component and 4 lost one pattern or the other at ES L4 (or at all ES levels). For 5 NOV subjects the low frequency pattern changed and for 2 it was lost. For 6 NOV subjects the high frequency pattern changed and for 2 it was lost. These results confirm the prediction of our first hypothesis that (i) the SHIM and HIPSLD require different coordination patterns in the ES, and that (ii) superposition causes modifications in timing patterns, as well as our second hypothesis that the types of switching and pattern changes are affected by TRG.

5.3.4 Modulation of the low frequency component in the COMBO

The one-sample Wilcoxon signed rank test to evaluate Euclidean distance between NOV (n = 9) and TRD (n = 9) for HIPSLD-D pattern showed no difference due to TRG (N = 81, *Mdn* = 8.35) T = 205, z = -6.85, p = .100.For this test, 4% of Lag%T values for L1 and L2/3 were missing and replaced with the column means of the respective TRG groups. The one-sample Wilcoxon signed rank test of within-subject Euclidean distance between HIPSLD and COMBO-LF patterns showed that with superposition, the timing pattern of the low frequency component was significantly altered in the NOV group (N = 7, *Mdn* = 45.71, 4% missing L1 and L2/3 lags filled with column means) T = 25.0, z = 1.86, p = .032, but not in the TRD group (N = 12, *Mdn* = 4.84, 8% missing L1 and L2/3 lags filled with column means) which fell significantly below the median threshold of 13% for pattern change T = 12, z = -2.12, p = 0.017. These results reflect the pattern switch from D to S for the NOV group while the TRD maintained the D pattern in both conditions, confirming hypotheses 1 and 2: combining the movement patterns causes a change in the low frequency pattern of ES activation timing, but only in the NOV group. Figure

5.6 compares the ES muscle timing patterns between the isolated HIPSLD and the low frequency component of the COMBO. In the COMBO, 10 of 12 TRD subjects and only 1 NOV subject exhibited a low frequency component with the same relative timing pattern as the D pattern in the isolated HIPSLD (Fig. 5.6B, left panel). Six NOV and 2 TRD subjects displayed a low frequency coordination pattern in the ES that was simultaneous (S pattern - Fig. 5.6B, right panel). The remaining 2 NOV (N3, N11) did not show low frequency bursting in either right or left L4 ES (although the low frequency burst pattern was clear at other levels) and thus are not included in Fig. 5.6B.

5.3.5 Modulation of the high frequency component in the COMBO

The trend for the high frequency ES activation pattern was opposite to that found for the low frequency activation pattern (Fig. 5.6C, D). The one-sample Wilcoxon signed rank test to evaluate Euclidean distance between SHIM and COMBO-HF showed that for the TRD group there was a significant within-subject difference in high frequency timing patterns with superposition of the low frequency motion ($N = 12$, $Mdn = 21.40$, 8% filled missing L1 and L2/3 values) $T = 65.0$, $z = 2.04$, $p = .021$. The median Euclidean distance for the NOV group was similar to that for TRD, but was not significantly different from the threshold median of 13% ($N = 7$, $Mdn = 19.99$, 11% filled missing L1 and L2/3 values) $T = 23$, $z = 1.52$, $p = .100$.

Similar to what we found in the previous study for the SHIM at different tempos, subjects adopted simultaneous (S), diagonal (D) or asynchronous (A) patterns of rhythmic muscle activation along vertebral levels of the ES spanning T10 to L4. However, in comparing the COMBO-HF to the SHIM, there appears to be a tendency for the COMBO-HF to become a hybrid pattern intermediate between the S or A pattern and the D-cau or D-ros pattern of the shimmy. That is, at this frequency *we do not see the same timing separation at different vertebral levels* (T10-L1-L2/3 vs. L4) *as in the HIPSLD and COMBO-LF*. This finding provides additional confirmation that combining the movements alters the high frequency component.

As in our previous study, an effect of training was seen in the difference in maximum high frequency motion achieved in the two TRG groups. The median frequency of SHIM was 1.45 Hz higher for TRD ($N = 12$, $Mdn = 5.27$) compared to NOV ($N = 8$, $Mdn = 3.82$), $W_s = 47$, $z = -2.818$, $p = 0.005$ (two-tailed test). The median frequency of COMBO-HF was 1.58 Hz higher for TRD ($Mdn = 5.57$ Hz) compared to NOV ($Mdn = 3.99$ Hz), $W_s = 41$, $z = -3.279$, $p = .001$. (Subject N8 was not included in the tests).

