# LEARNING TO BALANCE AN INVERTED PENDULUM AT THE FINGERTIP

A WINDOW INTO THE TASK AND CONTEXT-DEPENDENT CONTROL OF UNSTABLE DYNAMICAL OBJECTS

### LEARNING TO BALANCE AN INVERTED PENDULUM AT THE FINGERTIP: A WINDOW INTO THE TASK AND CONTEXT-DEPENDENT CONTROL OF UNSTABLE DYNAMICAL OBJECTS

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TITLE: Learning to Balance an Inverted Pendulum at the Fingertip: A Window into the Task and Context-Dependent Control of Unstable Dynamical Objects

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## Abstract

Our ability to control unstable objects highlights the sophistication of voluntary motor behaviour. In this thesis, we used an inverted pendulum (i.e., stick) balancing paradigm to investigate the task, learning and context-dependent attributes of unstable object control. We hypothesized that learning would mediate the functional integration of posture and upper limb dynamics and expected changes in the task demand and context to be reflected in the control of posture and the upper limb. We found that training increased the average length of balancing trials and applied this result to further investigate the circumstantial properties of unstable object control.

We investigated the temporal structure of posture and upper limb dynamics using statistical and nonlinear time series analysis. We demonstrated that subjects used an intermittent strategy to control the inverted pendulum (Chapters 3 and 5) and found that motor learning modulated the statistical and spatiotemporal attributes of posture (Chapter 5) and upper limb displacements (Chapters 2, 3 and 5). We confirmed the balance control strategy was intermittent by showing that posture and upper limb time series are composed of two independent timescale components: a fast component linked to small stochastic displacements and a slow component related to feedback control (Chapters 3, 4 and 5). The interplay between timescale components was affected by the balancing context (Chapter 3) and task demand (Chapter 4).

Chapter 5 investigated the acquisition of individual and coupled posture-upper limb control mechanisms. We found that motor learning involved two independent adaptation processes. The first process modified the timescale composition of posture and upper limb displacements and was followed by incremental changes in the occurrence and duration of correlated posture-upper limb trajectories. In Chapter 6, we investigated learning-mediated changes in multijoint coordination and control. Motor learning led to the flexible, error-compensating recruitment of individual joints and we showed that the preferential constraint of destabilizing joint angle variance was the putative mechanism underlying performance.

This thesis performed a detailed examination of unstable object control mechanisms. The undertaken studies have provided knowledge about the acquisition and adaptation of control mechanisms at multiple levels of the motor system. Our data provide convergent evidence that the control mechanisms governing complex human balancing tasks are intermittent and modulated by the task and context.

**Keywords:** Inverted pendulum, motor learning, unstable dynamical objects, intermittent control, multijoint error compensation, focus of attention, motor variability, statistical mechanics, coordination dynamics, uncontrolled manifold.

CO-SUPERVISORS: Drs. Ramesh Balasubramaniam and Timothy D. Lee

# **Author Contributions**

This thesis consists of seven chapters, each of which constitutes original research conducted by the author, except for contributions made by the thesis co-supervisors, Timothy D. Lee and Ramesh Balasubramaniam, and by the co-authors of journal manuscripts arising from the research presented here. As primary author, I was involved in every aspect of the presented work, including study conception and design, data collection and analysis, and writing. For Chapters 4 and 6, I was assisted by undergraduate thesis students. Taher Gharib (Psychology, Neuroscience and Behaviour) helped with the data collection, preliminary data processing and interpretation of the results presented in Chapter 4, and provided editorial advice for the manuscript. Aspasia Manos (Psychology, Neuroscience, and Behaviour; Biology) helped with preliminary data treatment for Chapter 6 and provided advice for the manuscript. Chapter 3 was performed in collaboration with Michael A. Riley (University of Cincinnati), who was involved in interpreting the results and writing the manuscript. Jason Boulet assisted with data processing and helped prepare the manuscript presented in Chapter 5.

The work presented in this thesis has been published (Chapters 2, 3, 4, 5) or submitted (Chapter 6) for publication in peer-reviewed international journals. The publications associated with each chapter are listed below.

Chapter 2: Cluff T, Balasubramaniam R (2009) Motor learning characterized by changing Lévy distributions. PLoS ONE 4: e5998.

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Chapter 4: Cluff T, Gharib T, Balasubramaniam R (2010) Attentional influences on the performance of secondary tasks during postural control. Exp Brain Res 203: 647–658.

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Chapter 5: Cluff T, Boulet JW, Balasubramaniam R (2011) Task-specific coupling between posture and hand displacements develop while learning a novel visuomotor balancing task. Exp Brain Res 213: 55–65.

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Chapter 6: Cluff T, Manos A, Lee TD, Balasubramaniam R (in review) Multijoint error compensation mediates unstable object control (manuscript #: JN-00691-2011).

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# List of Symbols and Abbreviations/Acronyms

# Symbols

∈	is a member of the set
θ	Sagittal (xz) plane joint angle with respect to the y-axis (mediolateral)
Θ	Heaviside function
	Euclidean norm
$\Delta t$	Discrete time step
$\Delta s$	Discrete speed increment
χ	Recurrence radius
<i>r</i> <sub>COP</sub>	Transverse plane (radial) center of pressure position
τ	Generalized time lag or delay
$ au_c$	Critical time
$ au_e$	Embedding delay
$\vec{u}, \vec{v}$	Unit vector representation
$\omega_{ m H}$	Hamming window
$D_e$	Embedding dimension
%DET	Density of recurrent trajectory segments that form diagonal line structures in the recurrence map
ENT	Shannon entropy of recurrent trajectory segments
F	Fisher ratio
$F_s$	Sampling frequency
Н	Hurst exponent
$H_l$	Long-range Hurst exponent
$H_s$	Short-range Hurst exponent

$H_{\text{surrogate}}$	Hurst exponent of phase-randomized (surrogate) time series
J	Jacobian matrix
$K(\tau)$	Mean-squared displacement; two-point correlation function
l	Body segment length
LAM	Density of recurrent trajectory segments that form vertical line structures in the recurrence map
$L_{\max}$	Maximum diagonal line length from the recurrence map
Μ	Arithmetic mean
$\eta^2$	Partial eta-squared (normalized effect size)
$R^2$	Adjusted coefficient of determination
<i>RR</i> , %REC	Recurrence rate
$R_{i,j}$	Recurrence matrix or map
SE	Within-subjects standard error of the mean
TT	Trapping time
<b>UCM</b> <sub>ratio</sub>	$V_{UCM}/V_{ORT}$
<i>v</i> <sub>max</sub>	Maximum trapping time
V <sub>ORT</sub>	Joint angle variance in the orthogonal subspace (task-relevant motor variance)
V <sub>UCM</sub>	Joint angle variance in the invariant subspace (task-irrelevant motor variance)
$z(\tau)$	Linear cross-correlation function

# Abbreviations and Acronyms

AMI	Average Mutual Information
ANOVA	Analysis of Variance
AP	Anteroposterior
CDT	Cognitive Dual Task
CNS	Central Nervous System
СОР	Centre of Pressure
DOF	Biomechanical Degree of Freedom
fBm	Fractional Brownian Motion
FINGER	Finger trajectory
FNN	False Nearest Neighbour
ML	Mediolateral
MPF	Mean Power Frequency
ORT	Orthogonal variance component
Р	Posture
P-SB	Posture-Stick Balancing
P-SBCDT	Posture-Stick Balancing Cognitive Dual Task
P-SBEXT	Posture-Stick Balancing-Externalized Focus of Attention
P-SBINT	Posture-Stick Balancing-Internalized Focus of Attention
PSD	Power Spectral Density
RMS	Root-Mean-Squared
RQA	Recurrence Quantification Analysis
UCM	Uncontrolled Manifold

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**Chapter 1 – General Introduction** 

# **1.1 – MOTIVATION**

Dynamic object interactions are central to the tasks that we perform in daily life, and often, the objects that we control have unstable dynamics. Unstable objects impose a complex control problem because, by definition, the object must be stabilized through the interaction between applied forces (i.e., motor commands) and the intrinsic object dynamics. Common examples include riding a bicycle or balancing a tray of drinks, which require precise control because error can elicit abrupt and irrevocable changes in performance. We know very little about the neural strategies used to balance unstable objects because the predominant research focus has been to characterize the task and context-dependent attributes of firmly grasped, rigid object control (Imamizu et al. 2003; Milner et al. 2006). As a result, there are a number of important questions to be answered: What strategies are used to control unstable objects and how are these control mechanisms learned? Are common control processes shared between interacting motor systems? This thesis uses an inverted pendulum (i.e., stick) balancing task to investigate skill acquisition in relation to the task and context-dependent attributes of unstable object control.

# **1.2 – CONTROL OF UNSTABLE OBJECTS**

The stick balancing task imposes a complex control problem. Because the stick pivots freely, the effect of forces applied at the fingertip depends on the angular state of the stick (i.e., position and velocity) and small errors may translate to the abrupt loss of performance stability. The stick balancing paradigm has generated a number of important insights on the neural control of balance (Treffner and Kelso 1999; Foo et al. 2000; Mah

and Mussa-Ivaldi 2003a, b; Cabrera et al. 2004), which fall under the general classification of two theories: Internal model and intermittent feedback control.

An influential development in voluntary motor control and learning has been that the brain develops neural structures that encode the physical properties of our limbs (Wolpert et al. 1995; Singh and Scott 2003; Kurtzer et al. 2008), environment (Gribble and Scott 2002; Körding and Wolpert 2004) and manipulated objects (Ingram et al. 2010). Compelling evidence suggests that humans develop internal models to produce the systematic forces required to counter learned force perturbations (Lackner and DiZio 1994; Shadmehr and Mussa-Ivaldi 1994; Conditt et al. 1997) and that object manipulation tasks require an internal model of the relationship between forces applied to the object and the corresponding object motion (Ahmed et al. 2008; Ingram et al. 2010). It has been shown that the force-motion model for stick balancing can be learned in the absence of upper limb motion (Mah and Mussa-Ivaldi 2003a) and generalizes to novel limb configurations (albeit, imperfectly; Mah and Mussa-Ivaldi 2003b), but does not transfer to objects with different dynamics (Mah and Mussa-Ivaldi 2003b). The latter finding suggests that effective control requires knowledge of the specific object properties, which Mah and Mussa-Ivaldi (2003b) have argued is generated by approximating the transformation between upper limb joint torques and the angular stick motion.

Are internal models required to balance an inverted pendulum? Presumably, the task could be performed by relying on sensory feedback that provides information about the inverted pendulum's angular position and velocity. The sensory signals that convey this information, however, are subject to random corruption (i.e., noise) and time delay

(Faisal et al. 2008). In the presence of feedback uncertainty and delay, researchers have argued that internal models are used to estimate body, environment, and controlled object states by the weighted combination of descending motor commands (i.e., the applied force), obtained via efference copy, and time-delayed afferent feedback (Wolpert et al. 1998; Hwang and Shadmehr 2005). The principal idea is that an output error signal is computed by comparing the estimated object states with time-delayed feedback. According to the internal model perspective, this output error is scaled to the reliability of sensory and motor uncertainty, and used as feedback into the sensorimotor system to generate minimum variance state estimates (Kalman 1960).

Model-based control theories treat uncertainty (i.e., noise) and delay as the inconvenient consequences of limitations in sensory processing (Izawa and Shadmehr 2008) and muscular force production (Christou et al. 2002; Jones et al. 2002; Christakos et al. 2006). A common argument is that internal models circumvent the cumbersome effects of feedback delay and uncertainty to enable the adaptive responses that are characteristic of skilled behaviour (Shadmehr and Krakauer 2008). The finding that subjects can successfully balance a virtual inverted pendulum during 600-ms intervals of random visual feedback occlusion (in the absence of force feedback about the state of the stick) suggests that state estimation is fundamental to the control of unstable objects (Mehta and Schaal 2002).

There is ample evidence, however, that continuous balance control does not adequately describe the behavioural strategies used to control unstable objects. It has been argued that the difficulty of controlling an inverted pendulum arises due to limitations in simultaneously processing noisy time-delayed feedback while specifying

controlled motor responses (Milton et al. 2009a). In the wake of feedback uncertainty and delay, experimental evidence has shown that intermittent rather than continuous control strategies are used to balance unstable objects and a number of authors have contested the viability of continuous model-based control (Loram et al. 2006; Milton et al. 2009b; Gawthrop 2010; Gawthrop et al. 2011).

Experimental evidence in favour of intermittent balance control has been found in the statistical attributes of angular stick displacements, which show alternating intervals of small and large amplitude fluctuations with frequency (the power spectrum of stick fluctuations follows a -1/2 power law) and timescale (the distribution of laminar phases follows a -3/2 power law) composition that are characteristic of intermittent dynamical systems (Cabrera and Milton 2002; Cabrera and Milton 2004a). To this end, angular stick corrections are performed on all timescales, but are most prevalent over time intervals that are shorter than estimated human voluntary control delays (~100-ms; Cabrera and Milton 2002) and there is evidence that stochastic or open loop motor output is an important factor in the control of unstable objects (Cabrera and Milton 2004b; Cabrera et al. 2006). Recently, an intermittent balancing strategy was reported for the manual control of an unstable virtual load (Loram et al. 2009). The intermittent balancing strategy has since been modelled as a sensory event-driven process with ballistic corrective forces applied in response to threshold-crossing angular stick deviations (Gawthrop et al. 2011).

An emerging argument is that discontinuous balance control reflects the short latency, stochastic forcing of unstable objects across set-point stability boundaries (Cabrera and Milton 2002; 2004a), with corrective upper limb displacements interjected on much

slower timescales (~1–3 Hz, Loram et al. 2011). The observations that balancing time is reduced for short, light sticks and that periodic vibration may stabilize the inverted pendulum and otherwise facilitate the detection of small angular stick displacements show that intermittent control arises due to sensory resolution/uncertainty, delay, or their combined effect (Cabrera and Milton 2004; Milton et al. 2008; Milton et al. 2009c). However, current theorizing has not considered the possibility that intermittent control is predicated on an adaptive strategy and we know very little about the task, learning and context-dependent properties of unstable object control. Intermittent balance control may depend on the circumstantial adaptation of threshold stick deviations or changes in the interplay between open loop (i.e., passive; stochastic) and feedback control processes (cf. Wolpert et al. 1992; Treffner and Kelso 1999; Loram et al. 2009). Further investigation is required to understand how we control unstable dynamical objects.

This thesis examines the acquisition of unstable object control strategies. We examine task (Chapter 2 and 4) and context-dependent changes in the statistical and spatiotemporal attributes of upper limb control (Chapter 3), and determine how these processes are related to the systematic, error-compensating recruitment of individual joints (Chapter 6). We additionally investigate postural mechanisms that contribute to the control of unstable objects with the goal of specifying common task (Chapter 4) and learning-dependent posture and upper limb control mechanisms (Chapter 5). The processes by which control mechanisms are learned and integrated across interacting motor systems is an unresolved, but important question in movement neuroscience (Bingham 1988; Bernstein 1996; Newell et al. 2001).

# **1.3 – TASK AND CONTEXT-DEPENDENT PROPERTIES OF POSTURAL CONTROL**

The upright posture is stabilized by muscle activity that is scaled to the magnitude and direction of self-generated and environmental forces (Ting and Macpherson 2005). Despite the complexity of the neural mechanisms involved in postural control (Fitzpatrick et al. 1994; Creath et al. 2005), the mechanical basis of standing balance is to maintain (the vertical projection of) the center of mass within the area defined by the outer edges of the feet. To the extent this equilibrium requirement is satisfied, the postural system appears to be recruited to facilitate goal-directed behaviour. A cogent and emerging argument is that the diversity of voluntary control is inseparable from the postural mechanisms that support behaviour (Riccio and Stoffregen 1988; Marin et al. 1999; Stoffregen et al. 2000).

The task-specificity of postural control was investigated in an experiment by Riley et al. (1999) using an upright, eyes-closed posture task. The experiment required subjects to stand with their eyes closed and lightly touch a hanging curtain. The subjects were instructed either to minimize curtain motion or that curtain deviations were inconsequential to task performance (i.e., free standing). The results demonstrated that sway variability was reduced relative to eyes-closed standing when the instructed task goal was to minimize curtain motion, but was unaffected in the free standing condition. In a similar experiment (Balasubramaniam et al. 2000), subjects performed a precision aiming task that required directing a handheld pointer at peripheral targets of various sizes. Relative to eyes-open standing, manual aiming caused the dissociation and direction-specific minimization of sway variability in the fore-aft (i.e., anteroposterior) and side-to-side (i.e., mediolateral) directions. Although sway variability is to some

extent immutable, these experiments demonstrated that subjects can effectively scale the variability of postural sway to meet the precision demand imposed by goal-directed behaviour.

The spatiotemporal properties of postural control show similar task and contextdependency. Postural sway in quiet stance has been shown to exhibit stochastic properties that arise due to the interplay between open (i.e., stochastic) and closed-loop feedbackdriven corrections (Collins and De Luca 1994; 1995; Zatsiorsky and Duarte 1999; 2000; Loram and Lakie 2002). However, the temporal and spatial features of standing balance are flexible and can exhibit stimulus-correlated (i.e., frequency-locked) periodic motion when subjects track an oscillating visual stimulus (Marin et al. 1999) or stand upright in an illusory motion display (Peterka and Benolken 1995; Jeka et al. 2000; Kiemel et al. 2002). The task and context-specific control of standing balance has been extensively documented (van der Kooij et al. 1999; van der Kooij 2001; Peterka and Loughlin 2004).

It should be emphasized that the task and context-dependent attributes of postural control are not confined to voluntary behaviour. A comprehensive literature has investigated postural responses to external perturbation (Nashner and McCollum 1985) and demonstrated that compensatory muscle activity (70-100 ms post-perturbation) is governed by: the direction of perturbation (Nashner 1976; Nashner 1977), somatosensory function (Horak et al. 1990; Horak et al. 1994), postural alignment (Macpherson et al. 1989), platform length (Cordo and Nashner 1982), expectation (Maki and Whitelaw 1993), attention (Horak et al. 1989), environmental factors (Horak et al. 1989) and subject intent (Horak and Nashner 1986). The most intuitive of these findings is that when the translating platform is longer than the feet, subjects counter environmental

perturbation by the stereotyped recruitment of the ankle musculature (i.e., the "ankle strategy"), but selectively activate the hip musculature (i.e., the "hip strategy") when the platform is short. Modulating the postural response according to the perturbation context (i.e., platform length) is critical to task success—the ankle strategy would cause the subjects' feet to rotate off the small platform support surface. The ability to scale corrective muscle responses to the characteristics of environmental perturbation is acquired systematically across training trials and decays slowly following an abrupt change in the perturbation context (Horak and Nashner 1986).

The control of standing balance is influenced by goal-directed behaviour, contextual factors, motor learning and adaptation. A limitation of the abovementioned studies, however, is that discrete perturbations and the simplicity of the investigated goal-directed tasks prevented investigation of the learning processes that govern the control of posture and voluntary movement. This limitation is addressed in Chapter 4, where an integrated analysis of posture and upper limb control is performed to evaluate the influence of task instruction. In Chapter 5, we investigate simultaneous changes in posture and upper limb control during the acquisition of the novel stick-balancing task.

## **1.4 – DYNAMIC POSTURE-UPPER LIMB INTERACTIONS**

The task and context-dependency of posture and upper limb control are robust features of voluntary behaviour (Kurtzer et al. 2003; Diedrichsen 2007; Boulet et al. 2010; Ahmed and Wolpert 2009). This finding in part reflects the instability of the upright stance and the inherent need to address self-generated perturbations that arise during upper limb motor responses (Zajac and Gordon 1989; Zajac 1993). Recent findings, however, imply

an intimate functional link between posture and upper limb control that extends beyond the instability of standing balance.

Skilled motor behaviour often requires that we control and compensate for forces that compromise postural stability. For example, we produce force on environmental objects when we perform common motor tasks like throwing a baseball, swinging a golf club, or lifting a cup of coffee. In the process, voluntary movements accelerate our center of mass and cause postural disequilibrium. These gravitational forces, if uncorrected, produce destabilizing torques that compromise standing balance. Fortunately, when a straightforward mapping exists between postural disturbances and self-generated motion, voluntary movement is preceded by an anticipatory postural adjustment (APA). APAs have been reported for diverse upper limb movements and object manipulation tasks (Bouisset and Zattara 1987; Commissaris and Toussaint 1997), and have been shown to be tuned to the uncertainty and spatial characteristics of the impending motion (Pedotti et al. 1989; Bouisset et al. 2000). The onset of the APA precedes voluntary movement (Wing et al. 1997; Forssberg et al. 1999), which suggests that a shared representation of voluntary movement dynamics (e.g., direction and amplitude) is used for the anticipatory control of posture.

APAs typically precede well-practiced movements and are thought to reflect the outcome of motor learning and adaptation. Indeed, experimental evidence has shown that APAs are learned responses and adaptation of the spatial and temporal properties of the APA have been reported during the acquisition of novel object manipulation tasks (Wing et al. 1997; Toussaint et al. 1998; Forssberg et al. 1999). Similarly, the APA is adjusted

in response to novel limb (Lee et al. 1989; Li et al. 2007) and environmental loads (Kingma et al. 1999; Patron et al. 2005; Ahmed and Wolpert 2009).

Anticipatory postural adjustments speak to the integrated and adaptive organization of posture and voluntary movement, but the investigations have been confined to discrete movements with little variation in the onset or magnitude of perturbation. The simplicity of the load context has precluded investigation of the adaptation processes shared by postural control and voluntary movement. We address this limitation in Chapter 5 by investigating the relationship between posture and upper limb control while subjects learn the inverted pendulum balancing task. How posture and voluntary movement evolve into commonly encoded, task-specific organizations is an important scientific and pragmatic question.

## **1.5 – THEORIES OF MOTOR LEARNING**

While it is generally true that practice and performance are closely related, the diversity of skilled voluntary behaviour has generated interest in motor learning. The impetus has been to discover neurophysiological and behavioural processes involved in the acquisition (Karni et al. 1995; Shadmehr and Holcomb 1997; Doyon and Benali 2005; Huang and Shadmehr 2009), retention (Brashers-Krug et al.1996; Shadmehr and Brashers-Krug 1997; Reis et al. 2009) and transfer of newly acquired motor skills (Imamizu et al. 1995; Gandolfo et al. 1996; Conditt et al. 1997; Goodbody and Wolpert 1998; Shadmehr and Moussavi 2000; Seidler et al. 2001). The motor learning literature may be divided into (at least) two distinct approaches: sensorimotor adaptation and coordination dynamics.

Sensorimotor adaptation paradigms investigate the modification of motor commands to accommodate novel sensory and force environments (Sanes 1986; Shadmehr et al. 1993; Braun et al. 2009). Mathematical models, machine learning algorithms and neuroimaging techniques have been used to argue that motor learning reflects an (optimal) parameter estimation process that learns the task by reducing error on a trial-bytrial basis (Krakauer et al. 1999; Scheidt et al. 2000; Criscimagna-Hemminger et al. 2010). The cerebellum (Imamizu et al. 2000) and basal ganglia (Seidler et al. 2006) appear to be central to the acquisition, retention and generalization of sensorimotor transformations.

Most often, sensorimotor adaptation experiments characterize changes in the kinematics of reaching movements by examining the curvature of hand trajectories. A classic finding is that hand path trajectories are straight when subjects perform goal-directed reaching movements (Hollerbach and Flash 1982), but when a novel mechanical load is introduced, the subject's hand deviates in the direction of the force perturbation. When the load is suddenly turned off after learning, an after-effect is observed whereby the hand path deviates in the direction opposite of the learned force field. This after-effect shows that motor commands are modified in anticipation of the learned force perturbation. While the force-field adaptation paradigm has made a substantial contribution to our understanding of motor learning, there has been little investigation of the multi-element structure of the upper limb (i.e., individual joints) or the interacting subsystems that comprise the human motor system. Both are fundamental considerations and form the basis of the coordination dynamics perspective, which offers a powerful

framework to investigate the organization, stability and control of voluntary movement (Kelso et al. 1984; Haken et al. 1985).

Dynamical analyses characterize the task-dependent coordinative relationships between joints, effectors, and motor systems with the objective to specify how control is influenced by biomechanical constraint (Buchanan and Kelso 1993; Virji-Babul and Cooke 1995; Serrien and Swinnen 1998; Dounskaia et al. 1998), sensory feedback (Kovacs et al. 2009) and task difficulty (Fink et al. 1999; Sternad et al. 1999). A central approach has been to examine the change in coordination between effectors (Swinnen et al. 1997; Kelso and Zanone 2002), body segments (Bobbert and van Ingen Schenau 2001) and joint angles (Vereijken et al. 1997) that accompanies motor learning. Learning has been described by the evolution of the topological properties that characterize body segment relationships (Schöner and Kelso 1988; Schöner et al. 1992) and systematic changes in the recruitment and patterning of active muscular responses (Southard and Higgins 1987; McDonald et al. 1989; Vereijken et al. 1992; Broderick and Newell 1999).

