

Learning a stick-balancing task involves task-specific coupling between posture and hand displacements

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Received: 25 January 2011 / Accepted: 9 June 2011 / Published online: 26 June 2011
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Abstract Theories of motor learning argue that the acquisition of novel motor skills requires a task-specific organization of sensory and motor subsystems. We examined task-specific coupling between motor subsystems as subjects learned a novel stick-balancing task. We focused on learning-induced changes in finger movements and body sway and investigated the effect of practice on their coupling. Eight subjects practiced balancing a cylindrical wooden stick for 30 min a day during a 20 day learning period. Finger movements and center of pressure trajectories were recorded in every fifth practice session (4 in total) using a ten camera VICON motion capture system interfaced with two force platforms. Motor learning was quantified using average balancing trial lengths, which increased with practice and confirmed that subjects learned the task. Nonlinear time series and phase space reconstruction methods were subsequently used to investigate changes in the spatiotemporal properties of finger movements, body sway and their progressive coupling. Systematic increases in subsystem coupling were observed despite reduced autocorrelation and differences in the temporal properties of center of pressure and finger trajectories. The average duration of these coupled trajectories increased systematically across the learning period.

In short, the abrupt transition between coupled and decoupled subsystem dynamics suggested that stick balancing is regulated by a hierarchical control mechanism that switches from collective to independent control of the finger and center of pressure. In addition to traditional measures of motor performance, dynamical analyses revealed changes in motor subsystem organization that occurred when subjects learned a novel stick-balancing task.

Keywords Dynamics · Motor learning · Inverted pendulum · Centre of pressure · Dynamic coupling · Supra-postural task · Coordination

Introduction

The ability to acquire and perfect complex motor skills raises a number of questions about voluntary motor control and learning. An exemplary skill is balancing an inverted pendulum (stick) on the fingertip, which requires rapid but precise control of hand displacements. Experiments have therefore been developed to delineate control mechanisms underlying skilled behavior, and additionally, the processes by which these representations are learned. A standard approach has been to examine 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)—motor variables are combined into coordinative relationships that are modified by learning and facilitate task performance. Though a great

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deal of knowledge has been generated about learning and the organization of movement, little is known about coordination patterns 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 coordination of the upper limbs to bring 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 limb segments must be integrated and processed to enable feedback-based swing corrections. Batting performance is therefore dependent on time-varying contributions made by posture, sensory, and voluntary motor subsystems.

Task-specific subsystem interactions have been a topic of interest in theories of motor control and learning (Bingham 1988; Bernstein 1996). Recently, Newell et al. (2001) argued that changes in motor performance are the product of an evolving set of sensory and motor subsystems that are organized hierarchically. Their model distinguished between: (1) local physiological microphenomena (e.g., electromyography, cortical activity) that evolve on the temporal order of milliseconds to seconds, (2) coordination between subsystems (e.g., posture and limb movement patterns) that changes on the temporal scale of minutes to hours, and (3) macrophenomena that are defined by outcome performance and evolve over months to years. Newell et al. (2001) proposed that reciprocal coupling functions exist between levels of the hierarchy so that individual effectors are organized into functional subsystem interactions that support performance. Though the hierarchical learning model entertains a theoretical appeal, it leaves unresolved questions about coordinative subsystem interactions and how they influence 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 that make differential contributions to performance. Object manipulation tasks can therefore provide key insight about subsystem coupling when the physics and temporal

properties of limb movements are dependent on environmental objects (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 control principles underlying human interaction with unstable 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 initiate corrections is limited (proportional to the square root of stick length), finger displacements are characterized by a series of ballistic corrections that stabilize the vertical stick position (Milton et al. 2009; Cluff et al. 2009). Notwithstanding the merit of this approach, these studies were limited to processes that stabilize the vertical stick angle. Additionally, stick balancing requires control of the balancing posture. To account for this control duality, this study will address the following questions: (1) “Is the acquisition of stick-balancing skill accompanied by a 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 subsystem interactions in motor control and learning.