Neither group showed a difference in mean movement frequency for COMBO-LF compared to HIPSLD: TRD ($N = 12$, Mdn difference = 0) $W_s = 133.5$, $z = -1.1582$, $p = 0.2468$ (two-tailed test); NOV ($N = 9$, Mdn difference = 0) $W_s = 87.5$, $p = 0.9186$ (two-tailed test). In each TRG group, some subjects showed an increase in movement frequency of the shimmy component with superposition, while others showed a decrease. Nevertheless, neither group showed a significant change in mean movement frequency for COMBO-HF compared to SHIM TRD ($N = 12$, Mdn difference = 4.77 Hz), $W_s = 118$, $z = -1.8194$, $p = 0.069$ (two-tailed test). NOV ($N = 8$, Mdn difference = -0.175) $W_s = 55$, $p = 0.185$ (two-tailed test). These findings indicate that while the frequency of the shimmy increases with training, this factor is not modulated by combination with the low frequency motion.

5.3.6 Variance and smoothness/jerk in pelvic kinematics

Wilcoxon rank-sum tests were performed using the mean variance and normalized RMS jerk of pelvis (RASIS) movement in the *x*-direction for each subject. Comparison of movement variance in HIPSLD and COMBO with TRG pooled confirmed that the medio-lateral trajectory of the pelvis is more variable during the COMBO than in the HIPSLD ($N = 21$) $p = 0.025$. In the COMBO, variance in the NOV group ($n = 9$, $Mdn = 0.66$) was more than twice that of the TRD group ($n = 12$, $Mdn = 0.31$) ($N = 21$) $W_s = 2.74$, $p = 0.003$.These results confirm the prediction that the high frequency movement pattern would interfere with the low frequency pattern since the low frequency movement became more irregular, and that TRD performers would be better able to maintain the HIPSLD trajectory when combined with the SHIM, compared to NOV performers. The differences in movement variability between TRG groups can be seen in plots of the RASIS velocity in the medio-lateral (x) direction. Figure 5.8 shows the unfiltered pelvic x-velocity as well as the extracted high and low frequency components for 2 TRD and 2 NOV subjects.

Our analysis of the effect of superposition on smoothness of pelvic x-translation in HIPSLD and COMBO showed that overall the smoothness of the HIPSLD trajectory decreased in the COMBO compared to the isolated HIPSLD ($N = 21$, Mdn difference = 7.51) $W_s = 249$, $z = -5.08$, $p = .000$. For both groups the normalized RMS jerk for the COMBO-LF was higher than for the HIPSLD NOV ($N = 9$, Mdn difference = -24.91) $W_s = 45$, $p = .000$; TRD ($N = 12$, Mdn difference = -3.58) $W_s = 87$, $z = -3.61$ $p = .000$. There was no difference between NOV ($n = 9$, $Mdn = 12.53$) and TRD ($n = 12$, $Mdn = 12.48$) in the smoothness of the HIPSLD $W_s = 108$, $z = 0.60$, $p =.273$. However, the normalized RMS jerk for the low frequency motion of the COMBO-LF was more than twice as high for NOV ($n = 9$, $Mdn = 37.44$) as for TRD ($n = 12$, $Mdn = 16.05$) $W_s = 147$, $z = 3.38$, $p = .000$. These results provide evidence that the trained group superimposes two independent control signals which are each regular and smooth, whereas the novices use a single control signal that is irregular.