Task-specific coordinative relationships have led researchers to question whether similar organizations exist between specialized sensorimotor subsystems. Indeed, goal achievement in complex motor tasks often requires collaboration between upper limb motor responses and the neural mechanisms that stabilize the upright posture (Bouissett and Zattara 1987; Bouisset et al 2000). Thus, in the same way that performance depends on the coordinated engagement of individual body segments, motor learning requires the task-specific assembly of specialized motor subsystems.

In view of these considerations, motor subsystem interactions have been a topic of interest in theoretical treatments of motor control and learning (Bingham 1988; Bernstein

1996). Recently, Newell et al. (2001) have proposed that motor learning is instantiated by the evolving coordination of interacting motor subsystems. Their model distinguishes between three hierarchical levels of the motor system ranging from (1) individual effectors that operate and evolve within effector systems (e.g., individual muscles, segments or joints) to (2) coordinative relationships between motor subsystems (e.g., posture and upper limb movement patterns) that interact to collaboratively produce (3) outcome performance. Newell et al. (2001) have proposed that specialized motor subsystems are organized hierarchically and integrated into functional interactions that support outcome performance.

Newell et al.'s (2001) hierarchical learning model was recently investigated in a series of experiments by Huys et al. (2003; 2004a, b) that examined learning-mediated changes in the coordination of posture, vision, and hand movements in three-ball cascade juggling. The authors found clear evidence for the emergence and progressive coordination (i.e., frequency-locking) of vertical ball displacements and center of pressure trajectories (Huys et al. 2003). The incidence and expression of posture-hand coordination varied across individuals, but was found to increase systematically across training sessions for each subject. The authors reported similar coupling functions between ball and point of gaze adjustments (Huys et al. 2004a). This work confirmed Newell et al.'s (2001) learning model by showing that learning-induced changes in motor subsystem dynamics precede the development of correlated subsystem interactions.

The strength of Newell et al.'s (2001) learning model is that it provides a straightforward framework for interpreting the complex interactions that arise between specialized motor systems. This thesis builds on the Newell et al. (2001) learning model

by examining the correlative properties of posture and upper limb dynamics. In Chapter 5, we examine the convergence of posture and upper limb control caused by the development of expertise in the inverted pendulum balancing task. The objectives of this study were to determine how we learn to control unstable objects, to characterize these control processes at multiple levels of the voluntary motor system, and to specify how learning influences the integration of independent motor subsystems.

# 1.6 – SUMMARY

In the previous sections, task and context-specificity were discussed as common features of posture and voluntary behaviour. While an extensive literature has focused on adaptation to novel mechanical loads, few studies have considered how we control unstable objects (Mehta and Schaal 2002; Mah and Mussa-Ivaldi 2003a, b; Milton et al. 2009a, b). The intuitive hypothesis is that our repertoire of object manipulation skills is established through common learning and control mechanisms for posture and the upper limb motor system. Accordingly, the outstanding questions are

- i) How do we control unstable objects?
- ii) Are unstable object control mechanisms modulated by the context and task demand?
- iii) Are distinct motor systems, such as the control of individual joints, posture, and the upper limb linked through common learning and control processes?

The aim of this thesis is to address these outstanding concerns. The first question is entertained by investigating the statistical and spatiotemporal properties of upper limb control during the acquisition of the inverted pendulum balancing task. The objective was to particularize the learning-dependent properties of unstable object control. The second

question examines the task and context-dependent properties of unstable object control. Our objective was to elaborate how unstable object control is affected by the balancing context and task instruction. The third question examines whether distinct effector systems are linked through common learning and control processes. These questions are addressed using a behavioural approach to better understand the learning and control processes governing unstable object interactions.

### **1.7 – THESIS OVERVIEW**

In this thesis, motor learning and control are scrutinized using a behavioural approach and dynamically-oriented (i.e., statistical mechanics, phase space reconstruction/embedding, time series analysis, and manifold methods) mathematical analyses. In Chapter 2, the statistical properties of upper limb control are evaluated across a training period and in two alternate balancing postures—seated and standing balance. Chapter 3 investigates the spatiotemporal properties of upper limb control to further elaborate the context and learning-dependent properties of stick balancing. Chapter 4 extends the approach used in Chapters 2 and 3 to investigate whether the upper limb and postural control are modulated by explicit task instruction or simultaneous cognitive load. In Chapter 5, we use an innovative analysis to examine concomitant changes in posture and upper limb control that are mediated by motor learning. Finally, Chapter 6 investigates learning-mediated changes in the control of multijoint kinematics. These five basic studies were designed to elaborate control processes at multiple levels of the motor system and the processes by which they are established through motor learning.

# **1.8 – OUTLINE OF EXPERIMENTS AND HYPOTHESES**

The studies presented in this thesis are motivated by the hypothesis that multijoint kinematics, posture, and upper limb displacements are functionally integrated to control unstable objects. This conjecture was motivated by evidence that the control of posture and voluntary movement are ostensibly linked through common learning and control processes (Huys et al. 2004a, b). The principal analyses performed in Chapters 2, 3, 5 and 6 examine motor learning and contrast the dynamical attributes of upper limb (Chapters 2, 3, 5), posture (Chapter 5), and angular joint excursions (Chapter 6) across a training period. Chapter 4 examines modifications in the control of posture and the upper limb in response to variations in the task demand.

In Chapter 2, we devised an experimental paradigm to evaluate the learning and context-dependent control of unstable dynamical objects. Our stick-balancing paradigm was motivated by research on the control of balance in time-delayed systems (Cabrera and Milton 2002; Cabrera and Milton 2004a, b; Milton et al. 2009a, b). The work of Milton and colleagues has demonstrated that stochastic motor processes are implicated in fast timescale balance control. Provided parametric noise fluctuations are tuned to displace the stick trajectory across the vertical on fast timescales (as shown in Cabrera and Milton 2004b), we hypothesized that the statistical attributes of upper limb displacements would change with motor learning to show that subjects tune balance control to optimize performance. To address this question, we used regression techniques and fit individual subjects' transverse plane fingertip speed profiles to theoretical Lévy distributions. We analyzed changes in the scaling and truncation of the statistical

distribution of upper limb kinematics. The objective of this experiment was to investigate the context and learning-dependent adaptation of upper limb control.

Chapter 3 examined the spatiotemporal properties of upper limb control. Our experiment was inspired by research which demonstrated that angular stick fluctuations are governed by an intermittent control mechanism (Cabrera and Milton 2002). Importantly, > 98% of corrective stick fluctuations have been shown to occur on timescales shorter than estimated human voluntary control delays (~100-ms; computed by Cabrera and Milton 2002 using the cross-correlation function between angular stick and fingertip displacement time series). The work by Cabrera and Milton, in conjunction with our observation that hand displacements are Lévy distributed in stick balancing (Chapter 2; Cluff and Balasubramaniam 2009), suggested that stochastic processes contribute to the stabilization of the upright stick position on short timescales. We hypothesized that if stochastic motor processes indeed stabilize the upright stick position on short timescales, then hand displacements should show intermittent dynamics—we expected upper limb displacements to switch between two (phenomenological) states differentiated by their correlative properties and timescale composition.

In Chapter 4, we tested whether stick balancing performance is influenced by the allocation of attention to upper limb control (internal focus), outcome performance (external focus) and cognitive demand. Our experiment was prompted by the observation that execution-oriented (i.e., internal focus) attention destabilizes performance and interferes with the automaticity of corrective motor responses during the control of posture and unstable handheld loads (Shea and Wulf 1999; Wulf et al. 2001; McNevin et al. 2002; McNevin et al. 2003). We approached this problem from a novel perspective.

We hypothesized that if attention modulates corrective motor processes, then task instruction should be reflected on timescales specific to voluntary control-the slower varying corrections characteristic of feedback control. We additionally hypothesized that if cognitive load (external, task-irrelevant focus) facilitates the automaticity of motor performance (as shown in Weeks et al. 2003), then we expected cognitive dual-task performance to evoke differences in short timescale posture and upper limb displacements. We implemented the cognitive load using a silent arithmetic task derived from work by Weeks et al. (2003). To address our hypotheses, we manipulated the focus of attention by explicit task instruction and used a dynamical analysis capable of classifying two independent timescale components that contribute to outcome performance. We decomposed the correlative attributes of hand and postural displacements into two independent timescale processes: a fast, stochastic component (i.e., drift process) and a slow feedback control component (i.e., correct process). To our knowledge, this is the first study to perform a mechanistic analysis of the influence of attention on motor performance.

In Chapter 5, we investigated the functional organization of posture and upper limb control. Our study was motivated by research which suggested that the acquisition of novel motor skills involves a series of stereotyped modifications to the hierarchical organization of motor subsystems (Bingham 1988; Bernstein 1996; Newell et al 2001). Unlike the few previous studies on the topic (Huys et al. 2003; 2004a, b), we focused exclusively on the convergence of posture and upper limb control. We hypothesized that change in the dynamical attributes of upper limb displacements would be paralleled by corresponding changes in posture. We used an innovative analysis to quantify

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simultaneous changes in posture and upper limb control and their coupled interactions. This study provides a much needed focus on motor interactions and their role in learning.

Chapter 6 was motivated by the equivocal relationship between angular joint trajectories and motion at the end effector (Polit and Bizzi 1978; Lacquaniti and Soechting 1982). Due to the redundancy of the upper limb motor system, identical end-effector kinematics may be generated by infinite combinations of individual joint configurations. Rather than use rigid or stereotyped joint recruitment patterns, we hypothesized that skilled performers would co-vary and flexibly engage individual joints to stabilize the upright stick position (Scholz and Schöner 1999; Latash et al. 2002). To address our hypothesis, we examined error compensation (i.e., covariation) between joints using a geometric model that mapped six independent joint angles onto the time-varying fingertip position. We partitioned motor variance into two orthogonal components that corresponded to joint configuration variance that stabilized (UCM) versus destabilized (ORT) outcome performance.

The studies presented in this thesis demonstrate that unstable object interactions are supported by learning-dependent changes in the control of individual joints, posture, and upper limb displacements. A detailed elaboration of the experiments is presented in Chapters 2 through 6. The discussion of how these studies contribute to the literature is presented in the General Discussion section (Chapter 7). Concluding comments and future research directions are also outlined in Chapter 7.
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# Chapter 2 – Motor Learning Characterized by Changing Lévy Distributions

## 2.1 – ABSTRACT

In this experiment, we show that transverse plane changes in fingertip speed are Lévy distributed in human pole balancing. To investigate, six subjects learned to balance a pole on their index finger over two weeks while sitting and standing. The Lévy or decay exponent decreased as a function of learning, showing reduced decay in the probability for large fingertip speed steps. The decay exponent was smaller in the sitting condition, but the distribution was truncated so that the probability for large fingertip speed steps was reduced. These results show a learning-induced tolerance for large fingertip speed step step sizes and demonstrate that motor learning in continuous tasks can be characterized by changing distributions that reflect sensorimotor skill acquisition.

### 2.2 – INTRODUCTION

Traditionally, motor learning for continuous, goal-directed movements has been difficult to characterize. Although dynamical approaches have argued that motor learning results from the evolution of potential landscapes (Newell et al. 2001), what has been elusive is to quantify and interpret these changes behaviourally. On the other hand, motor learning for discrete movements can be classified on the basis of performance error, for example, from the end-effector position relative to some salient target (Körding and Wolpert 2004). These studies have a longstanding history in the literature and consequently, have revealed much more about motor learning for discrete tasks (Snoddy 1926; Crossman 1959).

More recently, studies that examined learning for continuous tasks have incorporated a technique from control systems theory—the Kalman filter. The Kalman filter is a linear estimator that in neural applications recursively determines the sensory consequences of movement based on the intended motor command (Wolpert 1997; Wolpert and Ghahramani 2000; Wolpert and Flanagan 2001). Computational theories of human motor control posit that the Central Nervous System (CNS) employs internal forward models in tasks such as visuomotor pole balancing. Predictive control can be favorable for the neural control of pole balancing because it can help circumvent sensorimotor processing delays to produce the short latency movements required for maintaining pole stability (Mehta and Schaal 2002). Predictive mechanisms enable perturbations/threats to stability to be anticipated and accordingly, corrections can be performed in anticipation of these disturbances. More generally, estimation mechanisms are thought to be implicated in minimizing body-state uncertainty during the continuous evolution of limb states in

response to motor commands (Mehta and Schaal 2002; Wolpert and Kawato 1998; Witney et al. 2000; Witney et al. 2001).

Contrary to the abovementioned mechanisms, pole dynamics may be stabilized by stochastic properties characteristic of motor control (Cabrera and Milton 2002; Cabrera and Milton 2004a, b). The findings of Cabrera and Milton have demonstrated that fingertip speed profiles in human pole balancing show power law scaling. Power law scaling was also evident in the laminar phases (time intervals) for successive corrective movements, which demonstrated that corrective movements were intermittent in human pole balancing. In confirmation of intermittent control, behavioral data have demonstrated that > 98% of corrective movements are shorter than our sensory processing delays. Numerical analyses have since shown that balance can be facilitated in time-delayed stochastic systems, provided the system is tuned near a stability boundary. In this case, control could result from stochastic processes that force the angular stick trajectory back and forth across the vertical on short timescales (Cabrera and Milton 2004a, b). On the basis of efficiency, intermittent or 'bang-bang' control might be favored to continuous estimation in stochastic, time-delayed systems since the computational burden incurred by the CNS would be minimized (Milton et al. 2008).

Systems characterized by on-off intermittency exhibit two distinct phenomenological states. In the "off" state, dynamic variables remain approximately constant over various time intervals. Conversely, the "on" state is characterized by intermittent bursting of the dynamical variable. Intermittency requires the underlying system to possess an invariant subspace, whereby provided the dynamical variable remains within the bounds of the invariant space, it remains relatively constant. This bound is manifest as a threshold, that

when crossed, results in subsequent bursting of the dynamical variable, i.e., the system transitions from the "off" to "on" state (Marthaler et al. 2001).

In this context, the stochastic process that characterizes fingertip speed profiles is given by a symmetric Lévy process  $L_{\alpha}(\Delta s, \Delta t)$  (Cabrera and Milton 2004a):

$$L_{\alpha}(\Delta s, \Delta t) = \frac{1}{\pi} \int_0^\infty \exp(-\gamma \Delta t q^{\alpha}) \cos(q \Delta s) dq,$$

where  $\Delta s$  is the speed step size,  $\Delta t$  is the interval between successive observations,  $\gamma$  is the scaling factor ( $\gamma > 0$ ) and  $\alpha$  is the Lévy index ( $0 < \alpha < 2$ ). The Lévy process is an unbounded, unconstrained random walk and the asymptotic character gives rise to an infinitely variant process that lacks first and second statistical moments. Additionally, the Lévy process is characterized by 'slow' and 'fast' components, which are similar to the 'rambling' and 'trembling' processes studied in postural control (Zatsiorsky and Duarte 1999; 2000). The slow and fast regimes of the Lévy process are demarcated by a critical threshold and the dynamic variable is free to vary within the confines of this threshold.

Previous research demonstrated that the probability for large fingertip speed steps increased with learning in a human pole balancing task (Cabrera and Milton 2004a), which the authors argued was indicative of tolerance to stochastic processes. This consideration has important ramifications for our understanding of motor learning. In the event that the distribution broadens with learning, this corresponds to a smaller decay in the probability for large step sizes. Behaviourally, this is manifest as tolerance to stochastic processes: the participant becomes tolerant to large changes in fingertip speed as proficiency in the pole balancing task increases. The purposes of this study were two-

fold: first, to determine whether the decay exponent for the probability of a given step size,  $\alpha$ , changed with learning, and second, to determine whether  $\alpha$  varied in a sitting versus standing condition. We include the seated versus standing balance contrast to highlight differences in control between two conditions that differ markedly in the availability of biomechanical degrees of freedom. We expected greater probability for large changes in fingertip speed in the standing condition.

#### 2.3 - METHODS

Six healthy subjects (2 male, aged 26–28 years; 4 female, aged 23–27 years) participated in this experiment. The subjects were undergraduate or graduate members of the Sensorimotor Neuroscience Laboratory (i.e., convenience sample). The procedures were performed in accordance with the Declaration of Helsinki and subjects provided written informed consent prior to the experiment. The protocol was approved by the University of Ottawa ethics review board.

Subjects balanced a wooden dowel with length 62 cm, diameter 0.635 cm and mass 50 g in two experimental conditions: sitting and standing. Sitting trials were performed with subjects seated comfortably in a chair at the subjects' preferred seat height. The subjects were required to balance the pole with their back remaining in contact with the seat. In the standing condition, subjects performed pole balancing with their feet approximately shoulder-width apart, but were able to move their upper body while maintaining a stationary stance. In the event that foot movement occurred, the trial data were discarded and excluded from further analysis.

Motion capture was performed with 8 VICON MX-40<sup>+</sup> infrared cameras sampled at 500 Hz (Denver, CO, USA). We tracked pole motion in three-dimensions using two

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spherical reflective markers (14 mm diameter) affixed to the top and bottom of the pole with double-sided adhesive. We processed the marker trajectories offline with the VICON Workstation software and exported the trial data to MATLAB<sup>TM</sup> (Mathworks, Natick, MA) for further analysis.

This study employed a learning paradigm and subjects learned to balance a small cylindrical pole on their fingertip over a two week period. Data collection was performed on the first day, followed by subsequent data collection every fourth day. The subjects performed 30 min of daily practice between data collection sessions (15 min per condition), which was distributed between conditions according to their preference. We avoided confounding learning effects by counterbalancing the order of conditions across subjects.

The Lévy process ( $\alpha < 1.2$ ) requires  $10^5 \cdot 10^6$  samples to be reliably distinguished from the Gaussian process ( $0 < \alpha \le 2$ ). With our sampling rate of 500 Hz, this corresponded to a minimum balancing time of 200 s. Individual trials for each condition and session were parsed into a single aggregate trial for each subject. All data presented here were derived from detrended, aggregate fingertip speed profiles > than  $5 \times 10^5$ samples (1000 s). We aggregated the two-point differenced fingertip speed data ( $\Delta s$ ). We believe this is the more effective means of aggregating individual trial data because it minimizes artifact that might result from introducing particular speed steps—the effect of parsing would be accentuated by making the aggregate trial with fingertip positions and two-point differencing to determine the fingertip speed. Moreover, the effect of parsing individual trials would be minimized by the number of data points in relation to the number of trials used in the aggregate time series (max 50 trials vs. > 500000 samples per

aggregate time-series). Similar to Cabrera and Milton (2004a), we examined the corrective movements that occurred on timescales shorter or on the same order as the neural delay.

We computed the 2-D fingertip speed, s(t):

$$s(t) \equiv \left\| \frac{\vec{r}(t + \Delta t) - \vec{r}(t)}{\Delta t} \right\|,$$

where  $\vec{r}(t)$  corresponded to the transverse plane 2-D fingertip position at time *t*,  $\vec{r}(t + \Delta t)$  was the fingertip position at time  $t + \Delta t$ ,  $\Delta t$  represented the time step between successive observations and  $\| . \|$  represented the Euclidean norm. Therefore, s(t) was the Euclidean fingertip speed. The detrended speed  $\Delta s(t)$  was computed as:

$$\Delta s(t) = s(t + \Delta t) - s(t),$$

where s(t) was the 2-D norm at time *t* and  $s(t + \Delta t)$  was the fingertip speed at time  $t + \Delta t$ . This expression removes time-dependent linear trends and is equivalent to the high-pass filtered fingertip speed (Segev et al. 2002).

We computed the probability of a given step size,  $P(\Delta s, \Delta t)$  by constructing histograms with the bin size set to 1 mm/s. To determine whether the probability of a given step size was influenced by the time between observations ( $\Delta t$ ), we decimated  $\Delta s(t)$ on a logarithmic scale by factors 1 to 1000. We plotted the probability of return (i.e., the probability of zero change in fingertip speed between observations),  $P(0,\Delta t)$ , as a function of  $\Delta t$  and computed the power law exponent  $\alpha$  from the relationship

$$P(0,\Delta t) \propto \Delta t^{-\alpha}$$
.

In other words,  $\alpha$  was computed by regressing  $P(0, \Delta t)$  onto  $\Delta t$  on a double-logarithmic scale. We contrasted the power law exponent ( $\alpha$ ) across sessions (3) and conditions (2) using a 3 × 2 ANOVA with repeated-measures. Post-hoc analysis was performed by paired *t*-tests with Bonferonni corrections for multiple comparisons. The significance level for statistical contrasts was 0.05. As a measure of performance, we quantified the mean balancing time and contrasted this dependent measure across training sessions (3) and conditions (2) using a 3 × 2 ANOVA with repeated-measures. The balancing time  $t_{bal}$ (in seconds) for individual trials was determined from the number of samples as

$$t_{bal} = \frac{\# samples}{Fs}$$
,

where *Fs* was the sampling frequency for data collection. The mean balancing time  $\bar{\tau}$  was defined as the average time spent pole balancing across trials in each session and condition,

$$\bar{t}_{bal} = \frac{1}{n} \sum_{i=1}^{n} t_{bal_i},$$

where n was the number of trials and  $t_{bal}$  was the balancing time (in seconds) for individual trials, respectively. Post-hoc analyses were performed using paired *t*-tests with Bonferonni corrections.



**Figure 2.1.** Changes in fingertip speed are Lévy distributed in the visuomotor stickbalancing task. Decimated time series show the probability of change in fingertip speed,  $P(\Delta s, \Delta t)$ , is dependent on the time between successive observations,  $\Delta t$  (0.002 to 2 s). Overlaid colors represent the decimated time series, with time steps ranging from 0.002 to 2 s. a) Sitting; b) Standing condition. Left to right: Sessions 1 to 3.

### 2.4 – RESULTS

Figure 2.1 shows the normalized histograms for the probability of a given step size  $P(\Delta s, \Delta t)$  in the sitting (top row) and standing conditions (bottom row) across experimental sessions (Session 1: left; Session 2: middle; Session 3: right). Figure 2.2 shows representative session data for Subject 1 in the sitting and standing conditions (Session 1: Red; Session 2: Blue; Session 3: Green). Both figures demonstrate that the distribution broadened with learning, rendering the probability of large speed step sizes  $P(\Delta s, \Delta t)$  significantly greater with experience. Figure 2.2 also plots theoretical Lévy distributions with parameters fit to the data from Session 1 (solid black line). For the sitting condition, the decay exponent was  $\alpha = 0.95$  and the scale parameter  $\gamma = 0.025$ , whereas for the standing condition  $\alpha = 0.98$  and  $\gamma = 0.025$ . As shown, the central regions of the distributions are reasonably well fit by the parameters, but the quality of fit decreases in the tail region. This suggests that both the decay exponent and truncation were influenced by learning.

We decimated the change in speed time series  $\Delta s(t)$  to determine the probability of return or zero-speed change  $P(0,\Delta t)$  when the time between observations was varied from 0.002 to 2 s. The decay exponent  $\alpha$  was estimated by regressing  $P(0,\Delta t)$  onto  $\Delta t$  on bilogarithmic plot (Figure 2.3). Statistical analyses demonstrated that  $\alpha$  was dependent on both session, F(2, 10) = 7.90, p = 0.009, and condition, F(1, 5) = 7.70, p = 0.039 where F corresponds to the Fisher statistic for the repeated-measures contrast (mean-square error within-subjects/ mean-squared error between-subjects) and (2, 10) represents the statistical degrees of freedom for the mean-squared error within and between-subjects, respectively. In this context, p represents the probability of observing the same or more

extreme results. With respect to the session effect,  $\alpha$  was reduced in session 3 (M = 0.935, SE = 0.009) relative to session 1 (M = 0.981, SE = 0.011), p = 0.046. The decay

exponent,  $\alpha$  was similar between session 2 (M = 0.964, SE = 0.014) and sessions 1 and 3



**Figure 2.** 2.  $P(\Delta s, \Delta t = 0.002 \text{ s})$  over three sessions in the seated (left) and standing (right) balance conditions. Red: Session 1; Blue: Session 2; Green: Session 3.

(p > 0.05). Lastly, the decay exponent  $\alpha$  was significantly larger in the standing (M = 0.973, SD = 0.011) relative to sitting (M = 0.947, SD = 0.009) condition, p = 0.039. The decay exponent  $\alpha$  was not influenced by the session × condition interaction (F (2, 10) = 0.942, p > 0.05).

The mean balancing time measure was defined as the average time spent pole balancing across trials within each session and condition. We contrasted the mean balancing time performance measure using a 3 (session) × 2 (condition) ANOVA with repeated-measures. The mean balancing time was influenced by both session, F(2, 10) =14.331, p < 0.001, and condition, F(1, 5) = 6.92, p = 0.05, but was not influenced by the interaction effect, F(2, 10) = 2.92, p > 0.05. Regarding the session effect, the average length of balancing trials was greater in session 3 (M = 73.69, SE = 12.72) relative to session 1 (M = 29.80, SE = 11.78) (p = 0.034) and session 2 (M = 44.50, SE = 11.82) p = 0.034, whereas mean balancing times for sessions 1 and 2 were not significantly different from one another, p > 0.05. Lastly, mean balancing time was significantly greater in the standing (M = 59.61, SE = 14.10) relative to sitting condition (M = 39.04, SE = 11.04), p = 0.047.