We examined how learning affected correlative movement properties within (autocorrelation) and between (crosscorrelation) 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 hypothesized that average balancing times would increase as a function of learning to demonstrate that subjects more effectively performed the task. Nonlinear time series and phase space reconstruction methods were used to determine how individual subsystem dynamics (COP, finger) and their interactions changed as a function of learning. Two experimental problems were addressed. First, we investigated whether learning influenced the relationship between COP and finger trajectories. Second, we examined the temporal structure of finger-center of pressure (F-COP) trajectories to determine the effect of learning on dynamical interactions between posture and finger motor responses. 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 a modification in postural mechanisms that stabilize the multisegmented body, 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 displacements.

Methods

Subjects

Eight (5 females, 3 males) healthy, university-aged subjects (24.5 ± 2.35 years) of similar height (173 ± 5.82 cm) and weight (67 ± 9.4 kg) participated in the study. Prior to the experiment, 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 prior to the experiment. Subjects were remunerated for their time and were free to withdraw from the study without penalty. All subjects completed the experiment.

Protocol

Subjects learned to balance a cylindrical wooden stick on their index finger while standing in an upright posture. Learning was quantified over four experimental sessions. Data collection sessions took place every fifth day and were about 90 min in duration. Subjects performed 30 min of daily practice between experimental sessions. A log was maintained by the experimenters to ensure that each subject maintained their practice schedule.

Prior to the first learning session, twenty trials were performed during the recruitment session to ensure that subjects 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 time available for the subject to make corrections, respectively. Subjects stood with their feet approximately shoulder width apart during trial performance. Each subject's preferred stance was recorded to

ensure their balancing stance was consistent across trials and learning sessions.

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, subjects were instructed to balance the stick for as long as possible and to engage lower and upper extremity segments while remaining stationary in their preferred stance. If this criterion was not met, the trial was excluded from further analysis, data collection was repeated for that trial, and the subject was reminded to maintain a stationary upright stance. 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, physical or attentional fatigue.

Equipment and apparatus

Reflective spherical markers (14 mm) were attached to the top and bottom of the stick. 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 autolabelled, and the three-dimensional marker positions were reconstructed from individual camera views offline with the VICON Nexus software. COP time series and vertical ground reaction forces were collected using two adjacent strain gauge force platforms (AMTI OR6-2000; Newton, MA, USA) sampled at 750 Hz. The force platforms were separated by a 5 mm distance. Ground reaction force and centre of pressure data were processed offline in MATLAB™ 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 spatiotemporal properties 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

neighborhoods 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 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 neighborhoods of phase space for finite time intervals. LAM measures the global 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 time duration of laminar trajectory phases. Transitions between constant and fluctuating dynamics are a defining feature 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 learning-induced changes in posture and finger dynamics, and cross-recurrence quantification analysis was used to investigate the evolving interaction between posture and stick balancing corrections.

Prior to the analysis, COP and finger time series were downsampled using a five-sample, windowed-moving-average with no overlap (effective sampling rate = 150 Hz). We downsampled the data to minimize the numerical sensitivity of phase space reconstruction methods to measurement noise. The first step in the phase space reconstruction was to compute the embedding delay (τ_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 (τ_e) corresponding to the minimum mutual information was selected because it is the best numerical approximation to the critical system delay. Median embedding delays were contrasted using a one-way analysis of variance (ANOVA) with repeated-measures over the session (4 levels) factor. Statistical analysis demonstrated that median embedding delays were similar between sessions ($P > 0.1$) and the pooled median embedding delay was used 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 neighbors method (Kennel et al. 1992; Abarbanel 1996). False nearest neighbors 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; the neighbors of a given point in phase space are mapped onto equivalent neighbors 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 repeated-measures over the session (4 levels) factor. D_e was not significantly different across sessions ($P > 0.05$). Therefore, we used the pooled median embedding dimension (Table 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 (τ_e), embedding dimension (D_e), and (cross-) recurrence radii (χ) for individual subsystem (COP and finger) and collective dynamics (F-COP) are reported in Table 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, COP_j represents the radial COP at point $j = 1, 2, 3, \dots, n$, 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 greater amplitude but 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.