FIGURE 5.8 Velocity of pelvic motion in x-direction

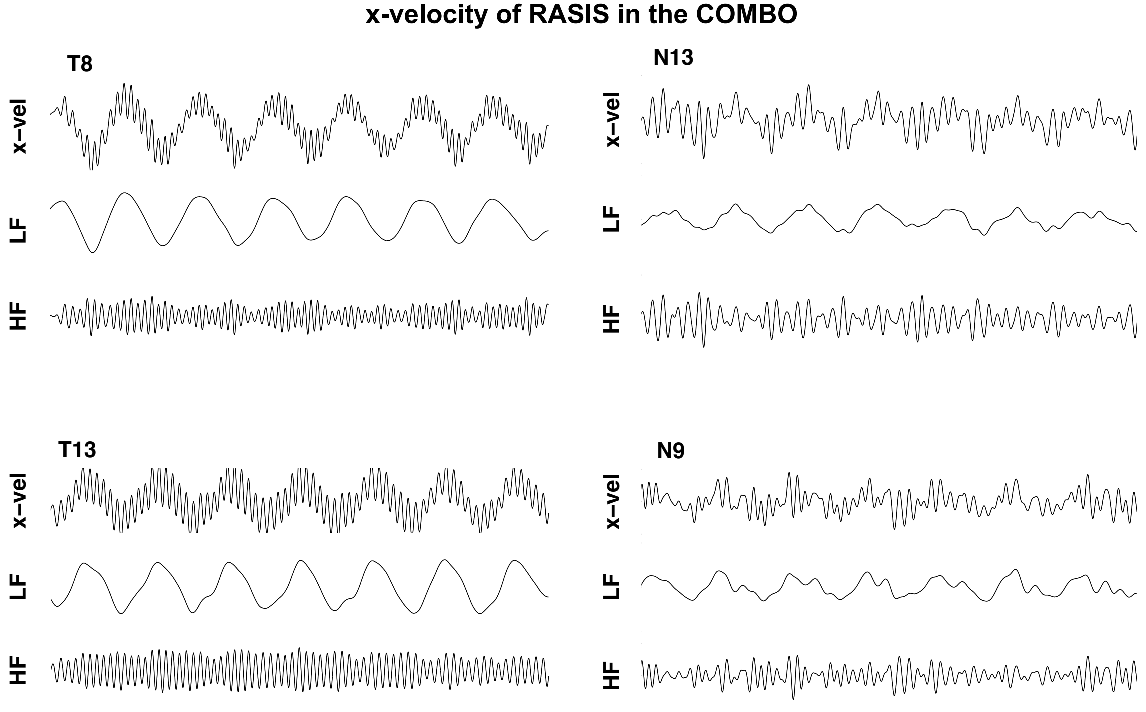

FIG. 5.8 Velocity of pelvic motion in the x-direction during the COMBO. Examples from one trial for two TRD (T8, T13) and two NOV (N13, N9). Kinematics are taken from the RASIS marker. X-vel = unfiltered velocity, HF = high frequency motion component, LF = low frequency motion component.

5.4. DISCUSSION

5.4.1 Timing patterns/signal independence

We confirmed our first hypothesis that superposition of two different frequencies of trunk oscillation to create a combination movement results from the merging of two independent control signals. Predictions (i)-(iii) were verified. Different patterns characterized high and low frequency movements (i). Comparisons between isolated movements and extracted COMBO components demonstrated that the two movement patterns interacted when combined (ii). Interaction between patterns was also clearly evident in the kinematics (iii). We also showed that the ability to perform the combination movement depended on training, confirming the second hypothesis.

5.4.2 Muscle activation timing patterns

Using a scheme developed in our earlier study (Nugent and Milner, in press) we classified muscle activation patterns as simultaneous (S), diagonal (D) or asynchronous (A). The patterns associated with low frequency motion in the current study were either D or S. The S pattern was exhibited by members of both TRG groups in HIPSLD and COMBO-LF. However, the dominant pattern for the TRD group for these movements was a new D pattern in which the 3 rostral levels of the ES were activated antiphasically to L4. The COMBO-HF displayed a greater variety of timing patterns. The S, D and A patterns previously observed at different SHIM frequencies (Nugent and Milner in press) were identified in the COMBO-HF for the TRD group. In the NOV group, the high frequency muscle timing patterns tended toward a hybrid version of the A and two D patterns characteristic of SHIM. Superposition also resulted in phase shifting of these patterns such that caudal Lag%T values tended to be intermediate between the classification cutoffs for the A pattern (31%) and D (50%) patterns.

5.4.3 Pattern interaction and mutual modulation

Superimposing the high frequency movement on the low frequency movement forced NOV subjects to switch to a simplified timing pattern (D to S). Whereas the majority of NOV showed a D pattern in the HIPSLD, only 1 of 9 was able to maintain this segmental specificity when the SHIM was superimposed. This pattern switch was seen only in NOV. In contrast, all 9 of the TRD subjects who employed the D pattern in the HIPSLD preserved the D pattern in the COMBO-LF, while one of 3 employing the S pattern in the HIPSLD switched to D in the COMBO-LF. Thus we conclude that this pattern switch is not an alteration demanded by the task, but a simplified version of the task. For the NOV group, the switch to the S pattern in the COMBO-LF was accompanied by an almost complete loss of HIPSLD lateral movement amplitude. For TRD subjects, the SHIM high frequency pattern was more susceptible to modification than the HIPSLD pattern when superimposed in the COMBO.