**Figure 2.3.**  $P(0, \Delta t)$  is power-law distributed for  $\Delta t = 0.002$  to 2 s in the seated balance condition.

### 2.5 – DISCUSSION

The objective of our study was to determine whether power law scaling in a human pole balancing task is dependent on learning. Previously, Cabrera and Milton (2004a) demonstrated that learning resulted in less severely truncated distributions for the probability of large changes in fingertip speed,  $P(\Delta s, \Delta t)$ . The authors proposed that this change was caused by differences in truncation. With truncation, the symmetric Lévy distribution becomes

$$P(\Delta s, \Delta t) = \begin{cases} c_1 L_{\alpha}(\Delta s, \Delta t) f(\Delta s) & \text{if } |\Delta s| \ge l_c, \\ c_2 L_{\alpha}(\Delta s, \Delta t) & \text{otherwise} \end{cases}$$

where  $P(\Delta s, \Delta t)$  is the probability of a given velocity step,  $c_1$  and  $c_2$  are normalization constants,  $L_{\alpha}(\Delta s, \Delta t)$  is the symmetric Lévy distribution,  $f(\Delta s)$  is the truncation function,  $\Delta s$  is the step-size and  $l_c$  is the threshold for truncation. The truncation function  $f(\Delta s)$ , can be approximated as (Gupta and Campanha 2002),

$$f(\Delta s) = \begin{cases} 1 & \text{if } |\Delta s| < l_c \\ \exp\left[-\left(\frac{|\Delta s| - l_c(\Delta t)}{k(\Delta t)}\right)\right] & \text{if } |\Delta s| \ge l_c \end{cases}$$

where  $\Delta s$  is the change in velocity,  $\Delta t$  is the time-step,  $l_c$  is the truncation threshold and  $\beta$  is ( $\alpha$ -2). Cabrera and Milton proposed the increased probability for large changes in fingertip speed ( $\Delta s$ ) resulted from changes in truncation and not scaling. We were concerned with whether the observed changes in the probability distribution for step size resulted not only from truncation, but also from a reduction in the decay exponent  $\alpha$  for  $P(\Delta s, \Delta t)$ . Our hypothesis was confirmed in that power law scaling was influenced by

learning: participants became tolerant of large changes in fingertip speed, and this tolerance was reflected in the decay exponent,  $\alpha$ .

Moreover, we contrasted decay exponents ( $\alpha$ ) for  $P(\Delta s, \Delta t)$  in sitting and standing conditions. Our results suggest that while the decay exponent for the probability of a given speed step size ( $\Delta s$ ) was significantly larger in the standing versus sitting condition, the distribution was truncated such that the  $P(\Delta s, \Delta t)$  distribution was broader for the standing condition. Therefore, individuals were relatively tolerant of large fingertip excursions when standing. We argue, in confirmation of the results presented by Cabrera and Milton (2004a), that truncation was more severe in the sitting condition—the physical capacities of the system were exhausted—and individuals were not capable of tolerating large speed step sizes to the same extent. The hypothesis is further supported by Figure 2.2, which demonstrated the experimental distributions for all three sessions were reasonably well fit in the central region by a theoretical distribution plotted using parameters  $(\alpha, \gamma)$  determined from Session 1 data, but the quality of fit was poor in the tail region. These results follow a more generalized form of truncation. With respect to the discontinuous truncation function  $f(\Delta s)$  mentioned above, there are three broad truncation classifications: (i) the distribution is truncated gradually from return (Koponen 1995),  $l_c = 0$ ; (ii) the distribution deviates from the symmetric Lévy and is truncated gradually from some critical change in fingertip speed,  $l_c \neq 0$ ; and (iii) the truncation gain is zero, k = 0, and the system's capacities are exhausted rapidly at the critical step size  $l_c$ (Mantegna and Stanley 1994). Physically, the truncation may have resulted from a reduction in degrees of freedom, ultimately reducing the range of motion and

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consequently, the truncation gain k. It would be beneficial to take up the specific truncation mechanism in future research.

Conceivably, changes in the distribution of fingertip speed changes  $P(\Delta s, \Delta t)$  could have occurred in the absence of learning; however, we quantified a performance measure for pole balancing based on balancing time. Balancing time was the mean time spent pole balancing for each session and condition. We found that learning did occur, since the time spent balancing was dependent on a session effect. Regarding the classification of participant skill levels, it is likely that our participants were still of low-moderate level since mean balancing times for the sitting condition were less than one minute (Milton et al. 2008). Future research should consider the differences in the examined distributions between low-moderate and expert pole balancers (mean balancing time >> 1 minute). As demonstrated, changes in the Lévy exponent certainly occur for the progression from low to moderate skill, but it is unlikely that these changes persist with further developments of expertise.

Our sit versus stand comparison was conducted to delineate the mechanisms by which individuals learn to accommodate noise in pole balancing. Power law scaling is known to arise in unstable physical systems influenced by parametric noise (Cabrera and Milton 2002, Cabrera and Milton 2004a; Hosaka et al. 2006; Cabrera et al. 2006). Balance control in unstable, time-delayed dynamical systems can benefit from the presence of parametric noise, provided the system is placed near a stability boundary. In such a way, the inverted pendulum with time-delayed (sensory) feedback is stabilized by parametric noise—stochastic forcing of a gain term back and forth across a stability boundary (Hosaka et al. 2006). The rationale for the sit vs. stand comparison can be summarized as

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follows. Sensorimotor noise is state-dependent (Harris and Wolpert 1998). The standing condition employed here capitalizes on more biomechanical degrees of freedom relative to the sitting condition, with state-dependent noise inherent to each additional degree of freedom. In alignment with the premise that balance control can benefit from noise, we hypothesized that pole balancing would be facilitated in the standing condition. The hypothesis was confirmed, since greater contribution from the distribution tails were observed in the standing condition and participants were capable of balancing for a prolonged period relative to when sitting. Though at present we know little about the underlying mechanism, one explanation might be that abundant dimensions along which the system can vary (muscle activations, joint kinematics) facilitate the pole balancing task.

Previous research into the mechanisms underlying postural control demonstrated that performance in a dual task (counting backwards by 3's) with eyes closed reduced postural fluctuations relative to an eyes-closed condition. Similarly, pole balancing performance improved for a moderately skilled subject in a dual-task situation (improvements were observed for both rhythmical and imaged leg movement) (cf. Ermentrout and Milton 2008 for exemplary video, Milton et al. 2008b for more detail). In short, these studies suggest that maintaining balance might be an exception, since dual task conditions typically have a deleterious effect on motor performance. Balance might be the exception since it appears to be facilitated by passive dynamics of the neuromuscular system (ligaments, joint capsules). However, there are also active contributions to the control of balance that are both reflexive (muscle spindles, golgi tendon organs) and voluntary (muscle contraction and tension at the tendon insertion) (Riley and Turvey 2002).

In summary, we demonstrated that motor learning resulted in increased tolerance for large pole displacements in a human pole balancing task. The decay exponent  $\alpha$  was influenced by learning, becoming significantly smaller with experience and resulting in less severe decay in the probability for a given fingertip speed step size,  $P(\Delta s, \Delta t)$ . Moreover, the decay exponent  $\alpha$  for  $P(\Delta s, \Delta t)$  was greater in a sitting versus standing condition. Our results show conspicuously that both decay exponents and truncation change with learning, resulting in an increased tolerance to large fingertip excursions in pole balancing.

Previously, Cabrera and Milton (2002) demonstrated that time intervals between corrective movements followed a -3/2 power law. These results were argued to be indicative of intermittent control. Cabrera and Milton (2004b) have argued that intermittent control is favorable to continuous estimation on the basis of efficiency since the intermittent control strategy would moderate the computational burden incurred by the CNS. In their view, pole balancing dynamics and the corresponding intermittent control regime does not require continuous estimation by the CNS since passive or noisy pole dynamics act to impart a dynamical stability. The CNS need only enact control when the pole dynamics cross a threshold stability boundary (Cabrera and Milton 2002; 2004a, b). Such dynamics have previously been reported in the control of upright posture (Collins and De Luca 1994).

In this model, the ability to sense threshold crossings for pole dynamics is bounded by the limitations of sensory processing. Sensory feedback involves processing delay, which incorporates limitations in transduction, conduction velocity, multimodal sensory integration, and neural processing to enable a control decision. When a movement

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decision is made, motor commands descend from the primary motor cortex to the distal effectors. Continuous estimation (predictive) can help circumvent sensory processing delay. In a recent experiment, manipulating an object with complex dynamics (subjects balanced a flexible weighted ruler by applying a force to the tip) was shown to cause greater activation of the ipsilateral anterior cerebellum relative to an object with simple dynamics (Milner et al. 2007). Activation of the ipsilateral anterior cerebellum was similar to that observed in a previous study (Milner et al. 2006) and was attributed to the acquisition of an internal representation of the task. The question is why cerebellar activity is modulated by task difficulty and shows increased activation when controlling objects with complex relative to simple dynamics. In the pole balancing task, the observed corrections are intermittent (Cabrera and Milton 2002), and it appears that the motion of the pole is corrected only when a fall is impending. It may be that the underlying sensory processing mechanism is continuous and predictive. With learning a representation of pole dynamics might be acquired and consequently used to estimate finger and pole states so as to circumvent neural processing delays.

Predictive control mechanisms can help circumvent neural processing delays by anticipating perturbations and performing corrective movements prior to or as these perturbations arise. However, whether an estimation model can replicate the intermittency observed in our experimental data is not yet known. Though an estimation strategy might represent a plausible control mechanism for the CNS, other scenarios might include a mixture of non-predictive and predictive mechanisms. In this context, participants might rely on passive dynamics until a stability threshold is surpassed, at which point a predictive strategy might be enacted for correction.

The present finding that the joint probability distribution for changes in fingertip speed over time intervals is Lévy distributed challenges any mechanism based solely on prediction. Typically, Lévy distributed processes are thought to be reflective of nonpredictive searches or foraging patterns (Viswanathan et al. 1996; Viswanathan et al. 1999), which is problematic for a theory of predictive control for pole balancing. As a further consideration, the current understanding of predictive mechanisms in motor control is grounded in Kalman filter-based models. The limitation of the conventional Kalman filter as applied to the context of the current results is that it implicitly assumes additive Gaussian process and measurement noise (Kalman 1960) and not the multiplicative noise that typically gives rise to power law distributed variables. These considerations are not easily explained by current predictive theories of motor control. Future endeavours should take these findings into consideration since important insights into the mechanisms governing the control of unstable systems may be proffered, including the possibility that the interplay between passive and predictive mechanisms (intermittency) might change as a function of expertise.

### **2.6 – REFERENCES**

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# Chapter 3 – Dynamical Structure of Hand Trajectories During Pole Balancing

# 3.1 – ABSTRACT

In this experiment, we examine the dynamics of fingertip displacements in a human pole balancing task. The purpose of this research was to determine how the dynamical structure of fingertip fluctuations evolved with learning. We analyzed fingertip time series using recurrence quantification analysis (RQA). Learning was accompanied by an increase in the stability of fingertip trajectories despite a reduction in the tendency for these movement trajectories to recur. Task manipulations, on the other hand, increased the intermittency of fingertip dynamics, which suggests that individuals were more tolerant of random fingertip displacements when the task was performed while standing relative to sitting. An intermittent balancing strategy might minimize the computational burden associated with stabilizing the pole.

## **3.2 – INTRODUCTION**

Complex perceptual-motor tasks such as pole balancing have received experimental and theoretical attention because they are representative of how the central nervous system (CNS) interacts with and controls unstable objects (Foo et al. 2000; Cabrera and Milton 2002; Mehta and Schaal 2002; Cabrera and Milton 2004a, b). Two competing perspectives have emerged for the neural control of pole balancing.

Computational approaches have argued that the CNS employs internal forward models for the neural control of pole balancing. The premise is that predictive control can help circumvent sensorimotor processing delays to produce the short latency movements required to stabilize the upright pole position (Mehta and Schaal 2002; Wolpert et al. 2002). An alternative argument, however, is that the stability of the inverted pendulum dynamics may emerge as a consequence of the stochastic properties of motor control (Cabrera and Milton 2002). In support of this argument, behavioural data have shown that > 98% of fingertip movements occur on timescales that are shorter than estimated human voluntary control delays (Cabrera and Milton 2002). Numerical analyses have since shown that balance can be facilitated in time-delayed systems if the dynamics are tuned such that small, stochastic displacements force the angular stick trajectory back and forth across the vertical on short timescales (Cabrera and Milton 2004a, b). Intermittent control might be favourable for the stabilization of time-delayed systems, since in comparison to continuous control, the computational burden would be minimized (Milton et al. 2008).

In support of the latter argument, we previously quantified decay exponents ( $\alpha$ ) and truncation for the distribution of fingertip speed changes in pole balancing (Cluff and Balasubramaniam 2009; Cabrera and Milton 2004a). We found that successive

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differences in fingertip speed were Lévy distributed and that learning caused an increase in the probability of large fingertip speed steps (Cluff and Balasubramaniam 2009). The observed decrease in the  $\alpha$ -parameter of the Lévy distribution reflects tolerance to fluctuations in the position of the pole over the course of learning. In other words, following extensive practice, large excursions of the fingertip are probabilistically rare, but enacted more frequently than in early-learning. These large amplitude corrections are initiated only when stability is threatened, as opposed to early in the course of learning, when fingertip excursions are performed continuously. Learning, in the context of the pole balancing task, can be characterized by changes in the statistical properties of movement kinematics.

The first goal of this study was to perform a detailed investigation of the Lévydistributed dynamics of pole-balancing fingertip trajectories. To investigate, we applied recurrence quantification analysis (RQA) to the fingertip displacement time series recorded during pole balancing (Webber and Zbilut 1992; Webber and Zbilut 2005). The objective was to substantiate the link between the gross statistical properties of movements and the time series dynamics of individual performances. This study was motivated by our previous work (Cluff and Balasubramaniam 2009), which demonstrated that individuals became tolerant of large amplitude fingertip displacements with pole balancing experience. This tolerance reflects an increased robustness to perturbations, a form of dynamical stability that is captured by the RQA variable  $L_{max}$  (this and the other RQA variables mentioned here are described in detail below). Therefore, we predicted that  $L_{max}$  would increase over the course of learning to reflect sensorimotor skill acquisition. The increase in the relative frequency of large fingertip excursions might also

be reflected in the magnitude of the variable TREND, which measures nonstationarity. In addition, RQA provides a method for quantifying change in the degree of relative determinism versus stochasticity (%DET) embedded in pole-balancing fingertip dynamics—a characteristic of the dynamics that might be expected to change over the course of learning (cf. Mitra et al. 1998; Riley et al. 1999; Balasubramaniam et al. 2000; Balasubramaniam and Turvey 2000). Finally, RQA provides a set of measures capable of indexing intermittency in the control enacted in pole balancing, including %LAM,  $v_{max}$ , and TTIME.

The second goal of this study was to determine the effects of available biomechanical degrees of freedom (DOF) for balancing, since previous research has shown that learning is accompanied by the progressive recruitment of biomechanical degrees of freedom (Vereijken et al. 1992a, b; Vereijken et al. 1997). These findings follow from Bernstein's stages of motor learning, whereby early learning is most aptly characterized by constraining degrees of freedom and eliminating motor redundancy. Effectively, this strategy translates to readily manageable, rigid patterns of movement. Practice tends to release restrictions, as degrees of freedom become organized in a coordinative unit that exploits the reactive forces of the task dynamics (Bernstein 1967).

*Quantifying Time Series Dynamics.* RQA is a nonlinear time series analysis that quantifies several dimensions of the time evolution of a signal. Importantly, RQA makes no assumptions about the statistical distribution or stationarity of time series and is wellsuited for the analysis of short time series. For detailed reviews of RQA including practical tutorials see (Pellechia and Shockley 2005; Webber and Zbilut 2005; Marwan et al. 2007).

The first step in RQA is to determine how frequently the movement trajectory revisits locations in reconstructed phase space (i.e., how frequently states recur). This is captured by the RQA variable %REC. Reductions in %REC reflect a decrease in the regularity of the system's behaviour—the system less frequently revisits states that it previously visited. The patterns of recurrence can then be used to quantify the dynamical structure of the time series as characterized by the following RQA variables.

%DET is the percentage of recurrent points that form diagonal lines in the recurrence plot of minimal length  $l_{min}$ . The rationale for %DET is that un- or weakly correlated stochastic processes (probabilistically) elicit many isolated recurrent points. Deterministic dynamics, however, manifest as longer diagonals and fewer isolated recurrent points (Marwan et al. 2007). As such, %DET reflects the deterministic (predictable) structure of the dynamics.

The maximum length of diagonal lines in the recurrence plot, excluding the main diagonal (where i = j and the distance between points is by definition zero) defines the  $L_{\text{max}}$  parameter.  $L_{\text{max}}$  is inversely proportional to divergence and thereby quantifies the dynamical robustness to perturbation (or to a change in initial conditions), since it approximates the lowest limit of the sum of positive Lyapunov exponents (Trulla et al. 1996; Gao and Cai 2000).

Entropy (ENT) is the Shannon entropy for the distribution of diagonal line segment lengths from the recurrence map. The ENT parameter quantifies complexity in the deterministic structure embedded in the signal (Webber and Zbilut 1992). Greater values of ENT indicate increased complexity (i.e., for uncorrelated noise, ENT is small, indicating low complexity).

Laminarity (%LAM) is analogous to %DET but measures the percentage of recurrent points forming vertical (with minimum length  $v_{min}$ ) rather than diagonal lines. %LAM quantifies the local time relationship between close trajectory segments (Marwan et al. 2002; Marwan and Kurths 2005) by demarcating time intervals where the state is relatively constant compared to intervals of sudden bursts of activity—a hallmark of intermittent systems (Marwan et al. 2005; Marwan et al. 2007). Recently, Kuznetsov and Riley (2010) used %LAM to distinguish between force production tasks where feedback modulated the intermittency of the enacted control.

Directly related to the %LAM parameter is the trapping time (TTIME), which quantifies the average length of vertical structures in the recurrence matrix. TTIME estimates the mean time (in samples) the system abides at a specific state—the average time for which the state is trapped. The final measure which considers vertical line structures from the recurrence map is the maximal length of vertical lines,  $v_{max}$ , which is analogous to the  $L_{max}$  measure for diagonal line structures.

In this study we present a reanalysis of data collected for a pole-balancing learning study (Cluff and Balasubramaniam 2009) that investigated how the statistical properties of pole-balancing kinematics were influenced by learning (Cluff and Balasubramaniam 2009). Participants learned to pole balance over three experimental sessions that spanned two weeks. Balancing performance improved progressively over the course of learning, as evidenced by an increase in the average time spent balancing in each trial. Experimental constraint of the available biomechanical degrees of freedom for balancing also influenced performance. Pole balancing was facilitated by the availability of biomechanical degrees of freedom, i.e., in the standing relative to sitting condition. In our previous study, we demonstrated that sensorimotor skill acquisition led to changes in the decay parameter for the probability of fingertip speed step sizes, which translated to tolerance for large, noisy pole displacements. In this experiment we use RQA to determine whether the evolution of fingertip displacement dynamics was modulated by motor learning and task-level balancing constraints.

### 3.3 – METHODS

Six healthy subjects (2 males, aged 26–28 years; 4 females, aged 23–27 years) participated in this study. Subjects were members of the Sensorimotor Neuroscience Laboratory. Participants had normal or corrected to normal vision and were free of neuromuscular and musculoskeletal disorders at the time of data collection. All procedures were performed in accordance with the Declaration of Helsinki. The protocol was approved by the University of Ottawa ethics review board and subjects provided written informed consent prior to the experiment.

Motion capture was performed with 8 VICON MX-40+ infrared cameras sampled at 500 Hz (Denver, CO, USA). Three dimensional pole kinematics were recorded using two spherical reflective markers (14 mm diameter) attached to the top and bottom of the pole with double-sided adhesive. Data acquisition was performed with the VICON Workstation software (v 4.6) and the marker trajectories were reconstructed and processed offline.

Subjects balanced a cylindrical wooden dowel (length 62 cm, diameter 0.635 cm, mass 50 g) in two experimental conditions: sitting and standing. Sitting trials were performed with subjects seated comfortably in a chair at their preferred seat height. Subjects were instructed to maintain contact with the backrest. In the standing condition, the subjects

balanced the pole with their feet approximately shoulder width apart and were free to move the upper body while keeping their feet stationary. When foot movement occurred, the trial was excluded from subsequent analysis.

This study employed a learning protocol. Subjects learned to pole balance over a twoweek period. Data collection occurred on the first day, followed by collection every fourth day. The presentation of trials was blocked by condition and counterbalanced across subjects. Subjects practiced pole balancing for 30 min per day (15 min per condition) between experimental sessions, distributed according to their preference. We did not enforce a predetermined learning regimen (i.e., massed vs. distributed practice).

RQA was implemented with the RQA software suite (v13.1; Webber 2009). We determined the embedding delay ( $\tau_e$ ) and dimension ( $D_e$ ) from a representative sample of trials using average mutual information (AMI) and false nearest neighbours (FNN) analysis. The embedding delay ( $\tau_e$ ) was the first minimum of AMI for the finger displacement series. The embedding dimension  $D_e$  was the dimension at which FNN were minimum (1% considered acceptable), which signifies the attractor has been sufficiently unfolded in the reconstructed phase space. The embedding delay parameters ranged from 34 to 108 samples, whereas the embedding dimensions ranged from 3 to 7. We used the median embedding delay  $\tau_e = 62$  samples and dimension  $D_e = 4$  for RQA. The line parameter, which specifies the number of successive points defining a line segment, was set to 5. We chose the more conservative line parameter to avoid saturation of %DET and a subsequent ceiling effect. The distance matrix was computed from the Euclidean distance between points, with the recurrence radius ( $\chi$ ) set to 10% of the mean distance between points. RQA was performed for fingertip time series in the transverse plane *x* and *y*-axes. Results for the *y*-axis fingertip trajectories are reported here since the *x*-axis displacements provided nearly identical results.

Dependent variables were contrasted with session (3) and condition (2) as independent factors using separate  $3 \times 2$  ANOVAs with repeated-measures. Post hoc analyses were performed using paired *t*-tests with Bonferonni corrections. The significance level for statistical contrasts was  $\alpha = 0.05$ .

### 3.4 – RESULTS

%REC (Fig. 3.1) was dependent on learning, F(2, 10) = 12.751, p < 0.01, and was significantly greater in Session 1 (M = 1.33, SE = 0.28) relative to Session 3 (M = 0.58, SE = 0.19), p < 0.05. %REC was also larger in the second (M = 0.90, SE = 0.19) relative to third session, p = 0.008. %REC was not different between Session 1 and 2 (M = 1.24, SE = 0.24).

 $L_{\text{max}}$  (Fig. 3.2) was influenced by learning, F(2, 10) = 9.10, p < 0.01.  $L_{\text{max}}$  was significantly larger at the third (M = 2356.60, SE = 434.76) relative to both first (M = 1619.36, SE = 376.05) and second sessions (M = 1354.86, SE = 267.73), p < 0.05.  $L_{\text{max}}$  was also dependent on condition, F(1, 5) = 4.98, p < 0.05, with greater maximum diagonal line length in the standing (M = 2270.85, SE = 420.19) relative to sitting (M = 1403.02, SE = 277.72) condition.



**Figure 3.1.** %REC was dependent on learning and the balancing condition. a) %REC decreased progressively across the training period (Session 1-3). b) %REC was greater in the seated relative to standing condition, which reveals greater tendency for the dynamic to revisit local neighbourhoods in phase space.

There was also a significant session × condition interaction F(2, 10) = 5.386, p < 0.05. The interaction showed that  $L_{max}$  was similar between conditions at the outset of learning, but increased disproportionately in the standing relative to sitting condition. Following learning, the dynamical stability of fingertip movements was greater when the task was performed while standing.

ENT was dependent on the condition for balancing, F(1, 5) = 27.97, p < 0.01. ENT was significantly greater in the standing (M = 4.71, SE = 0.12) relative to sitting condition (M = 4.18, SE = 0.21). Fingertip displacement series were nonstationary in the pole balancing task and the TREND variable was dependent on condition, F(1, 5) = 7.59, p < 0.05. Nonstationarity was greater in the sitting (M = -18.75, SE = 8.08) relative to standing condition (M = -8.13, SE = 4.43).

%LAM was influenced by condition, F(1, 5) = 20.32, p < 0.001, with significantly greater %LAM in the standing (M = 55.51, SE = 4.16) relative to sitting (M = 35.70, SE = 4.16) condition.  $v_{\text{max}}$  was also dependent on condition, F(1, 5) = 106.57, p < 0.001, with significantly greater vertical line length in the standing (M = 21.94, SE = 1.88) relative to sitting condition (M = 14.65, SE = 2.26), p < 0.01. Finally, TTIME was dependent on condition, F(1, 5) = 32.60, p < 0.01. TTIME was significantly greater in the standing (M= 7.35, SE = 0.37) relative to sitting condition (M = 6.05, SE = 0.41). Taken together, the latter three results indicate more intermittent control when the task is performed while standing.