We used the same downsampled (by factor 5) COP time series that were used for (cross-) recurrence quantification analysis. The first step in the dynamical intermittency analysis was to compute the COP speed. The COP speed was computed as the resultant Euclidean speed,

Table 1 Parameters for phase space reconstruction and (cross-) recurrence quantification analysis

	Embedding delay τ (ms)	Embedding dimension D_e	Radius, χ (% MAXDIST)	Minimum line length LMIN
RQA COP	36	4	10	5
RQA fingertip	45	4	10	5
CRQA	50	3	10	5

The embedding delay, τ , 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, χ , was chosen so that RR was between 1 and 3%

$s_{\text{COP}}(t) \equiv \|(\vec{r}_{\text{COP}}(t + \Delta t) - \vec{r}_{\text{COP}}(t))/\Delta t\|$, where $\vec{r}_{\text{COP}}(t)$ corresponded to the radial COP at time t , $\vec{r}_{\text{COP}}(t + \Delta t)$ was the COP at time $t + \Delta t$, Δt was the time step between successive observations (67 ms), and $\|\cdot\|$ represented the Euclidean vector norm. The detrended COP speed, $\Delta s_{\text{COP}}(t)$, was computed as the two-point difference in COP speed, $\Delta s_{\text{COP}}(t) = s_{\text{COP}}(t + \Delta t) - s_{\text{COP}}(t)$, where $s_{\text{COP}}(t + \Delta t)$ was the radial COP speed at time $t + \Delta t$ and $s_{\text{COP}}(t)$ was the COP speed at time t . This expression removed time-dependent linear trends of duration ≥ 67 ms. To ensure bins were adequately defined, the normalized frequency histograms for laminar phases were reconstructed from all trials collected within each session.

Threshold crossing changes in COP speed were determined according to the expression $\text{COP}(j) = \Theta(\varepsilon - |\Delta s_{\text{COP}}(j)|)$, where Θ was the Heaviside function and ε was the threshold change in COP speed, which we defined using the 95th percentile root-mean-square COP speed increment. Specification of the threshold COP speed is not a critical factor in the analysis but must be sufficient to enable detection of an adequate number of threshold crossings (Cabrera and Milton 2004). We chose the 95th percentile root-mean-square 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; 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 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 frequency histogram of laminar phase lengths with bin size set to 10 ms. The power law exponent α was computed by regressing $P(\delta t)$ onto δt on two logarithmic axes according to the relationship, $P(\delta t) \propto \delta t^{-\alpha}$. α determines the decay in the probability for laminar phase lengths: Reduced α -values correspond to 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. 1.

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 vector between states. In contrast, our dynamical intermittency analysis is a time series technique where dynamical states are considered constant if they are below the specified threshold. The intermittency and recurrence-based measures are expected to produce qualitatively similar results; however, recurrence analysis is performed in a reconstructed phase space with a dimension that is appropriate for the dynamics. It may therefore be expected that (cross-) recurrence analysis is more sensitive to changes in individual and coupled subsystem dynamics.

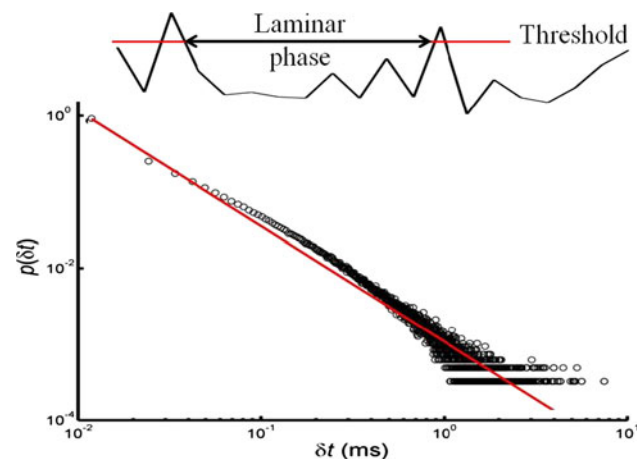


Fig. 1 Numerical method used to compute the occurrence, time duration and scaling law describing center of pressure laminar phase lengths. **a** Radial center of pressure time series with 95th-percentile change in speed threshold (horizontal black line). **b** Power law scaling for the probability distribution of center of pressure laminar phase lengths (δt). Similar numerical procedures were used for finger and finger-center of pressure trajectories (see text for further details)

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 our performance measure, mean balancing time, across learning sessions (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 (α) 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 ($\log_{10}(\delta t^{-\alpha})$). The statistical contrast was implemented using a one-way ANOVA with repeated-measures over experimental sessions. The scaling exponent (α) 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.