Half of the TRD subjects did not switch patterns at either frequency, underscoring their superior ability to maintain pattern stability in the composite movement. The remaining 6 only modified their patterns in the high frequency component, indicating greater overall stability of the low frequency component and/or a constraint on viable activation patterns for producing the movement. This suggests that in the isolated low frequency movement a muscle synergy is activated, that cannot be maintained when the high frequency component is superimposed without considerable skill. It may be that the low frequency pattern can only be maintained if the dancer is sufficiently adept that the SHIM can be controlled by low level automatic mechanisms. Although both groups showed a difference in pattern between SHIM and COMBO-HF, the lack of significance for NOV is probably due to the great variety of pattern changes in this group (inter-subject variability). In addition to loss of pattern, the NOV performances of the COMBO were characterized by higher movement variability. The relative smoothness of the low frequency component of the COMBO for TRD compared to NOV illustrates the degree to which the patterns interfere with each other and the role of training for instilling the capacity to separately specify and maintain the two motions when superimposed.

Sternad et al. (2000), investigating the superposition of discrete reach and rhythmic elbow movements, found that the oscillation frequency modified the duration of the discrete movement, whereas the discrete movement reset the phase of the rhythmic movement. In our study, superposition had no effect on the mean frequency of either high or low frequency components. It did, however, alter the relative timing of activation of the muscle compartments at different vertebral levels. Adamovich et al. (1994) combined fast discrete elbow flexion with rhythmic oscillations (4-6 Hz). The discrete movement was not affected by the ongoing rhythmical movement. However, frequency, phase and amplitude of the rhythmic movements was modified when the discrete movement was added. They concluded that the two movements were controlled sequentially because of conflicting stability requirements and that interaction between rhythmic and discrete movements could occur at both central and peripheral levels. In contrast, we have evidence from the TRD group that simultaneous control of superimposed movements at different frequencies is possible, although only with sufficient training.

Carter and Smith (1986a,b) investigated the interaction of paw shake and locomotor patterns in normal cats. This study is perhaps the closest analog to our paradigm for investigating two rhythmic patterns merged in the same effector. Clear superposition of high and low movement frequencies were apparent in kinematics and EMG, and these patterns were mutually modulating. The high frequency paw shake caused prolongation of the swing phase in the ipsilateral leg and homolateral forelimb, while prolonging stance duration of the opposite legs. The biomechanical demands for weight support and limb progression during locomotion imposed constraints on the phase relation between the two rhythms. Superposition of the paw shake caused a phase shift in ankle and knee muscle activation compared to the normal swing pattern. In contrast, SHIM muscle activity (right-left alternating extension) is congruent with weight-bearing. There are limited or no biomechanical constraints on the superposition of the two rhythms. The shift in activation timing seen in the NOV group could, therefore, not be explained by biomechanical constraints imposed by the task.

It seems likely that for the NOV group, interference between high and low frequency patterns occurs at a central level of control, during pattern selection. The evidence suggests that when novices attempt the COMBO, the CNS simplifies the control problem by harmonizing the HF and LF movements – combining elements of both movements centrally as a merged control signal. This could represent a failure in task conceptualization, due to the lack of a model for superimposing movements. In contrast, for the TRD group the two patterns appear to be defined separately at the central level involving different control centers, which limits interference between the two control signals before they reach the effectors. The slight reduction of the low frequency movement amplitude in the TRD group is likely necessary to permit the high frequency oscillation, which would otherwise stop if the hip joint neared the extremes of its range of motion.

We speculate that TRD subjects are capable of creating two separate signals that sum to produce the observed muscle and kinematic patterns, whereas NOV subjects try to generate both movements with a single controller. We propose that the low frequency motion is under descending, cortical control, while the high frequency oscillation could be generated at the spinal level by a central pattern generating network. The HIPSLD shows little variation and is slow enough to be under voluntary feedback control. The SHIM oscillates too quickly for voluntary cycle-to-cycle control, making it more likely to be under the control of an autonomous pattern generator. Extensive practice is required to achieve high SHIM frequencies. We interpret this as evidence that successful integration of the two rhythmic movements is not the superposition of one voluntary movement on another, but likely involves learning to gate a specific neural pathway that is innately oscillatory.