**Figure 3.2.** At the outset of the learning protocol,  $L_{max}$  was similar between standing and sitting conditions, which suggests the dynamic was equally stable between conditions. With the development of expertise,  $L_{max}$  increased disproportionately in the standing relative to sitting condition. \* p < 0.05; \*\* p < 0.01.

### 3.5 – DISCUSSION

The purpose of this study was to determine whether fingertip dynamics were influenced by learning in the pole-balancing task. This study follows from previous work carried out in our laboratory (Cluff and Balasubramaniam 2009). RQA revealed a number of changes in the dynamics of fingertip displacements that occurred over the course of learning. RQA also revealed a number of effects related to the availability of biomechanical degrees of freedom for task performance.

%REC is a measure of temporal correlation. It reflects the tendency for points that over time return to the same local neighbourhood of the reconstructed phase space. %REC decreased progressively with learning, suggesting that temporal correlation in fingertip displacement series decreased with experience. Therefore, as participants became more experienced in balancing, the trajectories in the reconstructed phase space were less likely to repeat.

 $L_{\text{max}}$  is the maximum diagonal line length in the recurrence matrix (aside from the main diagonal, where i = j) and is proportional to the positive Lyapunov exponent (Trulla et al. 1996).  $L_{\text{max}}$  thereby quantifies the stability of the underlying dynamics. In this experiment,  $L_{\text{max}}$  increased with learning, reflecting sensorimotor skill acquisition, but the interaction was such that the learning effect for  $L_{\text{max}}$  varied idiosyncratically across conditions. The relative stability of pole-balancing fingertip dynamics was equal prior to experience, but increased disproportionately for the standing balance condition. This result supplements our previous findings whereby performance in the pole balancing task saw an overall improvement with learning but was greater in the standing condition (Cluff and Balasubramaniam 2009).

Over the course of learning, fingertip displacement trajectories were less likely to repeat overall, but repeating values in the trajectories presented as longer strings of recurrent points. Several previous studies have employed dynamical measures to characterize motor skill acquisition. Those studies have revealed findings such as reduced movement system variability over the course of learning (Mitra et al. 1998; Newell and Vaillancourt 2001; Ko et al. 2003; Chen et al. 2005). Mitra et al. (1998) have also demonstrated that continued skill refinement led to further decreases in dynamical noise, which endured after the system dimensionality had stabilized. Broadly speaking, motor learning appears to involve the establishment and refinement of a stable dynamical structure for movement trajectory formation. Moreover, our finding that the stability of fingertip dynamics followed different learning trajectories suggests the availability of biomechanical degrees of freedom influenced the dynamical stability of fingertip displacements during pole balancing. These results suggest that control proffers from the motor abundancy that accompanies redundant biomechanical degrees of freedom (Bernstein 1967; Reisman et al. 2002a, b; Latash and Anson 2006). That is, the flexibility of abundant motor solutions leads to an increase in the stability of fingertip dynamics. *How is balancing affected by biomechanical degrees of freedom?* 

ENT, a measure of the complexity of the deterministic structure in the time series, was also greater in the standing relative to sitting condition, while TREND magnitude was greater in the sitting relative to standing condition. Additional biomechanical degrees of freedom for control led to stationary yet complex fingertip displacement dynamics. These results complement previous work (Cluff and Balasubramaniam 2009), which considered how the macroscopic variability of fingertip fluctuations in pole balancing was influenced

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by the availability of biomechanical degrees of freedom. Taking the results of these studies together, the increased variability in fingertip fluctuation magnitudes and  $L_{max}$  in the standing condition translate to increased probability for varied segment lengths, which is reflected as increased complexity by the ENT variable.

Our results demonstrate that %LAM,  $v_{max}$ , and TTIME, which index intermittency in the dynamics, were all larger in the standing relative to sitting condition. Collectively, these results suggest that the underlying control strategy is more intermittent for standing pole balancing, obviated by the relative amount of laminar phases in the observed dynamics. In other words, the system's propensity for intermittency was observed in relatively longer phases whereby the fingertip position was approximately constant. These results are consistent with a control mechanism that capitalizes on passive motor control dynamics and corrects for pole excursions only when these displacements threaten stability.

In summary, condition contrasts revealed drastic differences with regards to how biomechanical degrees of freedom affected performance. The %LAM,  $v_{max}$  and TTIME variables from RQA revealed that fingertip fluctuations were more intermittent in the standing condition. Intermittency in the dynamics reflects greater relative contribution from small amplitude, random fluctuations on fast timescales (passive vs. active dynamics). These results both corroborate and extend our previous work, which demonstrated that skill acquisition in the pole balancing task is reflected by the statistical properties of fingertip movement kinematics (Cluff and Balasubramaniam 2009).

The motivation for this research was to determine how the dynamical structure of fingertip fluctuations evolved with learning, and moreover, to determine how this might

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have contributed to improved balancing performance. To address this purpose, we analyzed our data using recurrence quantification analysis (RQA) and provided significant insight on the dynamical changes that accompanied learning. We also determined how fingertip fluctuations varied in response to the manipulation of biomechanical degrees of freedom for balancing. Learning was accompanied by the increased stability of movement trajectories despite a reduction in the tendency for movement trajectories to recur. Task manipulations, on the other hand, resulted in intermittent fingertip dynamics, which suggests that individuals were tolerant of random fingertip displacements when the task was performed while standing relative to sitting. The intermittent strategy would minimize the computational burden associated with maintaining pole stability.

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Chapter 4 – Attentional Influences on the Performance of Secondary Physical Tasks During Postural Control

# 4.1 – ABSTRACT

We examined the influence of attention and cognitive load on the performance of a stick balancing task during the maintenance of upright posture. Dynamical analysis of posture and fingertip time series revealed the existence of a drift and correct balancing mechanism with correlational properties that reflected the demands of the stick balancing task. The manipulated attentional foci (internal, external) did not affect the variability of posture or fingertip trajectories. In contrast, the variability of posture and fingertip time series was reduced for dual-task cognitive-stick-balancing performance. We interpret our results from the perspective of dual-timescale motor control models and the adaptive resource model of attention allocation.

### 4.2 – INTRODUCTION

Control of the upright posture is a complex physical task that requires the appropriate assembly of physical degrees of freedom in joint-muscle space (Ting 2007). While maintaining balance, however, we frequently perform concurrent physical and cognitive tasks. Superordinate to the control of posture, these tasks have been referred to as suprapostural tasks (Stoffregen et al. 1999; Mitra 2003). The influence of suprapostural task performance on balance control has received considerable attention (see Balasubramaniam and Wing 2002 for review). Of particular interest has been to determine the influence of attentional focus on the performance of physical and cognitive tasks during upright standing.

Several studies have contributed to a generalized theory of the influence of attention on motor performance (see Wulf and Prinz 2001 for review). Emanating from this research, the "constrained action" theory proposes that attention devoted to movement execution (i.e., internal focus) interrupts the automaticity of performance. A reproducible finding has been that the variability of motor performance is dependent on whether attention is devoted to motor execution or outcome (Wulf et al. 2001; McNevin and Wulf 2002). Within this body of research, a consistent finding has been that an external focus, defined as attention devoted to motor outcome, stabilizes performance. In contrast, an internal focus, where attention is directed to motor execution, inhibits learning and performance (Shea and Wulf 1999; McNevin et al. 2003). The stabilizing external focus is thought to minimize interference between conscious intervention and the automaticity of motor performance, which allows the motor system to self-organize more effectively (Wulf et al. 2001). Motor automaticity (Milton et al. 2004) has been supported by

reduced probe reaction times, which suggests that resource competition is reduced when the focus of attention is external (Wulf et al. 2001).

The attention–performance relationship can be investigated by experimental paradigms that impose cognitive (Lajoie et al. 1993; Dault et al. 2001; Doumas et al. 2009) or physical task load (Riley et al. 1999a, b). These studies have demonstrated that postural and suprapostural task performance, quantified in terms of posture and movement variability, are dependent on whether the focus of attention is internalized or externalized (Wulf et al. 2003). Furthermore, the prioritization of postural or suprapostural task performance is dependent on the congruency of task goals (Balasubramaniam and Turvey 2000; Balasubramaniam et al. 2000). A very good paradigm for studying the postural effects of attention and physical task performance is the stick balancing task.

Human stick balancing kinematics show complex, multi-scale dynamical properties (Milton et al. 2009a; Cluff and Balasubramaniam 2009). It has been shown that stick fluctuations with respect to the vertical conform to a generalized scaling law that is characteristic of on–off dynamical intermittency (Cabrera and Milton 2004). Dynamical intermittency reflects a discontinuous control mechanism that is characterized by periodic switching between approximately constant dynamical states and large-scale corrective movements. With experience, fingertip trajectories become less correlated but are convergent (within the recurrence radius  $\chi$ ), which demonstrates that stochastic fluctuations reflect and contribute to the performance stability (indexed by mean balancing time) that is acquired with stick balancing expertise (Cluff et al. 2009).

Here we examined the influence of attention on the statistical stability (movement variability) of fingertip (FINGER) and center of pressure (COP) trajectories in experienced stick balancers. Subjects balanced a wooden dowel on the index finger. We implemented the internal focus of attention by instructing participants to minimize fingertip displacements when stick balancing. In contrast, we implemented the external, task-relevant focus by instructing subjects to minimize stick deviations from the upright position. Finally, we implemented an external, task-irrelevant focus by imposing concurrent cognitive load in the form of a serial arithmetic task.

The attention-performance relationship was delineated through a series of experimental conditions that differed in terms of instructed foci. These tasks constituted dual-task suprapostural and postural performance (P-SBEXT: posture-stick balancing, externalized focus; P-SBINT: posture-stick balancing, internalized focus). We also implemented a triplicate condition through conjoint posture, stick balancing and cognitive task components (P-SB-CDT). The imposed cognitive task was motivated by evidence that cognitive load increases stick balancing survival times (Milton et al. 2008a). We also took into consideration that the acquisition of stick balancing expertise is characterized by stochastic fingertip deviations—the control is discontinuous and characterized by ballistic corrections (Milton et al. 2008a; Cluff et al. 2009). Fingertip deviations therefore show dynamical properties on distinct timescales. For short timescales, fingertip deviations fluctuate about a drifting equilibrium, but are corrective over longer timescales. We know little about whether cognitive load influences the stochastic (fluctuations) or deterministic component of serial fingertip and center of pressure increments. The purpose of this study was to determine the influence of focus of attention

and cognitive load on postural and suprapostural task performance. We also questioned whether suprapostural activity would mediate the interplay between the deterministic and stochastic posture and fingertip components of stick balancing (Collins and De Luca 1994, 1995).

The congruency of the statistical (i.e., reduced variability) and dynamical stability of trajectories has been a subject of debate in motor control (cf. Riley and Turvey 2002). While some authors access stability through a nonlinear embedding technique that indexes the spatiotemporal variability and dynamical structure of time series data (Riley et al. 1999a, b), others argue for the spectral decomposition of position increments. Scaling laws from the double-logarithmic power spectrum–frequency relationship are used to infer dynamical stability (Delignières et al. 2006). Other authors support the information theory perspective and consider variable increments favourable due to the inherent generation of proprioceptive information (Riley et al. 1997a, b). Finally, variability is often considered favourable because it facilitates flexible sensorimotor performance (Freitas et al. 2005).

In this experiment, we sought to identify attentionally-mediated changes in the global spatial variability of stick balancing FINGER and COP trajectories. We modeled COP and FINGER dynamics as two-dimensional random walks to probe the mechanisms underlying performance variability. We chose statistical mechanics methods for this analysis (Mandelbrot and van Ness 1968; Collins and De Luca 1995). In such a way, we combine a line of work focused on the statistical stability of performance and a timescale-dependent dynamical analysis. This analysis determines distinct variability components by quantifying the magnitude of correlation in series—persistent (i.e., positively

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correlated) versus anti-persistent (i.e., negatively correlated) displacements—and the characteristic timescales on which they operate. Finally, these analyses were supplemented by the spectral decomposition of COP and FINGER time series. Based on previous work (Weeks et al. 2003; Milton et al. 2008b), we predicted that the variability of fingertip and COP trajectories would be reduced in the triple-task posture, cognitive and stick balancing condition—trajectories would be less persistent on short timescales. Finally, we hypothesized that the temporal coupling between the COP and fingertip position would change as a function of the attentional focus for balancing. Specifically, we predicted that the external focus would evoke a temporal COP-finger relationship whereby fingertip deviations were prioritized. To our knowledge, this is the first study to perform a mechanistic, dynamical analysis of the influence of attention an motor performance. Second, we investigated distinct timescales over which attentional influences might facilitate (external focus) or detract (internal focus) from performance.

### 4.3 – METHODS

Ten healthy subjects (7 men; 3 women; aged 19–27) from the McMaster University student community participated in this experiment. The participants were sport science graduate and undergraduate students recruited from a learning study that examined the acquisition of stick balancing expertise (Cluff et al. *in preparation*). Participants had normal or corrected vision, with no history of neurological or musculoskeletal disorder. The protocol was approved by the Institutional Review Board and the participants provided written informed consent prior to the experiment.

We recorded the position of the COP (ML; AP) with a dual force platform arrangement sampled at 750 Hz (AMTI OR6 2000, Newton, MA). The preferred standing

position for individual subjects, corresponding to their foot width and angle, was recorded on the force platforms to ensure the physical support was consistent between trials and conditions. Motion capture was performed with 10 VICON<sup>TM</sup> T-40 cameras sampled at 750 Hz (VICON<sup>®</sup> Motion Systems, Lake Forest, CA). The experimental data were collected in a single session (~30 min) in which subjects balanced a 62 cm long, 0.65 cm wide, and 50 g mass cylindrical wooden dowel on their index finger. We attached reflective spherical markers (14 mm) to the top and bottom of the wooden dowel for kinematic motion capture.

There were six experimental conditions: (1) Posture condition (P): postural fluctuations were determined from five quiet standing trials (30 s). Participants did not receive explicit attentional instructions for the P condition (e.g., minimize sway, be as still as possible). (2) The Posture-Cognitive Dual-Task (P-CDT) condition required that subjects perform six serial arithmetic operations (addition, subtraction), one computation per five-second interval, while maintaining upright stance. The subjects were given a number between 0 and 100 before each trial. When the trial began, a sequence of integer operations was performed over five-second intervals according to the method of Weeks et al. (2003). The arithmetic operations were performed silently, with the final response verbalized after trial completion. (3) Subjects balanced the stick in upright stance without having received explicit attentional instructions (P-SB). This condition served as our attentional control for stick balancing. (4) In the Posture-Stick Balancing External focus condition (P-SBEXT), we instructed the subjects to 'minimize deviations of the stick from the vertical'. (5) In contrast, we instructed the subjects to 'minimize hand and finger movement' in the Posture-Stick Balancing Internal focus condition (P-SBINT). The

attentional instructions used for P-SBEXT and P-SBINT conditions resembled those implemented by Wulf et al. (2004). (6) The influence of the Posture-Cognitive Dual-Task on stick balancing dynamics was determined through the outlined arithmetic task (P-SB-CDT).

We preserved the task difficulty between P-CDT and P-SB-CDT conditions by using the same integer operations. However, for the CDT condition, subjects began with the initial number from a P-SB-CDT trial, with the order of operations randomized. Randomizing the sequence of integer operations minimized learning of the cognitive task between conditions. An example series for the P-SB-CDT condition follows: 40 (before trial) + 5 (trial onset) – 7 (5 s) + 4 (10 s) + 8 (15 s) – 3 (20 s) – 9 (25 s) = 38 (30 + s). A randomized sequence for the P-CDT condition was 40 (before trial) + 8 (trial onset) + 4 (5 s) – 7 (10 s) – 9 (15 s) + 5 (20 s) – 3 (25 s) = 38 (30 + s).

We used the silent arithmetic paradigm to minimize articulatory confounds on postural dynamics (Yardley et al. 1999). Subjects were allotted a break (~30 s) between trials. If the subject dropped the stick and the trial was not completed, the data were excluded from the analysis and the trial was repeated. The P-SB condition was performed first to prevent confounds resulting from attentional instructions for balancing. The remaining conditions were block-randomized with MATLAB<sup>™</sup> (Mathworks, Natick, MA).

We determined the statistical stability of performance using the root-mean-squared (RMS) variability of transverse plane COP and FINGER trajectories. RMS COP was contrasted between postural (marginal mean; P & P-CDT) and stick balancing conditions (marginal mean; P-SB, P-SBEXT, P-SBINT, P-SB-CDT) (paired samples *t*-test, two-tailed) to quantify the magnitude of postural variability attributable to stick balancing

performance. The attentional and cognitive influences on COP and FINGER trajectories were determined using a one-way (4 levels: P-SB, P-SBINT, P-SBEXT, P-SB-CDT) analysis of variance (ANOVA) with repeated measures. Huynh–Feldt corrections were used to correct sphericity violations (Mauchly's Test, p < 0.05). The RMS FINGER variability was contrasted across conditions using a one-way ANOVA with repeated measures (4 levels: P-SB, P-SBINT, P-SBEXT, P-SB-CDT). Prior to the numerical analysis, the COP and FINGER trajectories were resampled using a non-overlapping, 10 sample moving average, for an effective sampling rate of 75 Hz.

The power spectral density (PSD) of planar fingertip and COP trajectories was computed for individual trials using a Welch periodogram with a (75 sample) nonoverlapping Hamming window. The mean power frequency (MPF) of COP and FINGER trajectories was determined by weighted average from the PSD, ensemble averaged for each condition and analyzed using the outlined statistical analyses.

Stabilogram-diffusion analysis was performed on planar COP and FINGER increments according to the method of Collins and De Luca (1994). The COP and FINGER trajectories were considered two-dimensional random walks, defined by their mediolateral and anteroposterior components. The two-point correlation function for the planar stabilograms,  $K(\tau)$ , was computed for the lag  $\tau$  on [0.1, 10] s by

$$K(\tau) = \frac{1}{N-m} \sum_{i=1}^{N-m} \left[ (x(t) - x(t+\tau))^2 + (y(t) - y(t+\tau))^2 \right],$$
 (Eq. 1)

where  $t = i\Delta t$  and  $\tau = j\Delta t$ .

The critical time ( $\tau_c$ ) was defined as the first instance the Hurst exponent crossed H = 0.5. The critical times were determined for individual subjects from the ensemble-averaged stabilogram-diffusion plots in each condition. The critical time,  $\tau_c$ , defines the boundary between persistent (positively correlated,  $H_s > 0.5$ ) and antipersistent (negatively correlated,  $H_l < 0.5$ ) dynamical regimes. A linear regression was applied to the double-logarithmic plots of  $K(\tau)$  COP and  $K(\tau)$  FINGER versus  $\tau$  on  $[0.1, \tau_c)$  and  $(\tau_c, 10]$  s. The best-fit short and long-range scaling exponents were divided by 2 for fractional Brownian motion to render  $H_s$  and  $H_l$ .

The linear cross-correlation function was computed between COP and FINGER positions for a representative subject. COP and FINGER time series were normalized on the interval [-1, 1]. The cross-correlation function  $z(\tau)$  was computed for transverse plane COP and fingertip trajectories over the lags [0, 3] s.



**Figure 4.1.** Representative COP and fingertip position time series for a single subject in the stick balancing external focus condition (P-SBEXT). Transverse plane a) COP and b) Finger stabilograms showing mediolateral (ML; abscissa) and anteroposterior (AP; ordinate) time series. c) AP COP, d) ML COP, e) AP fingertip and f) ML fingertip time series. Transverse plane Finger and COP position series are irregular and nonstationary for the displayed 30 s interval.

### 4.4 – RESULTS

Figure 4.1 shows representative COP and FINGER time series for a single subject in the stick balancing external focus condition (P-SBEXT). Transverse plane COP (Fig. 4.1a) and FINGER (Fig. 4.1b) stabilograms depict mediolateral (ML; abscissa) relative to anteroposterior (AP; ordinate) positions. The corresponding AP and ML COP (Fig. 4.1c, d) and FINGER time series (Fig. 4.1e, f) are depicted in the right column subplots. Transverse plane FINGER and COP position series are irregular and nonstationary for the displayed 30 s interval. The following results were determined from the transverse plane stabilogram (Fig. 4.1a, b).

#### Variability analysis

Sway variability was influenced by balancing condition (F(1.82,

16.39) = 5.85, p < 0.05,  $\eta^2 = 0.39$ ), as shown in Fig. 4.2a. Explicit attentional focus did not influence the sway magnitude (RMS COP), since spontaneous sway was similar between P-SBEXT and P-SBINT conditions (p > 0.05). However, sway variability was reduced by conjoint cognitive and postural-stick balancing performance. In that regard, RMS COP was reduced in P-SB-CDT relative to the P-SB (p < 0.05), P-SBEXT (p < 0.05) and P-SBINT (p < 0.01) conditions. The variability of fingertip trajectories (RMS FINGER) was also affected by attentional instruction (F (3, 27) = 27.95, p < 0.001,  $\eta^2 = 0.76$ ; Fig. 4.2b). Fingertip displacements were least variable when performing the concurrent cognitive, postural and stick balancing task (P-SB-CDT; p < 0.05) and most variable in the P-SBINT condition (p < 0.05).



**Figure 4.2.** Task performance is dependent on the focus of attention for balancing. a) RMS COP and b) RMS FINGER were reduced in the stick balancing cognitive dualtask condition (P-SB-CDT). Of particular interest was the stabilizing effect of cognitive load for stick balancing performance. Finger trajectories were approximately half as variable in P-SB-CDT relative to other conditions. Error bars represent  $\pm 1$  standard error of the mean (SEM). \* p < 0.05, \*\* p < 0.01, \*\*\* p < 0.001. + P-SBINT > all other conditions (p < 0.05). † P-SB-CDT < all other conditions (p < 0.05).

#### Stabilogram-diffusion analysis

A representative subject, ensemble-averaged stabilogram-diffusion plot is depicted in Fig. 4.3 for both the posture (a) and fingertip (b) components of the stick balancing task. Figure 4.3 shows qualitative differences for the short-range scaling region and critical time (inflection) between incremental changes in the COP (a) and FINGER (b) position across balancing conditions. In contrast, the long-range scaling region was qualitatively similar for  $\tau > 1$  s.

The short-range scaling exponent for COP displacements,  $H_s$  COP, was influenced by condition ( $F(5, 45) = 2.99, p < 0.05, \eta^2 = 0.25$ ; Fig. 4.4a).  $H_s$  COP was reduced in the P-SB (marginal mean;  $H_s = 0.61$ ) relative to P and P-CDT conditions (marginal
mean;  $H_s = 0.69$ ) (p < 0.05). COP displacements were less persistent when stick balancing, which amounts to more stationary postural deviations.  $H_s$  FINGER was also dependent on condition (F(3, 27) = 7.48, P < 0.001,  $\eta^2 = 0.45$ ), as shown in Fig. 4.4d.  $H_s$  FINGER was similar between P-SB, P-SBEXT and P-SBINT conditions (p > 0.05). Cognitive load (P-SB-CDT) reduced the magnitude of serial correlation in fingertip trajectories (p < 0.05).



**Figure 4.3.** Double-logarithmic stabilogram-diffusion plots depicting a single subject, ensemble-averaged two-point correlation function  $(K(\tau))$  versus the time between observations  $(\tau)$ . a) COP and b) FINGER time series. Incremental changes in COP and FINGER position showed two distinct scaling regions in stick balancing. Stabilogram-diffusion analysis showed short  $(H_s)$  and long-range  $(H_1)$  scaling regimes, which characterize temporally-distinct persistent (drift) and anti-persistent (corrective) dynamical regimes separated by the critical time  $(\tau_c)$ .

The long-range scaling (Fig. 4.4b) exponent for incremental changes in COP position,  $H_1$  COP, was greater for the posture and posture-cognitive dual-task (P, P-CDT;  $H_1 = 0.24$ ) relative to stick balancing conditions (P-SB, P-SBEXT, P-SBINT, P-SB-CDT;  $H_1 = 0.11$ ) (p < 0.01). Therefore, the stringency of COP corrective displacements increased when stick balancing.  $H_1$  FINGER (Fig. 4.4e) was not affected by the balancing condition ( $F(3, 27) = 0.66, P > 0.05, \eta^2 = 0.07$ ).



**Figure 4.4.** Short ( $H_s$ ) and long-range ( $H_l$ ) scaling exponents revealed postural and stick balancing time series are composed of two distinct timescale components. a) Short ( $H_s$ ) and b) Long-range ( $H_l$ ) postural scaling exponents. d) Short and e) Long-range stick balancing scaling exponents. For short time intervals, incremental changes in COP and FINGER position were positively correlated (persistent), but negatively correlated for long intervals (anti-persistent).  $H_s$  was reduced for FINGER trajectories in the stick balancing dual-task condition (P-SB-CDT), resulting in more stationary time series. Surrogate analysis for both COP and FINGER trajectories revealed a single scaling region that was equivalent to classical Brownian motion ( $H \approx 0.5$ ). Error bars represent  $\pm 1$  SEM. + p < 0.05.