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 across sessions (Fig. 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 ($P < 0.001$), second ($P < 0.001$), and third ($P < 0.05$) learning sessions, and for the second and third relative to first session ($P < 0.05, P < 0.01$, respectively). These results corroborate our hypothesis that average balancing trial lengths would improve as a function of learning. In the ensuing sections, we will interpret our results in relation to these learning-dependent changes in performance.

Recurrence quantification analysis: centre of pressure trajectories

Recurrence rate (RR) is a nonlinear measure that quantifies the global regularity of time-varying states without accounting for the temporal properties of that regularity.

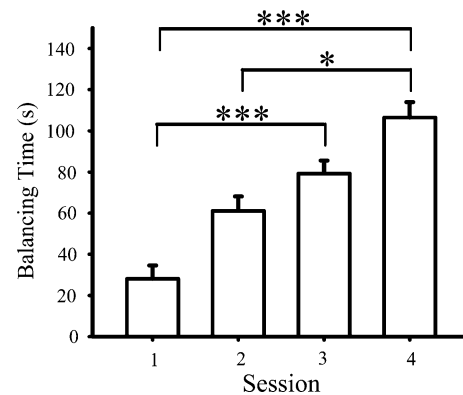


Fig. 2 Change in stick balancing performance across learning sessions. Results are reported as mean balancing times (in units of seconds) ensemble-averaged over individual subjects. Error bars represent the within-subjects SEM. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

We used RR to monitor the spatial regularity of COP trajectories (RR_{COP}) across experimental sessions. Figure 3a summarizes the learning effect observed for RR_{COP} . 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_{COP} 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 neighborhood of phase space. Practice increased the occurrence of laminar COP (LAM_{COP}) trajectory segments ($F(3, 21) = 3.68, P < 0.01$). Figure 3b summarizes the learning effect. LAM_{COP} was reduced at session 1 relative to every other session ($P < 0.05$). Further, the trapping time measure (TT_{COP}) demonstrated that the average length of laminar COP phases increased with learning ($F(3, 21) = 9.15, P < 0.001$). TT_{COP} was reduced in the first relative to third ($P < 0.01$) and fourth ($P < 0.01$) learning sessions (Fig. 3c). 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, COP excursions became discontinuous and increasingly separated in time. The results support our hypothesis that COP trajectories would be modified by learning to support stick balancing performance.

Recurrence quantification analysis: fingertip trajectories

Figure 4a shows a decrease in the regularity of finger trajectories with learning. Statistical analysis confirmed the learning effect for RR_{Finger} ($F(3, 21) = 11.37, P < 0.001$).

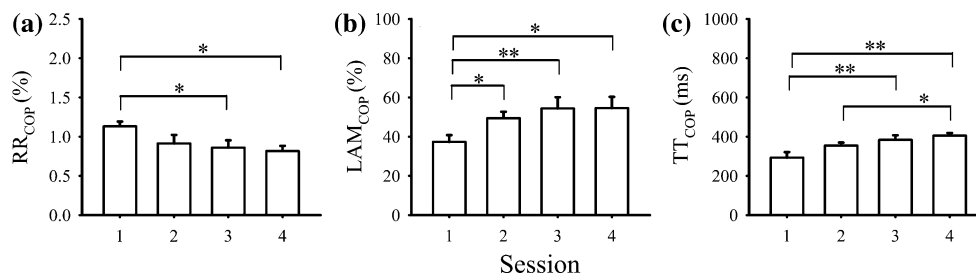


Fig. 3 Center of pressure dynamics were modified by learning. **a** Recurrence rate of center of pressure trajectories by session. Decreased RR_{COP} reflects a reduction in the regularity of center of pressure time series. **b** Discontinuity of center of pressure trajectories by session. Greater LAM_{COP} corresponds to an increase in the incidence of correlated center of pressure trajectory segments.

c Average trapping time (units of ms) of center of pressure trajectories across sessions. Greater TT_{COP} indicates a lengthening of the average time interval between successive center of pressure corrections. Error bars correspond to the within-subjects SEM. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