Trained belly dancers are able to specify complex biomechanical aesthetic movement goals through the central generation of two independent control signals in the superposition of two movement rhythms by the same effectors. The mitigating effects of skill on limiting the type and degree of interaction between patterns represents an important difference between our findings and those from experiments investigating hierarchical control of inter-limb and intra-limb dual task coordination. Mechanisms for control of the multi-segmental, polyrhythmic skill likely involve cortical descending control of the low frequency movement, activation of a central pattern generator for the high frequency movement, integration of the two signals at the spinal level, and modulation by sensory feedback according to biomechanical requirements. Prior to successful combination of the two movements, extensive practice is required to automate the high frequency shimmy. Integration of these two types of movements with practice likely involves learned modulation and gating of spinal neural oscillators, as well as learned refinement of the patterns through long-term use of sensory feedback to update an internal model, possibly at the cerebellar level.

Chapter 6

General Discussion

General Discussion

This research began with the establishment of compartmental specificity in lumbar spine extensor muscles, related to the biomechanical differences in the functional capabilities of muscle regions above and below L3. We were able to reveal this specificity due to the unique segmental characteristics of belly dance trunk isolation movements. This neuromechanical specificity of belly dance repertoire then provided the basis and rationale for investigating the neural coordination of rhythmic trunk motion: from the patterns of relative timing in the spine extensors we were able to infer recruitment of voluntary versus automatic control mechanisms depending on task (amplitude and plane(s) of motion), tempo and training. Comparisons of these activation patterns to locomotor patterns in animal models provided evidence for similarities in the spinal circuitry of humans. Mechanisms behind segmental control of complex trunk movements was further elaborated using the simultaneous performance of low frequency (voluntary) and high frequency (automatic) trunk oscillations. By comparing these two tasks performed in isolation versus superimposed, we were able to elucidate the capacity of the nervous system to specify two separate control signals generated centrally, with combination likely occurring at the level of the motoneuron, and preservation of both movement frequencies as expressed in the muscle activation patterns within a single effector. The interaction between task complexity and movement experience provides new insights into the capacity and degree to which the output from inherited genetic neural networks may be modified through training. Overall, the findings presented herein provide evidence of innate circuits in humans phylogenetically conserved, and further our understanding of the mechanisms underlying the control of complex human movement, including the interactions among different hierarchical levels. Finally, this thesis provides a testimonial to the usefulness and validity of belly dance as an experimental paradigm.

Belly dance appears to make use of root joint movements or motor primitives that can be flexible combined and performed in various ways. For example, segmental lateral motions include side-to-side lateral horizontal displacements of the head, ribcage or pelvis. Lateral head slides can be alternated with forward-backward horizontal movements to create horizontal head circles. Pelvic twists (rotation around the longitudinal axis) blended with horizontal hip displacements create horizontal pelvic figure 8s. The basic hip shimmy motion - alternating rotation/oscillation of the pelvis in the frontal plane - can be performed at different speeds and with different combinations of stepping patterns and rhythms.

Different dance forms have different specific control requirements. The complex stepping patterns and choreographic elements that represent more contemporary innovations in the dance are not dissimilar to these elements in ballet, ballroom or other contemporary Western dance forms. The specification of trunk segmental movements of the body core require similar control to isolations seen in many forms of latin, Polynesian, African and Indian dance styles. Motor control in ballet differs in the emphasis on postural stability and precision of limb shapes and reach directions, strength and power required for jumping, and very precise control of balance and equilibrium (as in turning and balancing on pointe). In belly dance, the cyclic segmental motion and rhythm and polyrhythmic entrainment require precise timing control in conjunction with fractionalization of global body movements - holding certain body segments or trunk regions relatively still while others are oscillated. This requires the neuromuscular capacity to decouple global spine motions to select which segments move versus which remain stable; to create fast, alternating patterns of antagonistic muscle activation; and to enhance instability (specify relative stiffness or compliance) of target joints such that oscillations are most easily maintained. Partner dancing, as in tango or ballet, requires high spatiotemporal precision and in order to match movements in time and space. In tango, there is a strong emphasis on movements of the lower limb - very fast footwork, both stepping (weight transfer) and open-chain (describing trajectories in space). By contrast, traditional belly dance movements (as opposed to traveling choreography) emphasizes trajectories of the proximal joints and pelvis, while the feet are usually more anchored to the ground.