**Figure 4.5.** The critical time  $(\tau_c)$  for switching between a) posture (COP) and b) stick balancing (FINGER) regimes. Critical times for switching postural regimes were increased for stick balancing relative to the upright stance (P) and dual-task postural condition (P-CDT). Critical times were similar between P and P-CDT conditions. In contrast, the critical time for switching between FINGER regimes was reduced in the stick balancing cognitive task condition (P-SB-CDT). Error bars represent  $\pm 1$  SEM.

The critical time for switching postural regimes ( $\tau_c$  COP) was not dependent on the attentional focus for balancing, (*F* (3, 27) = 0.25, *p* > 0.05,  $\eta^2 = 0.03$ ). Critical times for switching between the drift and correct postural regimes were similar for P-SB, P-SBEXT, P-SBINT and P-SB-CDT conditions. However,  $\tau_c$  COP was reduced in the P and P-CDT (marginal mean;  $\tau_c$  COP = 0.44 s) relative to stick balancing conditions (marginal mean;  $\tau_c$  COP = 0.74 s) (*t*-test, one-tailed, *p* < 0.05). The critical time for switching fingertip regimes,  $\tau_c$  FINGER (Fig. 4.5), was dependent on condition (*F* (3, 27) = 3.22, *p* < 0.05,  $\eta^2 = 0.27$ ).  $\tau_c$  FINGER was reduced in the P-SB and P-SB-CDT relative to P-SBINT (*p* < 0.05) and P-SBEXT (*p* < 0.05) conditions. Consequently, the critical times were reduced when the attentional focus was non-specific (P-SB) and external, but task-irrelevant (P-SB-CDT).

We computed surrogate time series by phase-randomizing the COP and FINGER increments (Theiler et al. 1992). The two-point correlation function,  $K(\tau)$ , was computed for the surrogate series to determine whether the computed correlations were the artifact of the time series length or the distribution and amplitude of incremental changes in the COP and FINGER position. Linear regression on the double-logarithmic stabilogramdiffusion plot on  $\tau \in [0, 10]$  s revealed a single scaling region for the phase-randomized COP (Fig. 4.4c) and FINGER (Fig. 4.4f) displacement series,  $H_{surrogate} \approx 0.5$ , rendering increments equivalent to classical Brownian motion. Therefore, the computed short and long-range scaling regimes and critical times reflected distinct dynamical regimes and not artifact.

### Spectral analysis

The mean power frequency (MPF) of transverse plane COP displacements was dependent on the balancing condition (F (1.91, 17.22) = 28.184, p < 0.001). Summary statistics are depicted in Fig. 4.6. MPF COP was reduced in P (p < 0.01) and P-CDT relative to stick balancing conditions (p < 0.01), suggesting the spectral composition of COP time series was increased for the balancing task. MPF COP was greater in the P-SB and P-SBINT conditions relative to P-SB-CDT (p < 0.001), reflecting higher frequency composition. MPF COP was similar for the P-SBEXT and P-SB-CDT (p > 0.05). MPF FINGER was also dependent on stick balancing condition (F (1.82,

16.40) = 4.51, p < 0.05,  $\eta^2 = 0.33$ ). MPF was reduced in the P-SB-CDT relative to P-SB (p < 0.01), P-SBINT (p < 0.05) and P-SBEXT (p < 0.05) conditions.



**Figure 4.6.** Spectral decomposition of COP and fingertip time series. a) The mean power frequency (MPF) of COP trajectories was reduced in quiet stance relative to stick balancing conditions and in the stick balancing dual-task relative to control (P-SB) and attentional focus conditions (P-SBEXT, P-SBINT). The MPF of COP trajectories was reduced in P, P-CDT relative to suprapostural conditions. b) The MPF of FINGER trajectories was reduced in the stick balancing dual-task condition (P-SB-CDT) relative to control (P-SB) and focus of attention conditions (P-SBEXT, P-SBINT). Error bars represent ± 1 SEM.

## Linear cross-correlation analysis

Figure 4.7 demonstrates that the manipulation of attentional focus evoked differences in the dynamical relationship between COP and FINGER positions. For the P-SBEXT condition, the COP and finger position were negatively-correlated for lags  $\tau \in [0, 1.5]$  s, suggesting that COP lagged FINGER position. The externalized focus, whereby individuals focused on the stick position with respect to the vertical produced compensatory COP displacements over longer intervals  $\tau \in [1.5, 3]$  s. In contrast, the COP and FINGER position were positively correlated for lags  $\tau \in [0,3]$  s in the P-SB, P-SBINT and P-SB-CDT conditions. Positively correlated trajectories demonstrate that the FINGER and COP followed the same spatiotemporal pattern. The externalized focus, therefore, saw the emergence of a distinct postural-suprapostural dynamic.



**Figure 4.7.** Ensemble-averaged cross-correlation function  $z(\tau)$  between COP and FINGER positions for a representative subject. The cross-correlation function  $z(\tau)$  was computed using the transverse plane, normalized COP and FINGER trajectories and is plotted for the lags  $\tau$  on the interval [0,3] s. Experimental manipulation of the attentional focus evoked differences in the dynamical relationship between COP and FINGER position. COP and FINGER position were negatively-correlated in the P-SBEXT condition for lags  $\tau \in [0, 1.5]$  s, suggesting that the COP lagged the FINGER position. For the externalized focus condition, individuals focused on the stick position with respect to the vertical. Compensatory COP displacements were produced over longer intervals  $\tau \in [1.5, 3]$  s. In contrast, the COP and FINGER positions were positively correlated for lags  $\tau \in [0,3]$  s in the P-SB, P-SBINT and P-SB-CDT conditions. Positively correlated trajectories demonstrate that relative FINGER and COP displacements were in the same direction. Externalized motor attention caused the emergence of a distinct postural-suprapostural temporal dynamic.

## 4.5 – DISCUSSION

## *Stick balancing dynamics*

The purpose of this study was to determine the dynamical influence of attentional foci on the postural (COP) and suprapostural (fingertip) components of human stick balancing performance. We sought to determine whether two variants of an external focus of attention (task-relevant, P-SBEXT; task-irrelevant, P-SB-CDT), increased the stability of center of pressure and fingertip time series. In the task-relevant external focus, we instructed participants to minimize the vertical displacement of the stick. In contrast, in the task-irrelevant external focus (P-SB-CDT), the participants performed a serial arithmetic task while stick balancing. In addition to summary statistics (RMS variability), we analyzed the COP and fingertip trajectories by method of spectral analysis and statistical mechanics methods (Rougier 2008).

We hypothesized that both the postural and suprapostural components of stick balancing would be stabilized by a task-irrelevant, external focus of attention (P-SB-CDT). We predicted that an internal focus of attention would compromise dynamical stability in the stick balancing task, resulting in variable COP and FINGER trajectories. In confirmation of the hypothesis, FINGER and COP trajectories were least variable when participants partitioned attentional resources between stick balancing and cognitive task components (P-SB-CDT). In contrast, COP and FINGER displacements were least stable when the focus of attention was internal (P-SBINT). Performance stability for the external, task-relevant condition was similar to control performance (P-SB).

The stochastic nature of human stick balancing has been discussed at length. Studies have shown that the fingertip control mechanism for stick balancing is performed

according to a drift and correct (Milton et al. 2009b) mechanism that reflects the scaleinvariant properties of the central nervous system (Werner 2009). The proposed mechanism consists of small amplitude, correlated changes in fingertip position, interspersed with corrective, negatively-correlated displacements.

In accordance with the drift and correct balance control mechanism, our stabilogramdiffusion analysis demonstrated that incremental changes in fingertip (FINGER) position occur on distinct timescales. For short intervals ( $\tau < \tau_c$ ), incremental changes in fingertip position are positively correlated. Positively correlated increments imply that for short timescales sensorimotor control is open loop and the finger tends away from relative equilibrium. In contrast, for long timescales ( $\tau > \tau_c$ ), incremental changes in fingertip position reflect feedback-driven control where the finger tends to equilibrium.

A novel contribution of this study was the observed influence of attentional manipulation on fingertip dynamics. The correlation for short time intervals ( $H_s$  FINGER) was similar regardless of whether attention was internal or external, task-relevant. However, cognitive load (P-SB-CDT) reduced the magnitude of short-range serial correlation, which defines the stochasticity of fingertip displacements in terms of jump amplitude and frequency (Mandelbrot and van Ness 1968). Reduced persistence in series was accompanied by a reduction in the critical time for switching between open and closed loop balancing regimes ( $\tau_c$  FINGER) for the external, task-irrelevant condition. In effect, reduced persistence in series and shorter time for switching regimes amounted to a more stationary process when the attentional focus was external and irrelevant to task performance (P-SB-CDT). This result corroborates our result for time

series variability, where RMS variability was reduced when the focus for balancing was external and task-irrelevant (P-SB-CDT).

The lack of difference in the long-scale Hurst exponent establishes that a similar corrective process was employed for stick balancing regardless of the focus of attention. This result likely reflects the permissible range of upper limb deviations or 'dead zone' for threshold upper limb deviations (cf. Collins and De Luca 1994; Milton et al. 2009c). Nonlinear control models have been implemented for postural control (Milton et al. 2009a, b, c) and a manual, stance-controlled inverted pendulum task (Lakie and Loram 2006). Our data suggest the dynamical threshold for fingertip displacements changes as a function of attentional foci, but participants correct with similar stringency when the permissible range of motion is exceeded. At present, we do not understand the extent to which the threshold deviation represents upper limb biomechanics (range of motion), sensory or central components (Mergner et al. 2001).

The mean power frequency of displacements was reduced in P-SB-CDT relative to all other conditions and reflects a slower dynamic. Fingertip dynamics for stick balancing were characterized by reduced frequency, reduced amplitude displacements with incremental changes in position that were only weakly correlated over short timescales for the external focus task-irrelevant condition. Regardless of the attentional condition, the long-range correlations in time series were very anti-persistent.

These results do not directly support the constrained action theory for motor performance (Wulf et al. 2004). Specifically, this theory predicts decreased variability, increased frequency components when the focus of attention is external and task-relevant, and increased variability, reduced frequency dynamics when attentional focus is internal.

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Though cross-correlation analysis demonstrated that a different dynamical relationship was evoked by the external, task-relevant focus, our data were inconsistent with the above predictions. This might represent the task familiarity of our participants and subsequent melding of the perceptual boundary to accommodate the balanced stick. This phenomenon is known as exproprioception (Maravita et al. 2002; 2003). It is important to consider the role of exproprioception with respect to constrained action theory. In studies that reported enhanced learning with external focus, the external/internal focus duality was established early in the learning process (McNevin et al. 2003). Additionally, most of the work related to the constrained action theory has dealt with tasks where the line between the actor and the controlled object is well defined. Hence, the manipulation of the attentional focus did not have to deal with issues of exproprioception. Future work should examine this issue in the context of the interplay between task familiarity, attentional focus and performance.

Our observation that performance was facilitated by the cognitive task corroborates the stabilizing effect of an external, task-irrelevant focus (Weeks et al. 2003). The benefit of the task-irrelevant focus is further supported by literature regarding sensorimotor expertise (Milton et al. 2008b; Beilock et al. 2002). Less experienced balancers are unlikely to benefit from an external, task-irrelevant focus (Milton et al. 2008b). *Postural Dynamics* 

COP displacements were more variable and composed of higher frequency components when stick balancing. In addition, the relative scaling of postural regimes was influenced by the stick balancing task. COP displacements were less correlated over short intervals, but more correlated for long intervals when stick balancing. Critical times

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for switching between short and long-range postural regimes increased when stick balancing but were similar regardless of the attentional condition. Postural corrections were therefore performed at longer timescales when stick balancing. For a given serial correlation, if the system drifts for prolonged time, the tendency is to migrate toward the support boundary. Corrective movements, when performed, prevent destabilization resulting from the COP traversing the base of support. When stick balancing, critical times increased and translated to a concomitant increase in the degree of anti-persistence. The degree of anti-persistence observed for COP increments in stick balancing ( $0 < H_l$ << 0.5) approaches the scaling exponent expected if the support boundary had been attained ( $H_l \approx 0$ ; Collins and De Luca 1994). These results are consistent with the facilitatory viewpoint of postural control, which considers sway subservient to suprapostural task performance (Stoffregen et al. 1999). Our results, therefore, recapitulate the importance of context in the optimal assembly of postural synergy (Balasubramaniam and Turvey 2000; Todorov and Jordan 2002).

We did not observe differences in postural dynamics when performing a cognitive dual task (P-CDT). This effect is not surprising, since postural control in healthy individuals is robust to secondary cognitive demand (Dault et al. 2001), and the efficiency of resource allocation to postural and cognitive task components reflects several factors. Consequently, perturbed (Pellecchia 2003), stabilized (Andersson et al. 2002) and unaffected (Dault et al. 2001) stability have been reported in dual-task paradigms. In our experiment, the participants performed a silent arithmetic task in a stable, well-learned postural context. Consequently, the neural pathways subservient to

balance were likely relegated to low-level reflexive and compensatory mechanisms (Torres-Oveido et al. 2006).

In our experience (Cluff and Balasubramaniam 2009; Cluff et al. 2009), skilled stick balancers use one of three balancing strategies. Proficient stick balancers position the hand so that it is either possible to see both the tip of the stick and hand simultaneously or, conversely, the hand is positioned sufficiently close to the body that it is possible to see only the tip of the stick. An intermediary strategy reflects a combination of the two. An elaborate methodology would be required to assess eve-hand coordination in stick balancing (Hayhoe and Ballard 2005) and is interesting topic for future research. We are confident, however, that our results reflect attentionally-mediated task dynamics and not a generalized inability to maintain the instructed attentional foci. Figure 4.7 shows a representative, ensemble-averaged cross-correlation function between radial COP and finger position for P-SB, P-SBEXT, P-SBINT and P-SB-CDT conditions. That COP and finger position were negatively correlated for lags  $\tau \in [0, 1.5]$  s suggests the COP lagged fingertip displacement—individuals focused on stick movement with respect to the vertical and produced compensatory COP movement over longer intervals  $\tau \in [1.5, 3]$  s. Conversely, for P-SB, P-SBINT and P-SB-CDT conditions, COP and fingertip position were positively correlated for lags  $\tau \in [0, 3]$  s, which suggests that finger and COP displacement paralleled one another. Consequently, the external focus, task-relevant condition saw the emergence of a balancing strategy that prioritized stick movement.

It is important to consider focus of attention in the context of Bernstein's ideas on expertise and its development (see Latash and Turvey 1996 for a review). While actors focus on moving body parts in the early stages of skill acquisition, attention shifts to

wielded objects in advanced stages of skill (Bernstein 1967). Advanced tennis players tend to focus on the ball or end point of the trajectory for a successful return, rather than the racquet or limb. In the stick balancing case, there is no clear boundary between where one ends and the other begins. A possible reason the instructed attentional foci did not reveal differences between the internal and external, task-relevant condition might reflect that the stick becomes an extension of the body as one acquires expertise (Maravita et al. 2003). Therefore, it is likely that motor attention more readily modulates the performance of novice stick balancers. We are currently exploring skill acquisition in stick balancing and its relationship to postural dynamics.

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Chapter 5 – Learning a Stick Balancing Task Involves Task-Specific Coupling Between Posture and Hand Displacements

# 5.1 – ABSTRACT

Theories of motor learning argue that the acquisition of novel motor skills requires the task-specific organization of motor subsystems. Here we examined the development of motor subsystem interactions as subjects learned a novel stick balancing task. We focused on learning-induced changes in fingertip movements and body sway and investigated the effect of practice on their coupling. We hypothesized that learning would elicit common changes in posture and fingertip control and evoke systematic increases in the sophistication of the posture-fingertip interaction. We quantified motor learning using the average length of balancing trials, which increased with practice and confirmed that subjects learned the task. We demonstrated that stick balancing skill acquisition involved two independent learning processes. First, we found that posture and fingertip displacements are governed by intermittent control strategies and that the time interval between corrections increased systematically across training. The second learning effect involved the incremental occurrence and lengthened coupling of posture-fingertip trajectories. We have argued that the abrupt (de)coupling of posture-fingertip control suggests that the control mechanism for stick balancing is hierarchical and switches from coupled to independent subsystem control. An important research direction will be to specify the precise mechanism(s) that give rise to the abrupt (de)coupling of the posturefingertip interaction.

## **5.2 – INTRODUCTION**

The ability to perfect complex motor skills raises a number of questions about voluntary motor control and learning. In response to these considerations, experiments have investigated the control mechanisms that govern skilled motor behaviour with the objective to specify how these representations are learned. A standard approach has been to examine the coordination between end-effectors (Swinnen et al. 1997; Kelso and Zanone 2002), body segments (Bobbert and van Ingen Schenau 1988; Rodacki et al. 2001; Hong and Newell 2006), joint angles (Vereijken et al. 1997; Adamovich et al. 2001; Chow et al. 2007; Hatzitaki and Konstadakos 2007) and muscle activations (Ting and Macpherson 2005; Torres-Oviedo et al. 2006). These studies have established the importance of motor synergy (Bernstein 1967) and shown that motor variables are combined into coordinative relationships that facilitate task performance. Though the coordination dynamics approach has generated a great deal of knowledge about motor learning, in comparison we know very little about the dynamical interactions that evolve between distinct sensory (e.g., vision) and motor (e.g., posture, voluntary motor) subsystems.

Perhaps the importance of sensory-motor interactions is best illustrated by example. Consider a baseball player up to bat. Batting requires precise upper limb coordination to direct the bat to the location of the ball with proper timing. In addition, lower limb segments and postural control should be coordinated so that peak energy generation coincides with ball contact. Finally, visual information about the evolving ball trajectory and proprioceptive feedback about the orientation of the upper limb segments must be integrated and processed to enable rapid feedback-based swing corrections. In short,

batting performance is dependent on the distinct contribution of posture, sensory, and voluntary motor subsystems.

Task-specific subsystem interactions have been a topic of interest in motor control and learning (Bingham 1988; Bernstein 1996), and recently, Newell et al. (2001) have argued that outcome motor performance reflects an evolving set of hierarchically-organized motor subsystems. Their model distinguished between: (1) physiological microphenomena (e.g., electromyography, cortical activity), (2) subsystem coordination (e.g., posture and limb movement patterns) and (3) outcome performance. Newell et al. (2001) have proposed that reciprocal coupling functions exist between levels of the motor hierarchy so that individual effectors are organized into functional subsystem interactions that support outcome performance.

The hierarchical structure and time scale specificity of motor learning were recently investigated by Huys et al. (2003, 2004a, b) in a series of experiments that examined learning-induced changes in coupling between posture, vision, and hand movements in three-ball cascade juggling. During practice, the coupling between center of pressure and vertical ball displacements increased progressively in strength (Huys et al. 2003) and similar relationships were present between ball and point of gaze adjustments (Huys et al. 2004a). Collectively, these studies demonstrated that skill acquisition is influenced by interacting subsystems and show that object manipulation tasks can provide key insight about motor subsystem coupling when the physics and temporal properties of limb movements are dependent on an evolving and circumstantial task demand (Dingwell et al. 2002; Nagengast et al. 2009).

In this experiment, we investigated skill acquisition in a novel stick-balancing task. Stick balancing requires that the central nervous system plan and generate appropriate time-varying positions of the hand in response to changes in the vertical angle of the stick. Initial studies have focused on finger and angular stick fluctuations to characterize the control principles underlying human interactions with unstable dynamical objects (Cabrera and Milton 2002, 2004; Cluff and Balasubramaniam 2009). Because the physics of the system are passively unstable and the time available to plan and execute corrections is limited, finger displacements are composed of a series of ballistic corrections (Milton et al. 2009; Cluff et al. 2009). Notwithstanding the scientific merit of these studies, the approach has been limited to processes that stabilize the vertical stick angle and we know little about the interaction between stick balancing corrections and the simultaneous control of posture. To account for this control duality, this study addresses the following questions: (1) "Is the acquisition of stick-balancing skill accompanied by the task-specific reorganization of postural control?" and (2) "What control mechanisms are used by the central nervous system to stabilize the upright posture and vertical stick angle, and are the control mechanisms influenced by learning?" These questions provide a much-needed focus on the role of (motor) subsystem interactions in motor control and learning.

To address these questions, we examined how learning affected correlative movement properties within (autocorrelation) and between (cross-correlation) posture and finger displacements. We defined learning as a relatively permanent change in the capability to perform the stick-balancing task (Schmidt and Lee 2005) and measured performance using average balancing trial lengths. We address two problems in this experiment. First,

we investigate whether learning influences the relationship between COP and finger trajectories. Second, we examine the temporal structure of finger-center of pressure (F-COP) trajectories to determine the effect of learning on dynamic posture-finger interactions. On the basis of our previous work (Cluff et al. 2009), we hypothesized that controlling finger displacements would become discontinuous, and additionally, that the average time interval between ballistic finger corrections would increase as a function of learning. We expected that learning-induced changes in finger displacements would require the modification of postural control, though we made no specific prediction about the time structure of these changes. Secondly, we hypothesized that learning would increase the confluence between center of pressure and finger displacements, which we measured using the occurrence and duration of coupled F-COP trajectories.

## 5.3 – METHODS

### **Subjects**

Eight (5 females, 3 males) healthy, university-aged subjects  $(24.5 \pm 2.35 \text{ years})$  of similar height  $(173 \pm 5.82 \text{ cm})$  and weight  $(67 \pm 9.4 \text{ kg})$  participated in the study. Prior to the experiment, the subjects reported to the Sensorimotor Neuroscience Laboratory for a briefing session that outlined the details of the study and time commitment. Subjects were right-handed, had normal or corrected-to-normal vision, and were free of musculoskeletal and neurological disorder. The protocol received ethical clearance from the McMaster University Research Ethics Board and subjects provided written informed consent. The subjects were remunerated for their time and were free to withdraw from the study without penalty. Every subject completed the experiment.

## Protocol

The subjects learned to balance a cylindrical wooden dowel on their fingertip while standing in an upright posture. The subjects performed 30 min of daily practice and we maintained a log to ensure that each subject satisfied the practice schedule. We monitored motor learning using four experimental sessions that we conducted in place of every fifth practice session (90 min).

Each subject performed twenty stick balancing trials during the recruitment session to ensure they were familiar with the task. The trials were separated into two blocks of ten trials in which subjects balanced a stick with different physical characteristics (length = 100 cm; diameter = 1.71 cm; mass = 150 g) than the stick used during the experiment and practice sessions (length = 62 cm; diameter = 1 cm; mass = 50 g). The familiarization task was less difficult owing to the inertia and mass of the stick, which increased tactile feedback and the time available for the subject to make corrections. Subjects stood with their feet approximately shoulder width apart and we recorded their preferred stance to control the balancing stance across trials and learning sessions.

The experimental sessions consisted of twenty trials (2 blocks  $\times$  10 trials) that ended when the subject dropped the stick. At the outset of each trial block, we instructed the subjects to balance the stick for as long as possible and to remain stationary in their preferred stance. If this criterion was not met, the trial was excluded from further analysis and data collection was repeated for that trial. The trial blocks were separated by 5 min and individual trials by a 30-s rest period. The rest breaks could be supplemented to alleviate temporary discomfort due to visual strain, and physical or attentional fatigue.

## Equipment and Apparatus

Spherical reflective markers (14 mm) were attached to the top and bottom of the stick and the three-dimensional marker positions were collected at a sampling rate of 750 Hz using 10 VICON T-40 cameras (Lake Forest, CA). The reflective markers were autolabeled and reconstructed offline with the VICON Nexus software. COP time series and vertical ground reaction forces were collected using two adjacent strain gauge force platforms sampled at 750 Hz (AMTIOR6-2000; Newton, MA, USA). The ground reaction force and center of pressure data were processed offline in MATLAB<sup>TM</sup> R2009a (The Mathworks, Natick, MA, USA) using the method outlined by Winter (2009).

## **Dependent Measures**

## Mean Balancing Time

Mean balancing time was computed as the within-subjects average of trial lengths performed in each learning session. Mean balancing time was used to infer changes in performance that occurred as a function of learning.

## (Cross-)Recurrence Quantification Analysis

(Cross-) recurrence quantification analysis was used to quantify change in the regularity and temporal structure of COP, finger and F-COP trajectories. We computed the recurrence rate (RR), laminarity (LAM), and trapping time (TT) of COP, finger and F-COP time series using (cross-) recurrence maps derived from individual trial time series.

