Perceptual and motor learning underlies human stick balancing skill

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We investigated the acquisition of skill in balancing a stick (52 cm, 34 g) on the fingertip in nine participants using three-dimensional motion analysis. After 3.5 hours practice over 6 weeks, the participants could more consistently balance the stick for longer durations with greatly reduced magnitude and speed of stick and finger movements. Irrespective of level of skill, the balanced stick behaved like a normal non-inverted pendulum oscillating under greater-than-gravity torque with simple harmonic motion about a virtual pivot located at the radius of gyration above the center of mass. The control input parameter was the magnitude ratio between the torque applied on the stick by the participant and the torque due to gravity. The participants utilized only a narrow range of this parameter, which did not change with practice, to rotate the stick like a linear mass-spring system. With increased skill, the stick therefore maintained the same period of oscillation but showed marked reductions in magnitude of both oscillation and horizontal translation. Better balancing was associated with 1) more accurate visual localization of the stick and proprioceptive localization of the finger; and 2) reduced cross-coupling errors between finger and stick movements in orthogonal directions, i.e., finger movements in the antero-posterior plane became less coupled with stick tip movements in the medio-lateral plane and vice versa. Development of this fine motor skill therefore depended on perceptual and motor learning to provide improved estimation of sensorimotor state and precision of motor commands to an unchanging internal model of the rotational dynamics.

Keywords: pole balancing, perception-action coupling, depth perception, kinesthesis, gravitational dynamics
INTRODUCTION

Balancing an object can be categorized as a continuous skill whereby an inherently unstable object has to be kept upright within the physical limitations and boundaries of the controller. When an object with a relatively small base of support has to be kept upright or transported, fine control is required to balance the object to prevent it from falling under the force of gravity. In one aspect at least, human adults are expert balancers since they can balance their own body well by achieving upright posture over a small base of support and can walk and run without falling. These feats seem natural for adults but to master the motor skills needed to perform these tasks certainly requires a significant amount of practice for infants (Payne and Isaacs 2008). Hence, to study the mechanisms of learning to balance through the behavior of infants requires long periods of observation. In this respect, the skill of balancing a stick on the fingertip is a challenging task that provides a good opportunity to investigate the mechanisms of skill learning since it is a skill that can be acquired in several hours of practice by young adults (Cabrera and Milton 2004a, 2012). To control an unstable object such as this requires constant vigilance and sustained visual attention. The subjective experience of the participants indicates that although it is possible to think about something else or to speak while balancing, if visual or proprioceptive attention is removed from the stick for more than a fleeting moment, stability is lost. Hence, even a skilled performer can maintain balancing for only a few minutes (Cabrera and Milton 2004b). Another interesting feature of the task is that augmented feedback from an expert trainer apparently cannot be used to guide the learner and no obvious ‘rules’ can be expressed to aid skill acquisition, which instead appears to depend on implicit learning (Stevens et al. 2012).

Since the work of Barto, Sutton and Anderson (1983), object balancing, also known as the inverted pendulum problem, has been a benchmark problem in the field of control systems engineering. The object to be kept upright is usually a pole which pivots on a
motorized cart that moves on a one-dimensional track. Investigators in numerous studies have successfully designed various controllers that can be trained to balance and stabilize such an object rapidly with high efficiency (Connell and Utgoff 1987; Guez and Selinsky 1988; Koza and Keane 1990; Lee and Berenji 1989; Widrow 1987).

While the mechanism(s) underlying the learning behavior of these machine controllers can in principle be specified, it remains unclear how relevant they are to learning in humans. Lakie and colleagues have shown that a large inverted pendulum with low intrinsic stiffness can be controlled via anticipatory hand movements, with stability being provided by a neurally-generated, intermittent pattern of impulses despite irregular and aperiodic pendulum sway (Lakie et al. 2003). In a previous study of balancing a stick on the fingertip by skilled performers (Lee et al. 2012), we observed that the movement of the stick tip was only about half of that of the finger. This fundamental kinematic finding showed that the balanced stick pivoted more like a normal non-inverted pendulum than the conventional inverted pendulum model from control systems engineering, a point also noted in previous studies (Cabrera and Milton 2002; Treffner and Kelso 1999). Indeed, the behavior of the balanced stick resembled angular simple harmonic motion of a normal pendulum, but operating under greater-than-gravity torque (applied by the balancer) and with a translating pivot point. Oscillatory movements between the finger and stick tip also have been emphasized in other studies of stick balancing, using time-delayed inverted pendulum models (Milton et al., 2009a,b), but the non-inverted pendulum model is purely a mechanical description of the behavior of the balanced stick and therefore is independent of the issue of time delay (see Lee et al. 2012).