6.1 SUMMARY OF CONCLUSIONS AND KNOWLEDGE GAINED

- Our research provides an example of the possibility of using complex, full body motor skills as study objects for rigorous experimentation in motor control. Despite the obvious issue of individual differences, possible error in electrode placements, and technical constraints and limitations in EMG, results were remarkably robust and consistent.
- Belly dance provides a viable study object for 1) evaluating task dependence of muscle roles in complex trunk motion and for 2) exploring the organization and mechanisms of control of complex trunk movements.
- Differential activation above and below L3 likely represents the different activity, due to different biomechanical functions (recall the opposing fiber directions and locations of insertions) of the lumbar vs. thoracic portions of the lumbar ES. This finding confirms predictions made by (Macintosh and Bogduk 1987) in their anatomical study, and may be an

important consideration for diagnosis and rehabilitation, as well as in biomechanical models of spine and back muscle function.

- This capacity for segmental control in the lumbar spine extensors is innate, using genetically determined neural circuits. With extensive practice, humans can learn to modify their output, resulting in increases in movement frequency and simultaneous rhythmic task performance.
- Fast and slow trunk movements are not the same, but are generated by different mechanisms, located in different levels of the nervous system. Additional evidence has been provided confirming a change in the control source with learning, depending on the type of task.
- Rhythmic lateral undulations in trunk curvature are a common aspect of trunk locomotory motion, across environments (aquatic and terrestrial) and limb arrangements (swimming, tetrapod stepping, mammalian quadrupedal and bipedal locomotion) and orientation with respect to gravity (horizontal or vertically oriented body axis).
- It is highly likely that primal neural circuits are phylogenetically preserved in humans, and that the patterns of activity originally developed for aquatic propulsion are flexibly recruited in bipedal stance to produce novel and learned behaviors.
- The neural circuits underlying rhythmic lateral undulations of the spine appear to be conserved across species - lamprey, salamander, rat, human. The fundamental functional arrangement of these networks - intrinsic segmental capacity for bilateral and intersegmental phase lag, longitudinal coupling and cross-cord connections - produce intersegmental phase lag and bilateral antiphase alternation patterns which underlie the control of the movements observed in these studies.

- The conclusion that at the central level, two movement patterns are conflated by novices and treated as one voluntary signal, but specified independently by experts as two separate voluntary (supraspinal) and automatic (spinal) signals, suggests that the freezing vs. freeing degrees of freedom often used to describe differences with learning, can occur even at an abstract (cognitive) level.

6.2 LIMITATIONS

Limitations of the study include typical factors in EMG and kinematic data collection that can contribute to error. As mentioned in Chapter 2 General Methodology, placement of electrodes to record selectively from different parts of the lumbar spine extensor muscles involves a certain amount of imprecision. Accurate placement is dependent on being able to see and/or feel the individual spinous processes to identify the vertebral levels. Because skin moves over muscle, a difference in posture between that adopted during electrode application and posture for the experimental trial conditions could mean the intended muscle is not being recorded. For example, I learned that, although having the subject curve their back made it easier to distinguish the spinous processes, a placement mark made on the skin in this position could be observed to shift by one-half a vertebral length when the subject straightened. I took great care to be as accurate as possible and practiced on a number of different subjects during pilot testing. I instrumented all the subjects in the study with electrodes and reflective markers, (except for when I was the subject) and I believe that error in longitudinal placement could not be more than one-half of a vertebral level. Individual differences in subject anthropometry also represents a source of error for electrode placement and signal differences. Accuracy of placement was sometimes constrained by the subject's stature: with those of shorter height, there was less space longitudinally and medio-laterally for placing the electrodes and Th12 marker frame. Sometimes optimal placement had to be shifted slightly to avoid sensors bumping together during trials and creating motion artifacts.

Adequate signal-to-noise ratio is always a concern when collecting EMG data. For this reason some of the subjects recorded were excluded from the study because the data were too poor to render reliable results. This occurred in those with a somewhat higher BMI (thicker skin folds at recording sites), and in one case when one subject sweated excessively. In the majority of cases most of the data were useable, but where I have sited missing data it was because there was not a clear enough pattern of phasic bursting, of sufficiently high amplitude to produce consistent inter-trial results in the cross-correlation analyses. Possible reasons for this were that either thick skinfold layers reduced the signal strength, the electrode was not placed over a motor innervation point, or a given subject was simply not recruiting those muscle regions phasically. Electrical noise was minimized by using two ground electrodes on subjects and placing a rubber mat on the support surface to insulate against noise coming from the force plates.