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 4b shows a learning-dependent increase in the discontinuity of finger trajectories. The learning effect for LAM_{Finger} was confirmed by statistical analysis ($F(3, 21) = 8.033$, $P < 0.01$). RR_{Finger} may have decreased as a function of learning, but these recurrent finger states evolved in correlated time segments. To supplement this finding, we examined the average duration of laminar finger trajectory phases (TT_{Finger}). Figure 4c shows that learning caused an increase in TT_{Finger} across sessions. TT_{Finger} was reduced in the first compared with the third ($P < 0.01$) and fourth ($P < 0.001$) sessions. In summary, learning resulted in a monotonic increase in the length of laminar finger phases. The data support our hypothesis and previous learning data (Cluff et al. 2009) by demonstrating that stick-balancing finger inputs become less correlated (RR) as a function of learning, discontinuous and increasingly separated in time (LAM and TT).

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 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 coupling between finger and COP displacements would increase as a function of learning.

Figure 5b demonstrates that LAM_{F-COP} increased as a function of learning ($F(3, 21) = 10.59$, $P < 0.001$). LAM_{F-COP} 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 sessions ($P < 0.05$). Similar to the effect reported for LAM_{F-COP} and consistent with our hypothesis, learning resulted in prolonged (TT_{F-COP}) intervals of coupled finger and COP dynamics ($F(3, 21) = 3.33$, $P < 0.05$). TT_{F-COP} was

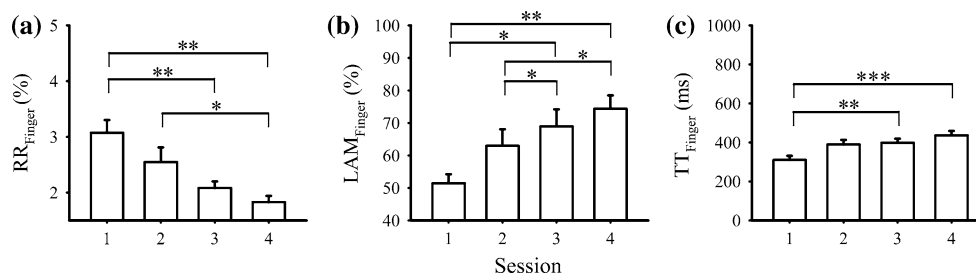


Fig. 4 Finger dynamics across the learning period. The interpretation of dynamical variables is as in Fig. 3. **a** Regularity of finger trajectories (RR_{Finger}) across learning sessions. **b** LAM_{Finger} by

session. **c** Average length of laminar finger trajectory segments (TT_{Finger} ; units of ms) across sessions. Error bars represent the within-subjects SEM. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

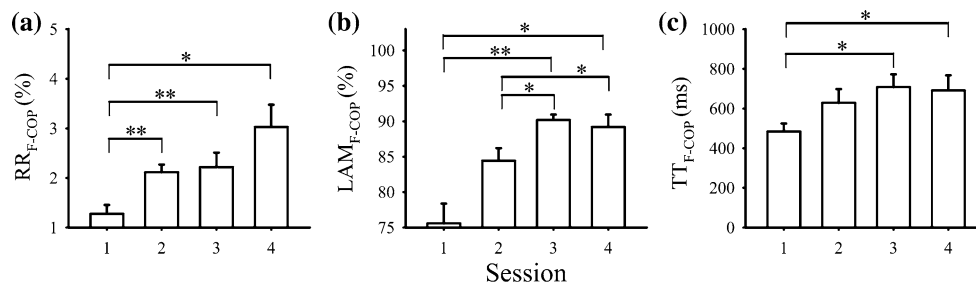


Fig. 5 Coupling strength and dynamical properties of the finger-center of pressure interaction. **a** Recurrence rate of coupled F-COP trajectories by session. An increase in RR_{F-COP} reflects the tendency for collective control over finger and COP displacements. **b** LAM_{F-COP} measures transitions between coupled and uncoupled F-COP

trajectories. Greater LAM_{F-COP} reflects an increase in the density of coupled F-COP trajectory segments. **c** Average length of coupled F-COP trajectories by session (TT_{F-COP} ; units of ms). Error bars are the within-subjects SEM. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