In this descriptive model of a pendulum, the relevant input control parameter was the magnitude ratio between the active torque applied by the participant and the torque due to gravity. This parameter determined the distinctive location of the virtual pivot point of the pendulum, which was approximately at the radius of gyration (measured about the CoM).
above the CoM of the stick. This location pointed to the importance of knowledge of the
gravitational dynamics and mass distribution of the stick for the interaction of the participants
with the movement of the stick. A subsequent control-theoretical interpretation of this non-
inverted pendulum model (Gawthrop et al. 2013) showed that the virtual pivot is the key to
successful balancing, enabling humans to simplify the control by approximately splitting the
fourth-order dynamics of the system into two non-interacting second-order systems: control
of angle (stick rotations) using finger acceleration at an appropriate frequency to create the
virtual pivot and control of the horizontal position of the virtual pivot (stick translations)
using the pendulum angle controller set point. The structure of the two subsystems is such
that they are amenable to cascade control and it is known that humans can successfully
control two non-interacting second-order systems simultaneously (Oytam et al. 2005).

Although there have been a number of previous studies of stick balancing (Cabrera
and Milton 2002, 2004a,b, 2012; Cluff and Balasubramaniam 2009; Cluff et al. 2009, 2011,
2012; Foo et al. 2000; Mehta and Schaal 2002; Milton 2011; Milton et al. 2008, 2009a,b;
Reeves et al. 2013; Treffner and Kelso 1999), there has not been extensive study of the
changes in stick balancing behavior with practice. Cabrera and Milton (2004a) had
participants practice stick balancing over a number of days. The change in the speed of hand
movements was used to estimate the “corrective” movements of the hand and they observed
faster changes after practice. Cluff and Balasubramaniam (2009) also reported faster changes
in fingertip speed after practice and concluded, in agreement with Cabrera and Milton, that
learning resulted in an increased tolerance for larger speed step sizes of the finger. Cluff et al.
(2009) analyzed the time series dynamics of the finger displacement data of Cluff and
Balasubramaniam (2009) and found that learning was accompanied by increased dynamical
stability of movement trajectories.
While these studies provided insights into skill-related changes in the statistical properties of hand movements, two further studies by Cluff and colleagues examined concomitant changes in postural and limb control. Cluff et al. (2011) showed that the trajectories of both finger and center of pressure displacements became more variable and discontinuous with practice, and that the coupling of finger displacements with postural sway increased. They suggested that this coupling resulted from the development of a hierarchical control mechanism that switches intermittently between coupled and independent control of the finger and posture. Cluff et al. (2012) analyzed the stick angle and six upper and lower limb joint angles in the sagittal plane as subjects learned to balance. They found a reduction in individual joint angle variation concomitant with an increase in multijoint covariation, indicating that subjects relied less on the control of individual joints and more on distributed error compensation, a transition that was correlated with improved balancing performance across subjects.

In our previous study of skilled stick balancing (Lee et al. 2012), we presented detailed three-dimensional (3-D) kinematic and kinetic measures that are not available from other studies to date. Here we apply these measures to identify hitherto unreported basic behavioral changes with practice, with the aim of extending understanding of the learning mechanisms for skilled balancing. In addition, the pendulum model proposed previously (Lee et al. 2012) was investigated further to determine whether changes in the behavior of the model occurred as a result of learning.
Glossary: CoM: center of mass, MoI: moment of inertia, PL: pendulum length, \( r_g \): radius of gyration

MATERIALS AND METHODS

Participants

Fourteen right-handed young adult participants (6 female, 8 male: age 18-35) with no history of motor disorders volunteered to participate in the study. All were naïve to the stick balancing task. The experimental procedures were approved by the Human Research Ethics Committee of The University of Sydney and written informed consent was obtained. Each participant received a pair of cinema vouchers at the beginning of the study and another pair upon completion.