The implications for missing data or error in electrode placement for the study are possible ambiguities in the identification ES activation patterns, which could affect the distribution of a given pattern across subjects/conditions. Nevertheless, I believe that given all the potential sources of error, the results are remarkably consistent and robust.

With regard to kinematics, joint movements in the trunk and hips are not actually constrained to movement in one plane, and so analysis of only frontal plane, lateral flexion elements of spine motion represents a simplification. Although there was an element of transverse rotation in many of the movements, this motion has not been addressed in this research. The assumption is that deeper muscles of the spine are responsible for rotation, which was also likely generated to large degree by the actions of the knees moving forward and backwards in the sagittal plane, and that effort to constrain actions to the frontal plane ensured that the dominant activity was related to lateral flexion - while some of the activity recorded in the lumbar spine extensors may have been involved in transverse rotation of the trunk, their prime roles are extension and lateral flexion, due to the larger moment arms in these planes. With regard to kinematics, segmental motion data were represented in the lab reference frame rather than an anatomical reference frame. Since relative motion was of main concern and subject position was standardized between subjects and within movement conditions, this was not deemed deleterious to analysis or interpretation. Actual and virtual (reflective marker issues) movement artifact are sources of noise in kinematic data. Trajectories were all filtered to extract only task relevant motion frequencies. Custom script was used to accurately calculate the relative motion between segments from the marker frames. The task-dependent distinctiveness in x-, y-, and z-trajectories of the RASIS marker justify its use to assess pelvic motion.

Another limitation involves the method of analysis for determining relative activation timing based on cross-correlations between EMG signals. The filtered EMG signal does not produce a nice smooth sinusoid and the shape of the EMG profile can vary between movements and between muscles. These inconsistencies limit the reliability of the lag values. This has been mitigated by computing the cross-correlation over many cycles and averaging across a number of trials. The within-subject standard deviation of lags for ES electrode sites across trials ranged from 0 to 10% mean cycle duration, with the majority lying between 0-5%. Since the threshold for significance in differences in timing between electrode recording sites and for differences in activation timing patterns was greater than 5% this limitation does not affect the validity of the results. The method used for classifying activation timing patterns also has some limitations since some subjects' patterns fell on the borderline between pattern classifications, or differed noticeably from the majority.

6.3 FURTHER INVESTIGATIONS USING EXISTING DATA SET

I believe my current data set has the potential to yield many additional interesting findings. I have yet to conduct an analysis of the coordination and integration between leg and trunk patterns. I have not yet analyzed the 0.5 Hz and 1 Hz sagittal plane undulation trials that were recorded during the same session. It would be interesting to compare patterns of bilateral ES activation in these movements with the right-left antiphasic patterns of the movements addressed in this thesis. The goal would be to create a more complete picture of how the coordination multi-segmental trunk muscle activity is altered to produce movements in different planes of motion. In addition, I would like to investigate the integration of posture/stability and segmental trunk motions in more depth. Since I have recorded EMG from ankle knee and hip muscles of the right leg, in addition to the ES sites, it would be possible to make comparisons between the patterns involved in hip slide and undulations with results from previous studies on synergy differences between voluntary and reflex postural changes (Nashner and Cordo, 1981; Oddsson and Thorstensson, 1987).

The role of coordination between trunk and leg movements in belly dance is still an open question. In the shimmy, hip slide and serpentine, direction of activation sequencing in the spine extensor muscles in the A pattern is rostral-caudal. The direction is reversed in the maya, similar to the reversal in pattern seen in vertebrates for backward swimming. Observations of leg EMG in the shimmy show that the order of activation is distal-proximal, with VM activity occurring usually just prior to ipsilateral ES activity. In the D pattern, the synergy appears to be VM-ES L4 and contralateral ES T10, which suggests coordinated signals from axial and leg CPGs. It is unclear whether the legs drive at all frequencies of the shimmy or if their role diminishes in favour of axial dominance at the higher frequencies. A biomechanical analysis of muscle onsets and durations in relation to the phases of the movement cycle may reveal aspects not derived through the cross-correlation analysis used in these studies for determining relative activation timing.