We used RR to quantify regularity because it is an index that measures the tendency for trajectories to return to local neighbourhoods in phase space (cf. Marwan et al. 2007). Greater recurrence rate corresponds to greater correlation in time series. Though RR provides a global measure of correlation it is not sensitive to the temporal properties of

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the time series dynamics. To acquire information about the temporal structure of the dynamics, we used the LAM measure. LAM quantifies the density of recurrent points that form vertical line structures in the recurrence map-dynamical states that remain within neighbourhoods of phase space for finite time intervals. LAM measures the tendency for dynamical states to remain within the recurrence radius and thereby quantifies the tendency for the "smooth" time evolution of the dynamics (Zbilut et al. 2002; Marwan et al. 2007 for a detailed review). We used TT to quantify the average duration of laminar trajectory phases. Transitions between constant and fluctuating dynamics are a defining characteristic of intermittent dynamical systems (Marwan et al. 2007) that exhibit two states: (a) "Stasis" or "Off" regime: dynamical states are correlated and approximately constant for variable lengths of time, and (b) "Bursting" or "On" regime: dynamical states fluctuate and are only spuriously correlated over finite time intervals. Therefore, recurrence quantification analysis was used to provide information about learningmediated changes in posture and finger dynamics, and cross-recurrence quantification analysis was used to investigate the evolving interaction between posture and upper limb corrections.

We downsampled the COP and finger time series using a five-sample, windowedmoving-average with no overlap (effective sampling rate = 150 Hz) to minimize the numerical sensitivity of the phase space reconstruction method to measurement noise. The first step in the phase space reconstruction was to compute the embedding delay ( $\tau_e$ ). The embedding delay was determined using the first minimum of the time-delayed average mutual information function (Fraser and Swinney 1986) computed for individual trials. The time delay ( $\tau_e$ ) corresponding to the minimum mutual information was selected

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because it is the best approximation to the critical system delay. Median embedding delays were contrasted using a one-way analysis of variance (ANOVA) with repeatedmeasures over the session factor (4 levels). Statistical analysis demonstrated that the median embedding delays were similar between sessions (p > 0.1) and we used the pooled median embedding delay for phase space reconstruction.

The second step was to determine the appropriate embedding dimension for phase space reconstruction. The embedding dimension was determined by the false nearest neighbours method (Kennel et al. 1992; Abarbanel 1996). False nearest neighbours analysis can be summarized as follows. Suppose the minimal sufficient embedding dimension for a given time series is  $D_e$ . Then, in a  $D_e$ -dimensional delay space, the topological properties of the phase space are preserved and the neighbours of a given point in phase space are mapped onto equivalent neighbours in delay space. In contrast, suppose the time series is embedded in a D-dimensional delay space with  $D < D_e$ . When the embedding dimension is not sufficient, the topological properties are not preserved and the dynamics are projected onto regions of phase space where they do not belong. We used a 1% tolerance and computed the embedding dimension for individual trials. The embedding dimension was contrasted using a one-way ANOVA with repeatedmeasures over the session factor (4 levels).  $D_e$  was not significantly different across sessions (p > 0.05). Therefore, we used the pooled median embedding dimension (Table 5.1). Cross-recurrence quantification analysis between fingertip and postural trajectories was performed using the same method.

The line parameter, which specifies the number of successive points required to define a line segment in reconstructed phase space, was set to 33.3 ms (5 points). (Cross-)

Recurrence quantification analysis was implemented with the Commandline Recurrence software (version 1.13z; Marwan 2006). The median embedding delay ( $\tau_e$ ), embedding dimension ( $D_e$ ), and (cross-) recurrence radii ( $\chi$ ) for individual subsystem (COP and finger) and collective dynamics (F-COP) are reported in Table 5.1.

## Dynamical Intermittency Analysis

Identical numerical procedures were used to analyze finger, COP and F-COP trajectories, but for the sake of brevity only procedures for the analysis of COP trajectories are outlined in this section. It should be noted; however, that prior to the analysis of F-COP trajectories, we were required to compute the scalar product F-COP time series. F-COP time series were computed for individual trials as,  $r_{\text{F-COP}(j)} = F_j \text{COP}_j$ , where  $F_j$ 

corresponds to the radial finger position,  $\text{COP}_{j}$  represents the radial COP at point j = 1, 2, 3, ..., n, and n was the length of the data series. We used the scalar product to quantify changes in the interaction between center of pressure and finger trajectories. Our rationale can be explained as follows: simultaneous changes in finger and COP time series would correspond to the smooth temporal evolution of the scalar product F-COP trajectory. Changes in independent subsystem dynamics would correspond to rapid and spurious fluctuations in the F-COP trajectory.

	Embedding delay $ au_e$ (ms)	Embedding dimension D <sub>e</sub>	Radius, χ (% MAXDIST)	Minimum line length LMIN
RQA COP	36	4	10	5
RQA Fingertip	45	4	10	5
CRQA	50	3	10	5

**Table 5.1.** Parameters for the phase space reconstruction and (cross-) recurrence quantification analysis. The embedding delay,  $\tau_e$ , was the first minimum of the average mutual information (AMI) function. The embedding dimension,  $D_e$ , was chosen as the dimension at which false nearest neighbors (FNN) were minimal. The threshold for neighborliness or radius,  $\chi$ , was chosen so that RR was between 1-3%.

We used the downsampled (by factor 5) COP time series for the dynamical intermittency analysis. The first step in the analysis was to compute the COP speed. We defined the COP speed as the resultant Euclidean speed,  $s_{COP}(t) \equiv ||(\vec{r}_{COP}(t + \Delta t) - \vec{r}_{COP}(t))/\Delta t||$ , where  $\vec{r}_{COP}(t)$  corresponded to the radial COP at time t,  $\vec{r}_{COP}(t + \Delta t)$  was the COP at time  $t + \Delta t$ ,  $\Delta t$  was the time step between successive observations (67 ms), and  $||\cdot||$  represented the Euclidean norm. The detrended COP speed,  $\Delta s_{COP}(t)$ , was computed as the two-point difference in COP speed,  $\Delta s_{COP}(t) = s_{COP}(t + \Delta t) - s_{COP}(t)$ , where  $s_{COP}(t + \Delta t)$  was the radial COP speed at time  $t + \Delta t$ , and  $s_{COP}(t)$  was the COP speed at time t. This expression removed time-dependent linear trends of duration  $\geq 67$  ms. To ensure the bins were adequately defined, the normalized histograms for laminar phases were reconstructed each subject's trials collected in a given experimental session.

Threshold crossing changes in COP speed were determined according to the expression  $\text{COP}(j) = \Theta(\varepsilon - |\Delta s_{\text{COP}}(j)|)$ , where  $\Theta$  was the Heaviside function and  $\varepsilon$  was the threshold change in COP speed, which we defined using the 95<sup>th</sup> centile root-mean-

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squared COP speed increment. Specification of the threshold COP speed is not a critical factor in the analysis but must permit detection of an adequate number of threshold crossings (Cabrera et al. 2004). We chose the 95<sup>th</sup> centile root-mean-squared COP speed increment to place our threshold in the tail region of the distribution of incremental changes in COP speed. According to our formula, subthreshold changes in COP speed were assigned a value of 0, while suprathreshold changes in COP speed were assigned a value of 0, while suprathreshold changes in COP speed were assigned a value of 1. Suprathreshold changes in COP speed correspond to ballistic COP corrections, while subthreshold changes in COP speed represent time intervals when the changes in COP speed are small ("off" dynamical regime, see the description of LAM and TT variables).

We determined laminar trajectory phases by computing the time intervals between successive threshold crossings. The probability of a given laminar phase,  $P(\delta t)$ , was determined by computing the normalized histogram of laminar phase lengths with bin size set to 10 ms. The power law exponent  $\alpha$  was computed by regressing  $P(\delta t)$  onto  $\delta t$  on two logarithmic axes according to the relationship,  $P(\delta t) \propto \delta t^{-\alpha}$ .  $\alpha$  determines the decay in the probability for laminar phase lengths: Reduced  $\alpha$ -values correspond to the greater tendency for long laminar COP trajectory phases and indicate that successive corrections are separated, on average, by longer time intervals. The bilogarithmic regression and numerical technique are shown in Fig. 5.1.



**Figure 5.1.** Numerical method used to compute the occurrence, time duration and scaling of laminar center of pressure phases. (a) Radial center of pressure time series (black) with 95<sup>th</sup> centile change in speed threshold (red). (b) Power law scaling for the probability distribution of center of pressure laminar phase lengths ( $\delta t$ ). Similar numerical procedures were used for finger and finger-center of pressure trajectories (*see text for further details*).

Our dynamical intermittency analysis is qualitatively similar to the procedure used by (cross-) recurrence analysis to compute laminar trajectory phases. However, in recurrence analysis, correlated trajectory segments are defined using the  $D_e$ -dimensional Euclidean distance between states. In contrast, the intermittency analysis is a time series technique where dynamical states are considered constant if they are below the specified threshold. Both measures are expected to produce qualitatively similar results; however, recurrence analysis is performed in the reconstructed phase space with dimension appropriate for the dynamics. It may therefore be expected that (cross-) recurrence analysis is more sensitive to changes in individual and coupled subsystem dynamics. *Statistical Analysis* 

Statistical contrasts were performed with SPSS version 16.0 (SPSS Inc., Chicago, IL). A one-way repeated-measures ANOVA was used to compare the mean balancing time performance measure across learning sessions (4 levels: Sessions 1-4). Dependent measures for the (cross-) recurrence quantification analysis (RR, LAM, TT) were analyzed using separate one-way repeated-measures ANOVAs performed for each dependent measure (finger, COP, F-COP). For the dynamical intermittency analysis, we compared the power law exponent ( $\alpha$ ) from the line of best fit that described the relationship between the probability of a given laminar phase length  $(\log_{10}(P(\delta t)))$  and the laminar phase length  $\left(\log_{10}\left(\delta t^{-\alpha}\right)\right)$  The statistical contrast was implemented using a one-way ANOVA with repeated-measures over experimental sessions. The scaling exponent ( $\alpha$ ) was used to determine whether the duration of smooth trajectory segments was influenced by learning. We averaged individual subject data across trial repeats for each analysis technique. Post-hoc comparisons were implemented with paired *t*-tests using Bonferroni-Holm corrections for multiple comparisons. The significance level for statistical contrasts was 0.05. Significant statistical contrasts are presented in text with corrected *p*-values.

## 5.4 – RESULTS

## Mean Balancing Time

Mean balancing time was defined as the average length of balancing trials performed in each experimental session. There was a progressive improvement in balancing times

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across sessions (Fig. 5.2). The effect was confirmed by statistical analysis and demonstrated that subjects more effectively performed the task as a function of learning (F(3, 21) = 22.86, p < 0.001). The average balancing time was greater in the fourth than the first (p < 0.001) and second (p < 0.05) learning sessions, and for the third relative to first session (p < 0.001). These results corroborate our hypothesis that average balancing trial lengths would improve as a function of learning. In the ensuing sections, we interpret our results in relation to these learning-dependent changes in performance.

## Recurrence Quantification Analysis: Center of Pressure Trajectories

Recurrence rate (RR) is a nonlinear measure that quantifies the global regularity of timevarying states without accounting for the temporal properties of that regularity. We used RR to monitor the spatial regularity of COP trajectories (RR<sub>COP</sub>) across experimental sessions. Figure 5.3a summarizes the learning effect observed for RR<sub>COP</sub>. There was a significant main effect whereby the regularity of COP trajectories decreased progressively across learning sessions (F(3, 21) = 9.03, p < 0.001). RR<sub>COP</sub> was greater in session 1 and 2 relative to session 3 and 4 (p < 0.05).

Laminarity is defined as the density of states that are correlated for finite time intervals relative to the total density of recurrent states. Dynamical states adjacent in time are considered constant (equal) if they are within the vicinity of the same recurrence neighbourhood. Practice increased the occurrence of laminar COP (LAM<sub>COP</sub>) trajectory segments (F(3, 21) = 3.68, p < 0.01). Figure 5.3b summarizes the learning effect. LAM<sub>COP</sub> was reduced at session 1 relative to every other session (p < 0.05). Trapping time (TT<sub>COP</sub>) demonstrated that the average length of laminar COP phases increased with

learning (F(3, 21) = 9.15, p < 0.001). TT<sub>COP</sub> was reduced in the first relative to third (p < 0.01) and



**Figure 5.2.** Change in stick balancing performance across learning sessions. Results are reported as mean balancing times (in units of seconds) ensemble-averaged over individual subjects. Error bars represent the within-subjects SEM. \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001.



**Figure 5.3.** Center of pressure dynamics were modified by learning. a) Recurrence rate of center of pressure trajectories by session. Decreased RR<sub>COP</sub> reflects a reduction in the regularity of center of pressure time series. b) Discontinuity of center of pressure trajectories by session. Greater LAM<sub>COP</sub> corresponds to an increase in the incidence of correlated center of pressure trajectories segments. c) Average trapping time (units of ms) of center of pressure trajectories across sessions. Greater TT<sub>COP</sub> indicates a lengthening of the average time interval between successive center of pressure corrections. Error bars correspond to the within-subjects SEM. \**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001.

fourth (p < 0.01) learning sessions. In addition,  $TT_{COP}$  was greater in session 4 relative to session 2 (p < 0.05). Our data demonstrate that experience modified the temporal structure of corrective COP displacements. With learning, corrective COP excursions became discontinuous and increasingly separated in time. The results support our hypothesis that COP trajectories would be modified by learning to facilitate stick balancing performance.

### Recurrence Quantification Analysis: Fingertip Trajectories

Figure 5.4a shows a decrease in the regularity of finger trajectories with learning. Statistical analysis confirmed the learning-effect for  $RR_{Finger}$  (F(3, 21) = 11.37, p < 0.001). The density of recurrent finger trajectories was greater during the first relative to third (p < 0.01) and fourth sessions (p < 0.01). Moreover,  $RR_{Finger}$  was greater at session 2 in comparison to session 4 (p < 0.05). In summary, finger trajectories showed a learning effect similar to that of COP trajectories and were characterized by a decrease in their spatial regularity.

Figure 5.4b shows a learning-dependent increase in the discontinuity of finger trajectories. The learning effect for LAM<sub>Finger</sub> was confirmed by statistical analysis (*F*(3, 21) = 8.033, p < 0.01). RR<sub>Finger</sub> decreased as a function of learning, but recurrent finger states evolved in correlated time segments. To supplement this finding, we examined the average duration of laminar finger trajectory phases (TT<sub>Finger</sub>). Figure 5.4c shows that learning caused an increase in TT<sub>Finger</sub> across sessions. TT<sub>Finger</sub> was reduced in the first compared to third (p < 0.01) and fourth (p < 0.001) sessions. In summary, learning resulted in a monotonic increase in the length of laminar fingertip phases. The data support our hypothesis and previous learning data (Cluff et al. 2009) by demonstrating
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that stick balancing finger inputs become less correlated (RR) as a function of learning, discontinuous and increasingly separated in time (LAM and TT).



**Figure 5.4.** Finger dynamics across the learning period. The interpretation of dynamical variables is as in figure 5.3. a) Regularity of finger trajectories (RR<sub>Finger</sub>) across learning sessions. b) LAM<sub>Finger</sub> by session. c) Average length of laminar finger trajectory segments (TT<sub>Finger</sub>; units of ms) across sessions. Error bars represent the within-subjects SEM. \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001.

#### Cross-Recurrence Quantification Analysis

In addition to individual subsystem dynamics, we examined coupling between COP and finger displacements ( $RR_{F-COP}$ ). The regularity of F-COP trajectories ( $RR_{F-COP}$ ) showed a learning-dependent increase (F(3, 21) = 6.20, p < 0.01). Figure 5.5a shows that F-COP trajectories were least coupled when inexperienced subjects performed the stick-balancing task (session 1). Pairwise comparisons demonstrated that the spatial correlation between finger and COP dynamics was smallest during the first session relative to every other session (p < 0.05). This finding corroborates our hypothesis that the coupling between finger and COP displacements would increase as a function of learning.

Figure 5.5b demonstrates that LAM<sub>F-COP</sub> increased as a function of learning (F (3, 21) = 10.59, p < 0.001). LAM<sub>F-COP</sub> was reduced in the first relative to third (p < 0.01) and fourth sessions (p < 0.05), and in the second relative to third (p < 0.05) and fourth

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sessions (p < 0.05). Similar to the effect reported for LAM<sub>F-COP</sub>, and consistent with our hypothesis, learning resulted in prolonged (TT<sub>F-COP</sub>) intervals of coupled finger and COP dynamics (F(3, 21) = 3.33, p < 0.05). TT<sub>F-COP</sub> was reduced in session 1 relative to session 3 and 4 (p < 0.05). The data are summarized in Fig. 5.5c.



**Figure 5.5.** Coupling strength and dynamical properties of the finger-center of pressure interaction. a) Recurrence rate of coupled F-COP trajectories by session. An increase in RR<sub>F-COP</sub> reflects the tendency for collective control over finger and COP displacements. b) LAM<sub>F-COP</sub> measures transitions between coupled and uncoupled F-COP trajectories. Greater LAM<sub>F-COP</sub> reflects an increase in the density of coupled F-COP trajectory segments. c) Average length of coupled F-COP trajectories by session (TT<sub>F-COP</sub>; units of ms). Error bars are the within-subjects SEM. \**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001.

## Dynamical Intermittency Analysis

We computed the scaling relationship between laminar COP, Finger, and F-COP phases and the probability of laminar trajectory phases. We were interested in the sensitivity of time series measures to learning-induced changes in individual and collective dynamics. Figure 5.6b shows that learning caused a decrease in the scaling exponent  $\alpha_{\text{Finger}}$  (*F* (3,

$$21) = 7.56, \, p < 0.01)$$



**Figure 5.6.** Laminar COP, Finger and F-COP trajectory phases showed decay properties characteristic of on-off dynamical intermittency. Power law scaling in the decay of a) COP, b) Finger, and c) F-COP trajectories. A reduction in the scaling law ( $\alpha$ ) corresponds to an increase in the average time interval between successive corrections. Error bars correspond to within-subjects SEM. \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001.

The increase in  $\alpha_{\text{Finger}}$  corresponds to a small decrease in the average duration of laminar finger phases. The learning effect occurred primarily at the first session;  $\alpha_{\text{Finger}}$  was reduced at the first compared with the third (p < 0.05) and fourth (p < 0.01) experimental sessions.

In summary, the dynamical intermittency analysis was not sensitive to changes in COP and F-COP dynamics that occurred with learning (Fig. 5.6a, c; repeated-measures ANOVA, p > 0.05). However, the distributions were nevertheless well-fit by a power law decay function, which demonstrated that there were intermittent corrections present in COP and F-COP time series. Thus, recurrence-based measures were more sensitive to changes in the discontinuity of subsystem and interactive dynamics. This finding most likely reflects the specificity of the (cross-) recurrence methods to the dynamical properties of time series (e.g., embedding dimension, embedding delay).

# 5.5 – DISCUSSION

We conducted this experiment to examine interactions between posture and finger dynamics while subjects learned a novel stick-balancing task. We operationalized performance using the average length of balancing trials, which we expected to increase as a function of practice. Our hypothesis was confirmed. Balancing trial lengths increased progressively and were nearly four times longer after the 20 day training period. This performance improvement demonstrated that subjects learned the task and supported previous studies that examined stick-balancing skill acquisition (Cluff and Balasubramaniam 2009; Cluff et al. 2009). We additionally examined changes in posture and finger trajectories, as well as learning-dependent coupling between these subsystems. Though qualitative differences existed between the learned dynamics of posture and finger control mechanisms, the effect of practice was to progressively stabilize their coupling.

At the outset of the study, we hypothesized that learning would involve a reorganization of postural control to support stick-balancing performance. Across learning sessions, finger trajectories became more variable and discontinuous, and in agreement with our hypothesis, similar changes were reflected in center of pressure time series. This finding corroborates a substantial body of work, which has shown that postural control mechanisms are modified to accommodate secondary task performance (Stoffregen et al. 1999, 2000; Balasubramaniam et al. 2000; Stoffregen et al. 2007). In agreement with these studies, we have shown that postural control mechanisms are specific to the behavioural context in which they are generated; however, the novelty of our study was to outline the specific form of the posture-finger interaction and determine

how the central nervous system satisfies these simultaneous (and often conflicting) task goals. In the ensuing sections, we discuss our results in relation to theoretical models of motor learning.

Central to Newell et al.'s (2001) motor learning model is that motor subsystems become assembled into coordinative relationships that support performance. Our data were consistent with this proposition and demonstrated that improved performance was the product of two distinct learning processes. The first learning process encompassed a series of modifications in individual subsystem organizations and arose between the first and second experimental sessions. Large decreases in the regularity and discontinuity of corrective finger and COP displacements were observed. In addition, intermittent fluctuations in finger and COP states became separated by longer intervals of time. The second process corresponded to the lengthened coupling of posture and finger displacements that emerged at the third experimental session. According to the hierarchical learning model (Newell et al. 2001), these distinct processes demonstrated that early-learning was facilitated by changes in the organization of individual subsystems and later-learning by their progressive coupling. In other words, individual subsystems at lower-levels of the motor hierarchy were progressively organized into a coordinative relationship that improved performance. The progressive strengthening of posture-finger coupling raises an important question: Did posture-finger coupling arise due to the anticipatory or reactive control of posture, or were coupled center of pressure and finger displacements the product of a hierarchical control mechanism? Although each of these mechanisms could account for our results, the latter mechanism corresponds to a superposition of motor subsystems to simultaneously satisfy the dual posture and stick-

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balancing task goals. We argue that center of pressure and finger displacements were controlled by a hierarchical mechanism that intermittently switched between coordinative and individual subsystem control.

The anticipatory postural adjustment has been described as a mechanism that minimizes the destabilizing effects of self-generated forces that arise during voluntary behaviour (Bouisset and Zattara 1987; Ahmed and Wolpert 2009; Cordo and Nashner 1982; Bouisset et al. 2000). Although cogent arguments have been provided for anticipatory postural control mechanisms and their role in motor learning (Flanagan and Wing 1997), only discrete movements such as reaching have been considered. In comparison, stick balancing is a continuous motor task in which corrective displacements are issued to stabilize an external object with intrinsic, unstable dynamics. APAs are likely infeasible in this context because they would require the prediction of destabilizing stick movements prior to their occurrence. It is more probable that postural corrections stabilize the upright stance in reaction to upper limb displacements.

The present data, in conjunction with a recent study conducted in our laboratory (Cluff et al. 2010) provide evidence against coupling mechanisms that are based solely on anticipatory or reactive postural control strategies. Our argument is substantiated by the fact that center of pressure displacements in stick balancing, on average, are positively correlated with finger displacements but switch to weaker negative correlation over longer time intervals. In other words, finger movements are time-locked to postural displacements over short intervals, but postural control switches to a compensatory mechanism presumably when upper limb motion destabilizes the upright stance (Cluff et al. 2010, P-SB condition, figure 7). Therefore, we argue that stick-balancing skill is

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related to the development of a control hierarchy whereby subjects learn to drive finger displacements with postural excursions but intermittently dissociate this control to individual subsystems when necessary.

Why does control switch from coupled to individual subsystem dynamics? One possibility is that the abrupt and intermittent (de)coupling of posture and finger displacements is performed in response to instabilities that arise in the subsystem dynamics. Intermittent dynamics are characteristic of systems with threshold stability criteria that lead to rapid fluctuations or discontinuities in variables of interest (Platt et al. 1993; Landa et al. 1998). In human motor control, the recruitment and suppression of individual segments has been described as an intermittent control mechanism that stabilizes motor performance (Buchanan et al. 1997; Buchanan and Kelso 1999) in response to perturbation (Newell and Vaillancourt 2001). The observation that intermittency existed at all levels of our analyses suggests that the central nervous system may (de)couple individual subsystems to satisfy concurrent task goals. Our rationale is consistent with evidence that human feedback parameters are often tuned to correct threshold-crossing perturbations that arise during voluntary behaviour (Kelso 1995; Buchanan and Kelso 1999; Cabrera and Milton 2004). We supplement these studies by demonstrating that coupling functions can be selectively dissociated to control individual subsystems in a similar state-dependent manner.

In conclusion, we have shown that the dynamics of posture and finger displacements are altered by learning a novel stick-balancing task. In addition, we demonstrated that practice caused a systematic increase in the occurrence and duration of coupled posturefinger displacements and recurrence-based measures were more sensitive to these

changes than dynamical time series measures (Rhea et al. 2011). We suggest that this coupling resulted from the development of a hierarchical control mechanism that switches between controlling coupled to individual posture and finger displacements. Future work will examine how individual segments contribute to postural control and hand displacements, and whether these contributions evolve as a function of learning. This research would enable detailed comparison between dynamical methods that focus on outcome level analyses and statistical methods that decompose the contributions of individual segments to performance variability.