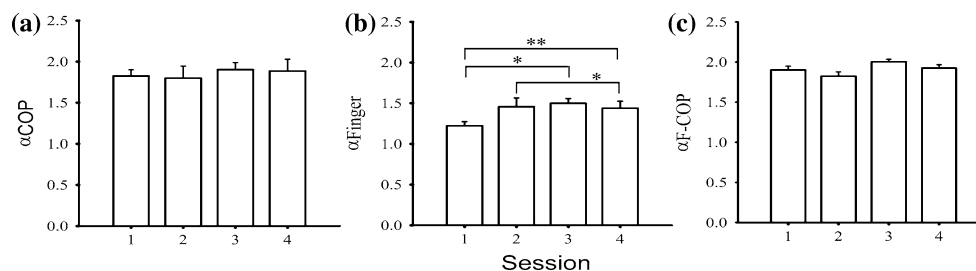


Fig. 6 Laminar COP, Finger and F-COP trajectory phases showed decay properties characteristic of on-off dynamical intermittency. Power law scaling in the decay of **a** COP, **b** Finger, and **c** F-COP trajectories. A reduction in the scaling law (α) corresponds to an

increase in the average time interval between successive corrections. Error bars correspond to within-subjects SEM. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

reduced in session 1 relative to session 4 ($P < 0.05$). The data are summarized in Fig. 5c. Our results demonstrated that F-COP coupling is present on multiple time scales in stick balancing.

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 6b shows that learning caused a decrease in the scaling exponent α_{Finger} ($F(3, 21) = 7.56$, $P < 0.01$). The decrease in α_{Finger} corresponds to an increase in the average duration of laminar finger phases. The learning effect occurred primarily at the first session; α_{Finger} was greater 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. 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).

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 as a function of practice and were nearly four times longer after the 20 day training period. This improvement in performance 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. It follows that learning-induced changes in hand displacements would likely require a modification in postural mechanisms that stabilize the multisegmented body. 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 facilitate secondary task performance (Stoffregen et al. 1999, 2000; Balasubramaniam et al. 2000; Stoffregen et al. 2007). In agreement with previous studies, we have shown that postural control mechanisms are specific to the behavioral 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 task goals. In the ensuing sections, we discuss our results in relation to theoretical models of motor learning.

Central to Newell et al. (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 processes. The first process corresponded to 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 earlier-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 anticipatory or reactive postural control, 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-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.

Anticipatory postural adjustments have been described in the literature as a mechanism that minimizes the destabilizing effect of forces that arise from self-motion (Bouisset and Zattara 1987; Ahmed and Wolpert 2009) and have been interpreted as evidence for neural mechanisms that encode task-specific movement dynamics (Cordo and Nashner 1982; Bouisset et al. 2000). Although cogent arguments have been provided for anticipatory postural control mechanisms and their role in learning novel motor tasks (Flanagan and Wing 1997), only discrete movements such as reaching have been considered. By contrast, 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. Importantly, both anticipatory and reactive postural strategies require time-lagged negative correlations between the finger and center of pressure.

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 weak 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, cf. P-SB condition, figure 7). Therefore, we argue that stick-balancing skill is 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 individual subsystem dynamics. Intermittent dynamics are characteristic of systems with threshold stability criteria that lead to rapid fluctuations or discontinuities in variables of interest (Landa et al. 1998; Platt et al. 1993). 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 destabilizing perturbations (Newell and Vaillancourt 2001). The observation that intermittency existed at all levels of our analyses complemented these arguments and demonstrated that the central nervous system may selectively (de)couple individual subsystems to satisfy concurrent task goals. Moreover, our arguments corroborate evidence that human feedback parameters are tuned to correct threshold-crossing perturbations that arise during voluntary behavior (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 posture–finger displacements and that recurrence-based measures are more sensitive to these changes than time series dynamical 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 end-effector analyses and statistical methods that decompose the contributions of individual segments to performance variability.

Acknowledgments TC was supported by an NSERC Alexander Graham Bell Canada Graduate scholarship. We thank members of the Sensorimotor Neuroscience Laboratory, the Motor Behaviour Group, and two anonymous reviewers for their helpful comments and suggestions.

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