Synergy and principal component analyses have been performed to investigate synergy combination in gaits in humans (Ivanenko et al. 2004) frogs (d'Avella and Bizzi, 2005; d'Avella et al., 2003), cats (Drew et al., 2008; Krouchev et al., 2006). A muscle synergy analysis of the data set collected for this thesis could provide a useful contribution for characterizing coordination patterns of trunk movements in different planes and degrees of segmental specification, as well as in coordination between trunk and leg function.

6.4 NEW STUDIES

A logical next step in the investigation of voluntary versus automatic control of these movements would be to use TMS stimulation to disrupt the cortical drive and see what effect it has on the hip slide, shimmy and combo. If stimulating in different brain structures has different disruptive effects, this could provide more information on hierarchical control in the functional integration of trunk and leg motion and coordination of complex trunk movements. TMS can be applied immediately prior to each activity trial, to avoid targeting inaccuracies that would occur during these movement oscillations. Another method for disrupting cortical drive would be to introduce cognitive interference tasks. These interventions could provide additional verification of the degree of voluntary versus automatic control involved in the different tasks and with different levels of training.

My current research project at the University of Florence is aimed at characterizing motorcycle rider motor behavior. The unique dynamics of motorcycles demand a more active form of control by the rider, compared to car driving - the mutual influence between the motions of vehicle and rider represent both the fun and the danger of this mode of transport. There is debate amongst engineers and riders as to the degree to which rider spine movement and position of center of mass are used to control direction of travel. A complicating theoretical factor is the lack of understanding amongst vehicle engineers with limited background in human research, of the role of automatic processes in the integration of spine and limb control. A common error in information gathering is to ask riders what they are aware of consciously doing by way of control actions. Because of the coupling between arms and handlebars, and between trunk and seat (frame) it may be that riders make use of innate circuits based on quadrupedal trunk-forelimb and inter-limb coordination. How riders control vehicle motion - the motion patterns recruited and distinctions between the roles of voluntary versus automatic mechanisms - are important questions to answer because they will inform design of motorcycle simulators (for rider training and experimentation), rider-bike control interfaces and new automatic safety systems for reducing incidence of crashes. I am very curious to compare my current findings with observations of spine control in balancing and steering a motorcycle. While it is unlikely that motorcycle race pilots will turn to belly dance as a cross-training complement, one never knows where the science will lead!

6.5 CLINICAL APPLICATIONS

As this study represents basic research, the findings leave open the question of whether these kinds of segmentally specific trunk movements could be used for rehabilitation in back and spinal cord injury. While being able to produce a D rather than an S pattern of back extensor activation during the hip shimmy may not seem an important functional goal, practicing different types and degrees of trunk segmental motion could possibly aid in rehabilitation or be used to diagnose type and source of dysfunction. A number of studies (Giszter et al., 2008; Song et al., 2009; Song and Giszter 2011; Oza and Giszter, 2015) have explored neural regeneration and the interaction (functional coupling) between trunk and leg controllers using spinally transected neonatal rats with robot assistance and partial weight support. Improvements in weight bearing were correlated with new cortical representations of the trunk, associated with extensive new synergy patterns. Thus they concluded that therapeutic interventions should focus on interactions between the trunk, pelvis and legs. The apparent role of cortical skill development for trunk function is interesting in light of our findings on the effects of practice on the ability to coordinate separate cortical and spinal control signals, integrated at the spinal level. Future studies could involve investigating whether performance of belly dance-like segmental movements, possibly with partial weight support and robot assistance, can stimulate elaboration of new cortical trunk representations any reorganization of spinal circuits post-SCI. These movements may have particular value as rehab interventions because subsets of motor patterns associated with locomotion and postural adjustment could be performed separately and specifically, following a progression of easier to more difficult, with and without assistance and partial weight support. Leg flexion-extension patterns and other rhythmic movements to activate CPGs can be performed while weight bearing in double stance - without the perturbing effects of stepping (the shimmy). Different forms of coupling between trunk and legs can be performed (e.g. hip slide, pelvic tilts), including postures that challenge and stimulate balance centers. I believe these exercises would operate on multiple levels of the nervous system: improving cortical representation and model of trunk, stimulation of rhythmic pattern generators underlying locomotor patterns, and production of different types of afferent inflow about weight-bearing, rhythmic entrainment, position of center of mass, to aid balance recovery to shape output.

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