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Zbilut JP, Zaldivar-Comenges JM, Strozzi F (2002) Recurrence quantification based Liapunov exponents for monitoring divergence in experimental data. Phys Lett A 297: 173–181. Chapter 6 – Unstable Object Control Is Mediated by Multijoint Error Compensation

# 6.1 – ABSTRACT

The purpose of our study was to determine whether skill acquisition was mediated by the stereotyped recruitment of individual joints (i.e., task sharing) or multijoint error compensation. We monitored stick balancing performance in four experimental sessions (1 session/5 days) and confirmed that subjects learned the task by showing that the length of balancing trials increased with training. A key finding was that motor learning mediated multijoint error compensation. We found that with training, subjects preferentially minimized joint variance that destabilized the fingertip position time profile. Importantly, we found that the selective constraint of destabilizing joint variance correlated to task performance. We additionally examined the variance and coupling of paired joint angle excursions to verify that improved performance could not be attributed to changes in the recruitment of individual joints. We found no evidence for an explicit task sharing strategy and reported a complex set of joint angle correlations that were unaffected by skill acquisition. We interpret our results from the viewpoint of optimal feedback control and propose a learning mechanism that is based on the accurate estimation of sensory states. Our data encourage future work to examine the relationship between the integrity of sensory information and the structure of joint configuration variance.

# **6.2 – INTRODUCTION**

Object manipulation is central to many of the activities that we perform in daily life, and often, the objects that we control are unstable. Common examples include the waitress that balances a tray of drinks while maneuvering through a crowded restaurant, or cyclists who navigate rush-hour traffic, avoiding pedestrians and vehicles while staying upright on their bicycles. In each of these tasks, the object is balanced at an unstable equilibrium and controlled indirectly through the interaction between applied forces (i.e., motor commands) and the intrinsic object dynamics.

A number of studies have investigated unstable object control using an inverted pendulum (stick) balancing task (Cabrera and Milton 2002) and demonstrated that performance is mediated by state estimation processes (Mehta and Schaal 2002; Mah and Mussa-Ivaldi 2003) and time-delayed feedback control (Milton et al. 2009). We know little in comparison about how individual joints are recruited and coordinated to control unstable objects. Here we examined motor learning in a (physical) inverted pendulum balancing task with the objective to investigate two aspects of coordination and their role in skill acquisition: Task sharing and multijoint error compensation.

The task-sharing perspective was pioneered by Bernstein's (1967) treatise on the coordination and control of voluntary movement. Bernstein proposed that skilled motor behaviour is acquired through three incremental stages that involve learning to control and progressively incorporate joint-space degrees of freedom into task performance. Joint angle variances and inter-joint correlations have subsequently been used to evaluate skill-dependent differences in task sharing between individual joints (Temprado et al. 1997). The recruitment of individual joints and the emergence of inter-joint correlations have

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been reported for the acquisition of diverse motor skills including ball bouncing (Broderick and Newell 1999), dart throwing (McDonald et al. 1989), simulated skiing (Vereijken et al. 1992) and the racquetball forehand shot (Southard and Higgins 1987).

The relationship between joint angle variance and outcome performance is confounded, however, by the equivocal mapping between angular joint trajectories and motion at the end effector (Polit and Bizzi 1978; Lacquaniti and Soechting 1982). Thus, it is conceivable that skilled performers engage a flexible and error-compensating joint control strategy to stabilize task performance (Latash 2000; Latash et al. 2002; Yang and Scholz 2005; Latash et al. 2007). A very useful technique to investigate multijoint error compensation is the uncontrolled manifold (UCM) method (Scholz and Schoner 1999), which partitions motor variance into two structural components: (a) variance that stabilizes performance ( $V_{UCM}$ ) and (b) variance that destabilizes performance ( $V_{ORT}$ ). In the context of our study, the subscript UCM refers to joint angle configurations within the UCM-subspace (i.e., task-irrelevant variance), while the subscript ORT refers to the orthogonal variance component that destabilizes outcome performance (i.e., task-relevant variance). If the time-varying fingertip position is controlled by multijoint error compensation, we expected that the neural controller would preferentially permit variance in the UCM-subspace (V<sub>UCM</sub>) while constraining joint angle variance that destabilizes performance (V<sub>ORT</sub>).

We investigated the structure of joint configuration variance using a link-segment model that mapped six independent joint angle configurations onto the time profile of the fingertip position control variable (i.e., the sagittal plane position of the inverted pendulum pivot). We hypothesized that unstable object control would be mediated by

multijoint error compensation and that the selective constraint of destabilizing joint angle variance would emerge across training. We show that stick balancing performance indeed correlates with the ratio of  $V_{UCM}$  to  $V_{ORT}$ , such that performers who minimize  $V_{ORT}$  perform best at the task. We additionally show that learning caused the selective minimization of destabilizing joint angle variance ( $V_{ORT}$ ) but did not influence variance aligned on the UCM-subspace ( $V_{UCM}$ ).

## 6.3 – METHODS

#### *Subjects*

Eight healthy subjects (5 males, 3 females; age =  $24.5 \pm 2.4$  years) participated in the study. The subjects were right-handed, had normal or corrected vision and reported no musculoskeletal or neurological disorders. Prior to the experiment, each subject attended a recruitment session that outlined the purpose of the study and time commitment. Participants gave written informed consent for the protocol, as approved by the McMaster University Research Ethics Board. The subjects were remunerated for their time in the laboratory and could withdraw from the study without penalty (none did so).

## Protocol

The subjects performed twenty balancing trials (2 blocks  $\times$  10 trials) during the initial recruitment/briefing session to become familiarized with the task. During the familiarization trials, the subjects balanced a cylindrical wooden dowel (stick) with different physical properties (length = 100 cm; diameter = 1.71 cm; mass = 150 g) than the stick used for the experiment and practice (length = 62 cm; diameter = 1 cm; mass = 50 g). The inertia of the stick moderated the task difficulty by providing additional time

for corrections. We recorded each subject's preferred stance to control the balancing posture between trials and learning sessions.

Each subject attended daily practice sessions conducted at the laboratory. We did not impose a fixed number of practice trials in each session, but required that subjects practice for 30 min/session. We maintained a log to ensure that each subject satisfied these practice requirements. We monitored motor learning in four experimental sessions (~90 min, including subject preparation time) that were substituted for every fifth practice session.

The experimental sessions consisted of twenty trials (2 blocks  $\times$  10 trials) that ended when the subject dropped the stick. We instructed subjects to balance the stick for as long as possible and attempted to achieve a consistent postural alignment for each trial by asking that subjects align their feet with their preferred stance. If the preferred balancing stance was not maintained during trial performance, we excluded the trial from further analysis and repeated data collection. Individual trials were separated by a minimum of thirty seconds and blocks of trials by a five minute rest period. The allotted rest breaks could be supplemented at the subjects' request to alleviate temporary discomfort due to visual strain, and physical or attentional fatigue.

## Equipment and Apparatus

Segment kinematics were recorded with 14 mm spherical reflective markers that we positioned over surface anatomical landmarks to provide an approximation to the joint centers of rotation (ankle joint: lateral malleolus; knee joint: lateral femoral condyle; hip joint: greater trochanter; shoulder joint: inferior to the lateral aspect of the acromion process; elbow joint: lateral humeral condyle; wrist joint: styloid process of the radius).

We also attached 14 mm reflective markers to the top and bottom of the stick. The marker coordinates were recorded at a sampling rate of 750 Hz using a ten camera VICON T-40 motion capture system (Lake Forest, CA, USA).

## Data Reduction

The three-dimensional marker coordinate data were reconstructed and autolabeled offline using subject-specific link-segment models that we constructed with the VICON Nexus software. The three-dimensional marker coordinate data were imported to MATLAB<sup>TM</sup> R2009a (The Mathworks, Natick, MA, USA) and low-pass filtered (5 Hz cutoff, 2<sup>nd</sup>-order, dual-pass Butterworth). We used a bidirectional digital filter to minimize artificial phase shifts in the data induced by the filtering algorithm. *Angle Calculations* 

We restricted our analysis to the right-side (balancing side) sagittal plane joint kinematics and calculated the ankle, knee, hip, shoulder, elbow, and wrist joint angles at each data sample using the filtered marker coordinates. The link-segment model and marker placements are outlined in figure 6.1. We calculated the sagittal plane joint angles using the general formula,

$$\theta_i = \arctan 2 \left( \frac{\vec{u} \times \vec{v}_i}{\vec{u} \cdot \vec{v}_i} \right),$$

where  $\theta_i$  corresponded to the joint angle about the *i*<sup>th</sup> joint, *u* corresponded to the unit vector directed along the right-horizontal, and  $\vec{v}_i$  was the unit vector corresponding to the limb segment proximal to the *i*<sup>th</sup> joint of the link-segment model. The joint angles were



**Figure 6.1.** Schematic of the experimental setup showing the reflective markers (*filled red circles*) used to construct the link-segment model (*black line*). Sagittal plane joint angles ( $\theta$ s) were calculated for the ankle, knee, hip, shoulder, elbow and wrist joints. Joint angles were defined relative to the right-horizontal (*broken horizontal lines*) and the angle of the stick was defined relative to the vertical (*broken vertical line*).

defined relative to the right horizontal with positive angles in the counterclockwise direction. We used the same formula to calculate the vertical stick angle; however, for the stick angle calculations  $\vec{u}$  corresponded to the unit vector directed along the upward-vertical and the unit vector  $\vec{v}$  represented the sagittal plane stick coordinates. Positive vertical stick angles were defined in the counterclockwise direction. We removed the first and last 3 s of trial data to confine the analysis to steady-state balancing processes and avoid transient adjustments at the start of the trial.

#### Dependent Measures

#### Mean Balancing Time

We computed the mean balancing time as the average trial length performed by each subject in a given experimental session. We used the average length of balancing trials to infer learning-mediated changes in stick balancing performance.

#### Variance of Individual Joint Angle Excursions

We used the variance of angular joint excursions to examine change in the recruitment of individual joints while subjects learned the task. We first determined the occurrence of successive corrections based on local maxima in the angular stick profile. For each trial, we partitioned the joint angle kinematics into time profiles with beginning and endpoints defined by the local angular stick maxima. We normalized each corrective displacement to 101 points by linear interpolation and calculated the variance of individual joint angles. We averaged the joint angle variances across corrections performed within each trial and then across trials within each session.

## Correlations between Individual Joint Excursions

To investigate change in the coupling of individual joint motions, we calculated the zero-lag cross-correlation coefficient between all combinations of paired joint angle time series. The cross-correlation coefficients were calculated for each individual trial and then averaged across trials in each session. The sign of the cross-correlation indicates the direction of coupling, while the magnitude indicates the degree of coupling between segments—the more independent the joint motions, the closer the coefficient would be to zero. Negative correlations reflect instantaneous error compensation between joint pairs. *Joint Variance and its Relationship to Performance Stability* 

The mathematical methods for the UCM analysis have been described elsewhere in detail (Scholz and Schoner 1999). In our study, the initial step was to specify a link-segment model that related individual sagittal plane joint angles to the hypothesized finger coordinate control variables (Milton et al. 2009). By restricting our analysis to the sagittal plane, we assume that a similar mechanism, if present, would control the frontal plane stick angle.

We used a link-segment model that consisted of six sagittal plane joint angles. The link-segment model relating the joint configuration to the sagittal plane finger coordinates at each sample was,

$$\begin{bmatrix} x_{\text{finger}} \\ y_{\text{finger}} \end{bmatrix} = \begin{bmatrix} l_{\text{shank}} \cos\theta_{\text{ankle}} + l_{\text{thigh}} \cos\theta_{\text{knee}} + l_{\text{trunk}} \cos\theta_{\text{hip}} + l_{\text{upperarm}} \cos\theta_{\text{shoulder}} + l_{\text{forearm}} \cos\theta_{\text{elbow}} + l_{\text{hand}} \cos\theta_{\text{wrist}} \\ l_{\text{shank}} \sin\theta_{\text{ankle}} + l_{\text{thigh}} \sin\theta_{\text{knee}} + l_{\text{trunk}} \sin\theta_{\text{hip}} + l_{\text{upperarm}} \sin\theta_{\text{shoulder}} + l_{\text{forearm}} \sin\theta_{\text{elbow}} + l_{\text{hand}} \sin\theta_{\text{wrist}} \end{bmatrix}$$

where  $\theta_{ankle}$ ,  $\theta_{knee}$ ,..., $\theta_{wrist}$  were the sagittal plane joint angles; and  $l_{shank}$ ,  $l_{thigh}$ ,..., $l_{hand}$  were the segment lengths that we calculated from marker coordinate data averaged over the first 3-s of each trial. Changes in the individual joint angles were mapped onto the finger

coordinates by constructing the Jacobian matrix, which is the system of first-order partial derivatives  $(J(\theta) = \partial F / \partial \theta_i)$ :

 $J(\theta) = \begin{bmatrix} -l_{\text{shank}} \sin \theta_{\text{ankle}} & -l_{\text{thigh}} \sin \theta_{\text{knee}} & -l_{\text{trunk}} \sin \theta_{\text{hip}} & -l_{\text{upperarm}} \sin \theta_{\text{shoulder}} & -l_{\text{forearm}} \sin \theta_{\text{elbow}} & -l_{\text{hand}} \sin \theta_{\text{wrist}} \\ l_{\text{shank}} \cos \theta_{\text{ankle}} & l_{\text{thigh}} \cos \theta_{\text{knee}} & l_{\text{trunk}} \cos \theta_{\text{hip}} & l_{\text{upperarm}} \cos \theta_{\text{shoulder}} & l_{\text{forearm}} \cos \theta_{\text{elbow}} & l_{\text{hand}} \cos \theta_{\text{wrist}} \end{bmatrix}$ 

The second step was to compute the linear approximation of the individual joint angles onto the invariant joint configuration subspace (UCM). This step required specification of a referent joint configuration at each data sample. For each trial, we used the local angular stick maxima to partition individual joint angle profiles into successive corrections (see the *Variance of Joint Angle Excursions* section). We ensemble-averaged the joint angle time series at each normalized time sample to determine the referent joint configuration. Our method is a within-trial UCM analysis that examines online error compensation between individual joint angles (Scholz et al. 2003; Ranganathan and Newell 2008).

The referent joint configuration was then used to compute the UCM. The linear approximation of the UCM was calculated by determining the nullspace of the Jacobian matrix with respect to the referent joint configuration at each normalized time sample. We calculated the nullspace of the Jacobian matrix by singular value decomposition in MATLAB. We then calculated the angular deviation matrix by subtracting each joint angle from their respective referent angle and projected it onto the nullspace of the Jacobian. We used this projection to provide a scalar estimate of how consistent the joint configuration was with the referent finger coordinate at that time sample, we used the complement to estimate the extent to which the joint configuration matrix destabilized the instantaneous finger coordinates. We normalized the variances within the UCM ( $V_{UCM}$ ) and orthogonal subspace ( $V_{ORT}$ ) to the dimension of the subspace

(DOF<sub>UCM</sub> = 4; DOF<sub>ORT</sub> = 1), the number of samples (n = 101 samples), and the number of corrections, which varied from trial-to-trial. We used the UCM ratio, which is defined as the variability on the UCM (V<sub>UCM</sub>) relative to the orthogonal joint configuration subspace (V<sub>ORT</sub>), to determine whether learning led to the development of a multijoint error compensation strategy (UCM<sub>ratio</sub> = V<sub>UCM</sub>/V<sub>ORT</sub>). An UCM<sub>ratio</sub> > 1 would demonstrate that selective error compensation is used to stabilize the time-varying finger coordinates. *Relationship between the Variability Ratio and Performance* 

We used Pearson's product moment correlation coefficient to examine the relationship between balancing time and the  $UCM_{ratio}$ . Positive correlation would demonstrate that performance is dependent on the degree of error compensation between individual joint configurations. We sought to determine if error compensation (i.e., feedback control) was a significant predictor of stick balancing performance.

## Statistical Analysis

For every dependent measure, we averaged subject data across trials performed in each session. We used a one-way repeated-measures analysis of variance (ANOVA) to determine the influence of learning on balancing time. Separate one-way repeated-measures ANOVAs were performed to determine whether the individual joint angle variances (6) differed across experimental sessions (4 levels: Sessions 1 to 4). We chose separate one-way ANOVAs in favour of the two-way ANOVA with joint (6) and session (4) factors because we were interested in learning-induced changes in joint variance and not the difference in variance across joints. Additionally, we performed a two-way repeated-measures ANOVA to determine how the organization of joint variance (2 levels: V<sub>UCM</sub> and V<sub>ORT</sub>) differed across experimental sessions (4 levels: Sessions 1 to 4). Finally,

we natural log-transformed the UCM<sub>ratio</sub> to correct for deviations from normality and contrasted it across sessions using a one-way repeated-measures ANOVA. The post-hoc means comparisons were performed using paired *t*-tests with Bonferroni-Holm corrections. We performed the statistical analyses in PASW version 18.0 (SPSS Inc., Chicago, IL) with the significance level set to  $\alpha = 0.05$ . The pairwise mean differences and corrected *p*-values are reported in the text and figures 6.2 through 6.6.

## 6.4 – RESULTS

## Mean Balancing Time

Mean balancing time showed a marked learning effect (F(3, 21) = 22.86, p < 0.001, Fig 6.2) and post-hoc comparisons demonstrated that the average balancing time was greater following training (Session 4) relative to early-learning (Sessions 1 & 2; *ps* < 0.05). In addition, mean balancing time was reduced in the first relative to third session (*p* < 0.001). We interpret the magnitude and structure of joint angle variance and the development of error-compensation mechanisms in relation to the changes in performance that accompanied learning.



**Figure 6.2**. Balancing time (in s) by experimental session. Error bars represent the within-subjects SEM. \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001.

## Individual Joint Excursion Variance and Relationship Between Individual Joints

The top three panels of Fig. 6.3 show the variability of the ankle (a), knee (b), and hip (c) joints ensemble-averaged across trials and sessions. In contrast to the variance of lower limb joints, the bottom panel shows that shoulder (d), elbow (e) and wrist (f) excursions were substantially more variable. Statistical analysis demonstrated that while the variance of ankle, knee, hip, shoulder and elbow excursions were approximately constant (*F* (3, 21) < 2.50, p = ns), learning led to diminutive changes in wrist joint variance (*F* (3, 21) = 5.58, p < 0.001). Wrist joint excursions were less variable at the end of training (Session 4) compared to the first training session (p < 0.05).

We performed cross-correlation analyses to determine whether changes in performance were related to a straightforward, consistent covariation between joint pairs. We analyzed the zero-lag cross-correlation coefficient for every pair of the six investigated joints and averaged this measure across trials. We corrected deviations from normality by *z*-transforming the correlation coefficients prior to the statistical analysis. The results demonstrated that performance was subserved by a complex set of inter-joint correlations and Table 6.1 shows that the paired joint correlations were unaffected by learning. To further understand the complex interdependence of individual joint kinematics, we performed an uncontrolled manifold analysis. The UCM analysis allowed us to interpret structural changes in joint variance induced by motor learning.



**Figure 6.3.** Variance of joint excursions at the ankle (a), knee (b), hip (c), shoulder (d), elbow (e) and wrist (f) joints by experimental session. Joint angle variance was small in the lower relative to upper extremity joints. Each vertical bar denotes the within-subjects standard deviation averaged across trials performed in that session. Error bars represent the within-subjects SEM. \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001.

Joint pair	Session 1	Session 2	Session 3	Session 4
Ankle-knee	$0.41 \pm 0.10$	$0.29\pm0.06$	$0.50 \pm 0.11$	$0.44 \pm 0.11$
Ankle-hip	$0.16\pm0.07$	$0.20\pm0.06$	$0.20\pm0.10$	$0.19\pm0.09$
Ankle-shoulder	$0.20\pm0.09$	$0.29\pm0.05$	$0.33\pm0.04$	$0.20\pm0.09$
Ankle-elbow	$0.15\pm0.07$	$0.19\pm0.06$	$0.27\pm0.05$	$0.19\pm0.06$
Ankle-wrist	$0.22\pm0.06$	$0.16\pm0.08$	$0.16\pm0.07$	$0.16\pm0.05$
Knee-hip	$0.27 \pm 0.18$	$0.26 \pm 0.14$	$0.28\pm0.18$	$0.28\pm0.07$
Knee-shoulder	$0.38\pm0.10$	$0.43 \pm 0.09$	$0.46 \pm 0.10$	$0.41\pm0.07$
Knee-elbow	$0.50\pm0.09$	$0.53 \pm 0.11$	$0.52 \pm 0.11$	$0.51\pm0.07$
Knee-wrist	$0.16 \pm 0.14$	$0.16 \pm 0.12$	$0.18 \pm 0.10$	$0.17 \pm 0.04$
Hip-shoulder	$0.19 \pm 0.10$	$0.20 \pm 0.08$	$0.15 \pm 0.09$	$0.24 \pm 0.07$
Hip-elbow	$0.40 \pm 0.08$	$0.30 \pm 0.09$	$0.29 \pm 0.09$	$0.45 \pm 0.05$
Hip-wrist	$0.24 \pm 0.09$	$0.21 \pm 0.05$	$0.24 \pm 0.07$	$0.28\pm0.05$
Shoulder-elbow	$0.52 \pm 0.06$	$0.62 \pm 0.07$	$0.67 \pm 0.02$	$0.62 \pm 0.05$
Shoulder-wrist	$0.11 \pm 0.06$	$0.15 \pm 0.09$	$0.09 \pm 0.11$	$0.14\pm0.08$
Elbow-wrist	$0.46\pm0.07$	$0.44\pm0.09$	$0.26\pm0.12$	$0.46\pm0.05$

Table 6.1. Average zero-lag cross-correlation function between pairs of joints.

\**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001

Ratio of Variability: Structure of joint configuration variability related to the stability of finger coordinate control variables

Figure 6.4 plots V<sub>UCM</sub> (a) and V<sub>ORT</sub> (b) derived from the link-segment model (6-DOF; Fig. 6.1) that related individual joint angles to the hypothesized finger control variables. The two-way ANOVA revealed that joint variance distributed along the UCM subspace (V<sub>UCM</sub>) was significantly larger than variance in the orthogonal (V<sub>ORT</sub>) direction (*F* (1, 7) = 7.42, *p* < 0.03, Fig 6.4). There was a significant session-by-variance component interaction (*F* (3, 21) = 8.46, *p* = 0.001) that we decomposed by planned univariate comparisons (i.e., simple main effects). The planned comparisons demonstrated that while there was no change in variance on the UCM-subspace (*F* (3, 21) = 0.64, *p* > 0.05, Fig 6.4a), learning caused a substantial reduction of V<sub>ORT</sub> (*F* (3, 21) = 8.00, *p* < 0.001, Fig 6.4b). V<sub>ORT</sub> was greatest at the outset of training but decreased monotonically with learning (*p* < 0.05) to demonstrate that multijoint error compensation minimized the deleterious effects of kinematic joint variance. This effect is further summarized in Figure 6.5.

We used the UCM<sub>ratio</sub> to quantify the relative variance per DOF in each subspace. The UCM<sub>ratio</sub> increased with learning to show that subjects learned to selectively constrain joint configurations that jeopardized outcome performance (F(3, 21) = 12.68, p < 0.001, Fig 6.4c). The UCM<sub>ratio</sub> was reduced in the first and second relative to third (p < 0.05) and fourth (p < 0.05) sessions, and in the second relative to fourth session (p < 0.05). In summary, the results confirmed our experimental hypothesis and demonstrated that learning caused the selective minimization of destabilizing angular joint variance. The underlying control mechanism was composed of flexible yet complex inter-joint coupling.



**Figure 6.4.** Mean joint configuration variability per degree of freedom aligned on the uncontrolled manifold (V<sub>UCM</sub>) (a), the orthogonal subspace (V<sub>ORT</sub>) (b), and the ratio of V<sub>UCM</sub> to V<sub>ORT</sub> (c) for the finger coordinate control hypothesis. Error bars represent the within-subjects SEM. \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001.



**Figure 6.5.** The structure of joint configuration variance was influenced by training. The variability ellipses show the distribution of joint configuration variance across repetitive corrections performed within individual trials. Comparison by session demonstrates that joint configuration variance changed from an approximately equal distribution on ( $V_{UCM}$ ) and orthogonal ( $V_{ORT}$ ) to the UCM (a); Session1) to progressive stabilization by the constraint of motor solutions that detracted from the stability of the fingertip position ( $V_{ORT}$ ). The ellipse in (a) (Session 1) shows weak covariation amongst individual joint configurations, while (b)-(d) show progressive strengthening of error compensation between joints (reduction in  $V_{ORT}$  from Session 2 through Session 4).



**Figure 6.6.** Relationship between mean balancing time and the variability ratio  $(V_{UCM}/V_{ORT})$ .  $V_{UCM}/V_{ORT}$  predicted the mean balancing time and subjects who selectively minimized  $V_{ORT}$  performed better at the stick balancing task. Red circles represent ensemble-averaged individual subject data.

## Relationship Between Error Compensation Mechanisms and Performance

There was a significant linear relationship between the UCM<sub>ratio</sub> and stick balancing performance (Fig 6.6). Independent of learning, subjects who controlled kinematic joint error minimized variance in the fingertip position and performed best at the task (Session 1: F(1, 6) = 8.07, p < 0.05,  $R^2 = 0.573$ ; Session 2: F(1, 6) = 15.31, p < 0.01,  $R^2 = 0.718$ ; Session 3: F(1, 6) = 8.33, p < 0.05,  $R^2 = 0.580$ ; Session 4: F(1, 6) = 26.63, p < 0.01,  $R^2 = 0.804$ ).

# 6.5 – DISCUSSION

We undertook this experiment to examine changes in the coordination and control of individual joints during the acquisition of an inverted pendulum balancing task. We examined the variance and coupling of paired joint angle excursions to investigate task sharing between individual joints. We additionally performed a within-trial uncontrolled manifold analysis to examine learning-mediated changes in the structure of joint configuration variance. We focused on the differential management of joint variance that stabilized ( $V_{UCM}$ ) and destabilized ( $V_{ORT}$ ) the time-varying fingertip position. Our objective was to determine how individual joints are coordinated to control unstable objects.

We examined the variance and coupling of paired joint angle excursions to determine whether improved performance was mediated by changes in the stereotyped recruitment of individual joints. An important finding was that the variance of joint angle excursions did not increase with learning, and in contrast, we reported a systematic reduction in wrist joint variance across training sessions. This result opposes Bernstein's (1967) argument that motor learning involves three incremental stages differentiated by the initial freezing (rigid control) and progressive recruitment (flexible control) of individual joints. We additionally reported that the zero-lag cross-correlations between joint angle pairs were constant and could not have accounted for learning-mediated changes in performance. Taken together, our data oppose a strict freezing-to-freeing progression in motor learning but corroborate a growing body of evidence which has shown that joint recruitment patterns are task-dependent (Buchanan and Horak 1999; Konczak et al. 2009). Our results show that learning-mediated changes in motor coordination are more diverse than a strict

freezing-to-freeing progression and more complex than correlated paired joint angle outputs.

There are two possible mechanisms that may account for the decrease in wrist joint variance reported in this study. The wrist joint may have compensated for balancing errors in early-learning and was recruited progressively less as participants learned the task. Similar mechanisms have been proposed for reductions in lower limb joint variance when participants learn to control posture in the presence of sinusoidal platform oscillations (Ko et al. 2001). The second mechanism is that destabilizing wrist displacements may have arisen due to the inappropriate control of interaction torques generated during the ballistic upper limb corrective movements (Atkeson 1989). However, since the mass of the stick is negligible, the effect of these perturbations would likely be offset by neural mechanisms that compensate for the complexity of upper limb joint motion (Gribble and Scott 2002; Kurtzer et al. 2008).

What changed with learning and led to the systematic reduction of wrist joint variance? Certainly our data are consistent with a number of studies that reported learning-induced changes in joint variance (Anderson and Sidaway 1994; Young and Marteniuk 1998) to reduce end-effector variability in both single (Gabriel 2002) and multijoint tasks (Timmann et al. 2001). These results are difficult to interpret, however, because there is no straightforward mapping between individual joint angles and fingertip kinematics (Latash 2000). In view of this limitation, we performed an uncontrolled manifold analysis to further understand the complex interdependence of the angular joint kinematics.

A noteworthy finding was the differential management of joint variance that developed across experimental sessions. We reported a progressive decrease in overall joint variance and demonstrated that this effect was caused by the selective reduction of variance in the subspace of destabilizing joint angle configurations. In comparison, there were no changes in the amount of variance distributed on the invariant UCM subspace (V<sub>UCM</sub>). A number of studies have shown that learning can change the partitioning of motor variance between task-relevant and task-irrelevant dimensions, but these studies have generated conflicting results and there has been a lack of consensus regarding the specific function of motor learning (Latash et al. 2007). To that end, larger (Domkin et al. 2002), equal (Domkin et al. 2005), and smaller decreases (Yang and Scholz 2005) in  $V_{UCM}$  have been reported relative to  $V_{ORT}$ . These findings have prompted a number of explanations ranging from optimization criteria imposed to constrain motor responses on the basis of efficiency (Domkin et al. 2002; 2005) to a lack of novelty or insufficient practice in the to-be-learned motor task (Domkin et al. 2002). In contrast, we have shown that motor learning caused the preferential reduction of V<sub>ORT</sub>. Thus, our results are most consistent with the Frisbee task investigated by Yang and Scholz (2005), where the decrease in motor variance was largely confined to solutions that jeopardized the outcome of the toss (Yang and Scholz 2005). This is an important finding because the magnitude of V<sub>UCM</sub> corresponds to the use of flexible, outcome stabilizing joint configurations. In consideration of these findings, two questions are left outstanding: What is the significance of V<sub>ORT</sub> and why does it decrease with learning?

The reduction of  $V_{ORT}$  may be attributed to a number of factors. Variance in the timevarying finger positions might have arisen from imprecise sensory judgments about the
angular position and velocity of the stick (Jacobs 2009) or during the neural computation and execution of motor commands (Faisal et al. 2008). Both of these considerations would cause variance in the time-varying finger position, and presumably, could be circumvented by learning. However, could either of these factors account for the > 50% reduction in V<sub>ORT</sub> across the training period? We propose that V<sub>ORT</sub> was affected by state estimation processes used during the ballistic upper limb corrections.

The goal-specific processing of sensory feedback is a decisive factor in skilled motor behaviour (Scott 2004). The confluence between sensory and voluntary control processes has been formalized by the optimal feedback control framework (OFC) (Todorov and Jordan 2002), which suggests that the CNS constructs modifiable feedback control structures that use multimodal sensory inputs to formulate optimal motor responses (Diedrichsen, Shadmehr and Ivry 2010). According to OFC, the parsimony of motor behaviour is influenced by the integrity of two interrelated neural processes: state estimation and feedback control. It has been demonstrated that state estimation processes rely on neural representations that encode the physical properties of our limbs (Flanagan and Lolley 2001), environment (Gribble and Scott 2002), and manipulated objects (Mah and Mussa-Ivaldi 2003). These internal force-motion models are typically acquired prior to the development of task-specific control policies (Flanagan et al. 2003).

In our study, it is possible that the diminutive changes in  $V_{ORT}$  reflect the acquisition of accurate state estimation processes. This would situate our data in the context of the work by Mehta and Schaal (2002) that used brief intervals of visual feedback occlusion (600-ms) and force perturbation to show that state estimation processes are intimately linked to human balance control. Because the hand is the terminal segment of the upper

limb and possesses the least segmental inertia, a high-gain (servo-) mechanism could enable rapid feedback corrections to be enacted at the wrist independently of other joint motions. As subjects learned the dynamical representation between applied upper limb forces and the motion of the stick, the corresponding motor commands would become tailored to the state of the stick, reduce error, and decrease emphasis on these compensatory wrist displacements. Our proposition that  $V_{ORT}$  is influenced by state estimation processes leads to a number of verifiable predictions. If  $V_{UCM}$  and  $V_{ORT}$  arise from distinct processes, then we anticipate that an increase in the uncertainty of sensory information (variability and not bias) will cause a selective increase in  $V_{ORT}$  while preserving the integrity of multijoint error compensation. The influence of sensory feedback on the task-specific distribution of motor variance will likely be an important direction for future research.

In conclusion, we have shown that the UCM<sub>ratio</sub> predicted stick-balancing performance. We additionally demonstrated that joint configurations that jeopardized the outcome of the task were selectively eliminated with practice to engender incremental changes in performance. Our data have implications in understanding the relationship between sensory feedback and motor variance. We anticipate this approach will be a fundamental step in linking the higher-order structural properties of motor variance to the underlying estimation and control processes.

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Chapter 7 – General Discussion

# 7.1 – THESIS SUMMARY

Goal-directed motor tasks commonly require the use of objects, tools and implements to interact with our environment. Dynamic object interactions can vary in terms of the rigidity, geometry and stability of manipulated objects, yet we formulate adaptive motor responses that accommodate differences in the task, context and object mechanics. Knowledge of the underlying control mechanisms and learning processes is imperative to understanding the basis of skilled object manipulation. The five studies presented in this thesis used an inverted pendulum (i.e., stick) balancing paradigm to investigate skill acquisition and elaborate the task and context-dependent attributes of unstable object control.

We hypothesized that learning would mediate the functional integration of posture and upper limb dynamics and expected changes in the task demand and context to be reflected in the control of posture and the upper limb. In addition, we examined joint angle variance with the expectation that skilled performers co-vary individual joint configurations to stabilize the position of their fingertip (i.e., inverted pendulum pivot). To address our hypotheses, we performed a comprehensive evaluation of posture (Chapters 4 and 5), upper limb (Chapters 2, 3, 4, 5 and 6) and individual joint kinematics (Chapter 6). Our behavioural approach has provided knowledge about the circumstantial properties of unstable object control at multiple levels of the motor system. The following sections provide a summary of each study and outline future research directions.

# 7.2 – LEARNING AND CONTEXT-MEDIATED ATTRIBUTES OF UNSTABLE OBJECT CONTROL

In Chapters 2 and 3, we devised a stick balancing task that required a cylindrical wooden dowel to be balanced at the fingertip. We examined the context-dependent attributes of unstable object control by imposing two alternate balancing postures— seated and standing. Compared to the standing posture, seated balance imposed a limitation on the biomechanical degrees of freedom to be recruited for task performance (Chapters 2 and 3). At issue in these studies was the investigation of how we learn to control unstable objects and to specify if learning and control are dependent on the balancing context.

Chapter 2 evaluated the learning and context-dependent attributes of upper limb control. We found that the length of balancing trials (i.e., outcome performance) increased systematically across training sessions and further explored this result in terms of the statistical properties of upper limb kinematics. We used a regression analysis to fit our data to theoretical Lévy distributions and evaluate the truncation and scaling of upper limb kinematics (Cabrera and Milton 2004b). We found that motor learning caused systematic changes in task performance and a corresponding increase in the prevalence of rapid upper limb displacements. Another important finding was the stringent constraint imposed on upper limb control by differences in the balancing context. We found that the distribution of upper limb kinematics was truncated in seated balance and large changes in fingertip speed were uncommon.

Chapter 3 was motivated by Cabrera and Milton's (2002) observation that angular stick fluctuations occur on timescales shorter than estimated voluntary control delays (~100-ms) and show amplitude variations that are characteristic of on-off intermittency—

periods of low amplitude fluctuations that alternate with epochs of feedback-driven corrections. Provided that angular stick fluctuations are intermittent, we hypothesized that upper limb displacements would be composed of two independent timescale components differentiated by their correlative properties. We additionally hypothesized that the temporal structure of upper limb corrections would be modulated by the balancing context. We used a numerical phase space reconstruction method (cf. Webber and Zbilut 1992; Marwan et al. 2007) to determine whether the switching time to feedback control was dependent on motor learning and the balancing context.

We demonstrated that upper limb displacements are indeed composed of two independent timescale components: a fast stochastic component and slow feedback control. On that note, we found that the discontinuity, stability and regularity of upper limb displacements changed systematically across training sessions. Another important finding was the differential control evoked by changes in the balancing context. We found that the average time interval between upper limb corrections was substantially shorter for seated balance. In accordance with previous research (Cabrera et al. 2006), we have argued that fast fluctuations transiently stabilize the inverted pendulum and over brief time intervals accomplish some of the nuanced properties of voluntary control (Cabrera and Milton 2002; Cabrera and Milton 2004a, b). In summary, we have shown that the distributional properties of upper limb kinematics (Chapter 2) and the interplay between stochastic and corrective motor processes are dependent on the balancing context and expertise (Chapter 3).

Collectively, Chapters 2 and 3 provided convergent evidence on three important features of unstable object control. First, learning-mediated changes in the scaling,

truncation and spatiotemporal properties of upper limb kinematics reflected the tuning of balance control to optimize performance (Chapters 2 and 3). Second, stick-balancing performance was dependent on differential upper limb control evoked by changes in the balancing context. Subjects switched more rapidly from fluctuating to corrective upper limb displacements in seated balance (Chapter 3) and the speed of corrections was substantially more variable for standing balance (Chapter 2). Third, while it has been argued that unstable objects are balanced using continuous model-based control mechanisms (Mehta and Schaal 2002), several studies have indicated that complex human balancing tasks are performed using intermittent corrections (Cabrera and Milton 2002; Milton et al. 2009; Loram and Lakie 2002; Loram et al. 2006; 2009; 2011; Gawthrop et al. 2011). Our observation that upper limb kinematics were composed of two independent timescale components (Chapter 3) corroborated that the stick balancing control mechanism is intermittent. In conjunction with Milton et al., we have argued that intermittent control likely arises from the expertise-dependent interplay between feedback control and motor variability (Cabrera and Milton 2002; Cabrera and Milton 2004a; Milton et al. 2009), but, importantly, we have shown that the interplay between stochastic motor processes and feedback control is modulated by differences in the balancing context.

In addition to elaborating the learning and context-dependent features of unstable object control, the results of Chapter 2 raised concern for computational studies that employ the Kalman filter algorithm (Kalman 1960). The problem is that motor noise is assumed to be Gaussian distributed and additive (Wolpert et al. 1995; Wolpert et al. 1998), while in comparison we have shown that upper limb kinematics are Lévy

distributed (i.e., heavy-tailed) for stick balancing. This is an important finding since the default state observer in sensorimotor control models is the Kalman filter (cf. Mehta and Schaal 2002; Denève et al. 2007). Our data indicate that the accuracy of the Kalman filter is likely dependent on contextual factors and subject expertise and indicate that these factors likely require explicit experimental control or the use of suitable estimation algorithms (Gordon et al. 2006; Sinha et al. 2007). Further investigation may help resolve the paradox where, on the one hand, it is well understood that the variability of muscular force production increases with the mean amplitude of force produced, yet it is commonly assumed that the state-dependent component of motor noise is negligible (cf. Todorov 2005 for a similar argument).

# 7.3 – TASK-DEPENDENT PROPERTIES OF UNSTABLE OBJECT CONTROL

Chapter 4 examined the task-dependent properties of posture and upper limb control. Our focus was to determine whether task instruction influenced the stochastic (i.e., drift or open loop) or feedback component (i.e., corrective or closed loop) of unstable object control (Milton et al. 2009). We expected that explicit task instruction would elicit differential feedback control and evaluated our hypothesis by decomposing posture and upper limb displacements into open loop and corrective feedback components based on the correlative properties of time series (Collins and DeLuca 1994; 1995).

An important result was that conjoint cognitive load caused a reduction in the average switching time from open loop displacements to feedback control. This change reduced the variability of posture and upper limb kinematics and elicited a shift toward lower mean power frequency composition. A notable finding was that cognitive load caused a reduction in the persistence (i.e., autocorrelation) of short timescale posture and upper

limb displacements. This was an intriguing result because in comparison to voluntary control, we know very little about the task-modulation of short timescale motor processes. Though numerical simulations have shown that fast control (i.e., short latency) may be linked to the tuning of parametric motor noise (Cabrera et al. 2006; Milton et al. 2009), further research is required to clarify the underlying neurophysiological processes. One possibility is that short timescale activity reflects joint impedance control achieved by the co-contraction of upper limb agonist and antagonist muscle pairs. Upper limb cocontraction is known to be modulated by the instability of mechanical loads and the accuracy demands of goal-directed behaviour (Gribble et al. 2003; Milner and Cloutier 1993; 1995; 1998; Osu et al. 2004; Visser et al. 2004), and a relevant finding is that elbow joint impedance is used to reduce the variability of hand motion caused by statedependent motor noise (Selen et al. 2005). If subjects use joint impedance (i.e., muscle co-contraction) to modulate the variability of short timescale upper limb displacements, then it is conceivable that joint impedance would scale to the task difficulty evoked by balancing short, light sticks. Further investigation may provide important insight about the control of short timescale motor variability in human balancing tasks.

An influential theory in motor control is that outcome performance is dependent on the focus of attention. A reproducible finding has been that task instruction or feedback that induces an external focus facilitates the self-regulatory processes or automaticity of motor performance (Kluger and DeNisi 1996; Lohse et al. 2010; Wulf et al. 2010). In contrast, self-focused attention has been shown to induce excessive, superfluous corrections. In Chapter 4, we used explicit attentional instructions to investigate the taskdependent properties of unstable object control. We found that performance variability

and the time interval for switching to corrections increased regardless of whether the focus of attention was outcome or execution-oriented. We speculated that this finding was caused by the shift to a slower (presumably conscious; cf. Loram et al. 2009) corrective mechanism. Thus, explicit instruction caused variable task performance and demonstrated that focused attention is counterproductive for skilled stick balancers (Beilock et al. 2002a, b; Beilock et al. 2004; Gray 2004; Beilock et al. 2008). Our data cannot rule out, however, that outcome-oriented motor attention may facilitate learning, and further research will be required to characterize the learning-dependent relationship between motor attention and performance (McNevin et al. 2003; Wulf et al. 2010; Freudenheim et al. 2010). One explanation for why we did not replicate the enhancing effect of outcome-oriented motor attention is that the relationship between attention and performance is confounded by expertise. In that case, two tenable hypotheses are that (1) naïve or novice subjects lack the task knowledge and resources to accommodate secondary task performance (Beilock et al. 2002b; Milton et al. 2004; 2008) and (2) outcome-oriented feedback facilitates motor learning and retention (Todorov et al. 1997; Shea and Wulf 1999; Malone and Bastian 2010).

In short, an important component of this thesis was to evaluate posture and upper limb mechanisms that are involved in the control of unstable dynamical objects. A key result in Chapter 4 was that task instruction and cognitive load evoked similar modifications in posture and upper limb control. The task-mediated similarity of posture and upper limb control supports the emerging argument that voluntary control is supported by the task-dependent recruitment and control of posture.

# 7.4 – POSTURE-UPPER LIMB COUPLING IS MEDIATED BY MOTOR LEARNING

Complex motor tasks often require the coordination of postural control and voluntary movement. In view of these considerations, a comprehensive theory of motor learning is required to explain how specialized motor systems are integrated into goal-specific interactions (Bingham 1988; Bernstein 1996; Newell et al. 2001). In Chapter 5, we asked whether stick balancing expertise would mediate the reorganization of postural control, and also, if motor learning influenced the sophistication of posture-upper limb interactions. Building on work by Huys et al. (2003; 2004a, b), we hypothesized that learning would elicit common changes in posture and upper limb control and evoke systematic increases in the sophistication of posture-upper limb interactions. To address our hypothesis, we performed an innovative analysis that investigated the learning-dependent coupling of posture and upper limb dynamics (cf. Marwan et al. 2007). We interpreted our results from the perspective of a hierarchical learning model (Newell et al. 2001) and this study was among the first to quantify learning and control at multiple levels of the motor system.

Our results corroborated Newell et al.'s (2001) model and demonstrated that skill acquisition involved two independent learning processes. First, we found that posture and upper limb control were governed by intermittent balancing strategies (as shown in Chapter 4) and that the time interval between corrections increased systematically across the investigated training period. The second learning effect involved the incremental occurrence and lengthened coupling of correlated posture-upper limb trajectories. In agreement with Newell et al.'s (2001) model, our data have shown that independent

subsystems at lower levels of the motor hierarchy are organized into task-specific interactions that stabilize outcome performance (Newell et al. 2001).

We argued that posture-upper limb coordination is likely contingent on a statedependent (de)coupling mechanism and we have additionally proposed that the abrupt decoupling of posture-upper limb trajectories is caused by the instability of subsystem dynamics. Our rationale is supported by the observation that human feedback parameters are often tuned near instability (Kelso 1995). Thus, we anticipate that perturbing forces applied to the tip of the stick would induce the abrupt dissociation of posture-upper limb coupling to enable independent subsystem corrections. State-dependent posture-upper limb coupling is a plausible control mechanism and is similar to the spontaneous recruitment of body segments that has been shown to intermittently stabilize intereffector coordination (Buchanan et al. 1997; Buchanan and Kelso 1999).

In summary, we have provided novel insight about the sophistication of posture-upper limb interactions, but an important direction will be to specify the precise mechanism(s) that give rise to the abrupt (de)coupling of posture and upper limb control. This question can be addressed by extending the method developed in Chapter 6 to investigate the learning-dependent interplay between posture and upper limb corrections. Our finding that fingertip and postural displacements are on average positively correlated over short time intervals suggests that subjects may destabilize posture to facilitate rapid changes in the upper limb position (Chapter 4; Fig. 4.7). In comparison, it appears that compensatory postural adjustments are performed much later in the correction. In short, stick balancing is a complex task that involves ballistic upper limb corrections that cause postural

disequilibrium. Further investigation is required to specify how the central nervous system stabilizes these simultaneous but conflicting task goals.

Another interesting possibility is that object manipulation requires the task and context-dependent modification of posture-upper limb coupling. It is conceivable that posture-upper limb coupling shows much, if not all, of the circumstantial properties of posture and upper limb control. A key step for addressing this hypothesis will require the investigation of posture-upper limb coupling in alternate balancing postures—e.g., while standing upright in a heel-to-toe stance or on altered or reduced base of support. A tenable hypothesis is that modification of the support surface will cause the differential and direction-specific control of posture and the upper limb. An important development will be to determine whether the dynamical properties of the posture-upper limb interaction show similar context modulation.

# 7.5 – MOTOR LEARNING ALTERS THE STATISTICAL PROPERTIES OF MULTIJOINT CONTROL

A common theory in motor learning is that skill acquisition is dependent on intereffector coordination. In Chapter 6, we asked whether unstable object control is mediated by changes in the variance of individual joint excursions (i.e., task sharing) or multijoint error compensation (i.e., flexible joint control). To address this question, we computed the variance and coupling of paired joint angle excursions and examined the expertisedependence of individual joint recruitment patterns. We additionally investigated differences in the structural properties of joint angle variance across training sessions. We developed a simple technique to quantify the within-trial structure of motor variance and used this measure to implement an uncontrolled manifold analysis. Based on previous work, we hypothesized that the time-varying fingertip position would be controlled by

multijoint error compensation. Accordingly, we expected that the neural controller would selectively minimize joint angle variance that destabilized outcome performance (Latash 2000; Latash et al. 2002; Yang and Scholz 2005; Latash et al. 2007). This was the first study to investigate the joint coordination mechanisms that govern unstable object control.

We found that changes in individual joint angle excursions were inconsistent with those predicted by the task-sharing perspective. Specifically, we showed that joint angle excursions were relatively constant, but reported a systematic reduction in wrist joint variance across training sessions. This result opposed Bernstein's (1967) classic theory that motor learning involves three incremental stages based on the initial freezing and progressive recruitment of individual joints. In conjunction with other authors, we have argued that joint recruitment patterns are task-dependent and do not necessarily follow a freezing-to-freeing progression with motor learning (Buchanan and Horak 1999; Ko et al. 2001; Konczak et al. 2009).

An important finding was the differential management of joint variance that emerged across training sessions (Scholz and Schöner 1999; Todorov and Jordan 2002). In confirmation of our hypothesis, we found that the selective constraint of destabilizing (i.e., task-relevant) joint angle variance was the mechanism underlying incremental changes in performance. Our results are consistent with a number of studies that reported the selective control of task-relevant motor variables in load stabilization (Sun et al. 2011), object transport (Gera et al. 2010) and postural control tasks (Hsu et al. 2007). The common finding that motor variability ellipses are elongated on the uncontrolled manifold indicates that neural control mechanisms preferentially minimize variance in

task-relevant movement parameters while satisfying the task demand via the flexible recruitment of individual effectors (Liu and Todorov 2009). A logical extension of this work would be to determine whether the differential management of joint variance scales to the specific task and contextual demands of behaviour. Future work could use our paradigm to determine whether the selective constraint of destabilizing joint variance scales to the task difficulty associated with balancing shorter sticks.

We argued that the reduction of wrist joint variance likely reflected the acquisition of sensorimotor transformations that relate the forces applied at the fingertip to the corresponding angular stick motion. Our rationale is supported by the observation that state estimation processes are implicated in the control of unstable objects (Mehta and Schaal 2002; Mah and Mussa-Ivaldi 2003) and we anticipate that the reduction in wrist joint recruitment paralleled the acquisition of the stick-balancing force-motion model. It would be beneficial for future research to delineate the relationship between state estimation and the enigmatic structural features of motor variance. This would be a fundamental step in linking the higher-order structural properties of motor variance to the underlying neurophysiological processes.

### 7.6 – CONCLUDING COMMENTS

In summary, we examined posture, upper limb and multijoint control processes involved in the control of unstable dynamical objects. This thesis has provided an innovative approach for the investigation of motor subsystem interactions and we are among the first to quantify learning at multiple levels of the voluntary motor system. Our technique has provided important insight about the mechanisms that bind posture and upper limb control into functional, task-specific interactions. Another important facet of this thesis

was to underscore the task and context-dependent properties of unstable object control. We have provided knowledge about the functional attributes of unstable object control and specified how they were modulated by the balancing task and context. A promising focus for future work would be to further investigate the influence of physiological, task and contextual factors to the event-driven control of unstable objects. The final focuses of this thesis were to delineate multijoint control processes, to specify how they were refined through motor learning, and to relate these processes to the integrity of unstable object control. We demonstrated that flexible, error-compensating joint coordination mechanisms stabilize the inverted pendulum and take precedence over the rigid recruitment of individual joints. We showed that the differential management of destabilizing joint variance was an important determinant of stick balancing performance. This finding encourages future work to investigate structural variability changes and their functional significance in motor skill acquisition.

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