Task and practice

The task goal was to balance a stick on the pad of the middle finger of the right hand while standing upright for at least 20 seconds without taking a step. The participants were given 10 minutes of familiarization immediately before data collection was begun. At the beginning of each trial the participants supported the stick with their left hand, which they released once they were given the ‘Go’ signal for data collection. Trials were stopped once 20 seconds had been reached. Twenty trials were performed and the whole experiment took about one hour to complete. An identical procedure was repeated for the post-practice trials.

To acquire the skill of balancing, each participant was provided with a stick and asked to practice at home for a total of three and a half hours distributed over six weeks. They were instructed to practice for at least five minutes daily and given a logbook to encourage compliance with this schedule. An extra pair of cinema vouchers was promised if they were able to 1) double the number of successful trials they had achieved in the pre-practice session
or 2) succeed at all trials in the post-practice session. The logbooks indicated that all participants achieved the target hours of practice.

Apparatus and data acquisition

The experimental methods used in the current study are the same as those reported in Lee et al. (2012) and will be presented only in summary form here. The stick was a telescopic television antenna (length: 0.52 m, diameter: 5-7 mm, mass: 0.0338 kg, MoI: 0.0029 kg m², distance from base to CoM: 0.27 m). A semi-cone shaped base (diameter: 8 mm), originally the tip of the antenna, was in full contact with the finger pad, preventing slippage between the finger and the base of the stick while balancing. Two retro-reflective markers (0.56 g Styrofoam spheres) were attached to the stick, one at the tip and another 9 cm above the base, to track the 3-D movement of the stick. In order to track the 3-D movement of the participants’ left and right arm and head, five reflective markers (25 mm diameter) were attached on the left and right radial styloid process, the forehead, and the left and right zygomatic bone. Ten cameras (Eagle Cameras, Motion Analysis Corporation, Santa Rosa, USA) were used to track the movements of the stick and participants with 100 Hz capture frequency. The laboratory coordinate system was defined as ML (medio-lateral), AP (antero-posterior) and V (vertical) axes, paralleling the orientation of the participants at the start of the task. Captured trial data were imported for analysis into Matlab 7.0 software (The MathWorks Inc).

Trimming of the raw data was necessary in order to ensure that only data from true balancing of the stick were analyzed. The starting point of each trial was chosen when the supporting left hand released the stick, identified from the onset of movement of the marker on the left radial styloid process. For trials less than 20 seconds in duration, the end point was selected by examining the sway cycles between the upper and lower markers on the stick. A
failure of balancing was easily identified by the desynchronization of the trajectories of the 
two markers on the stick in the ML and/or AP axes. The end point of such trials was chosen 
two sway cycles prior to the initiation of such a desynchronization. Only trials comprising 
more than 5 seconds of data were analyzed.

Data analysis

The variables measured are described briefly below. All variables except the head-
centered coordinate system were described in detail by Lee et al. (2012). In addition, 
frequency domain and linear systems analyses were used to investigate the relations between 
kinematic and kinetic variables, in order to garner further insights into the effects of practice 
on stick balancing performance.

ASSESSMENT OF BALANCING PERFORMANCE. The number and duration of successful stick 
balancing trials were the most basic performance measurements. The duration of balancing is 
perhaps the most telling measure of level of skill because balancing can be maintained for 
only a limited duration even by a skilled stick balancer (Cabrera and Milton 2004b). The 
range of movement in each 3-D direction (the maximum – minimum position) of the stick 
and finger was measured to assess the stability of the stick and the amount of finger 
movement. The total distance traveled in the laboratory space by the stick tip and finger was 
calculated for each trial by summing the 3-D distance traveled across sample intervals. The 
normalized length of path (LoP) was then defined as the total distance traveled by the stick 
tip or finger divided by the duration of each trial in seconds.

KINEMATIC VARIABLES. The position, velocity and acceleration of the finger and stick tip 
were measured in each axis. To reveal how the finger and stick tip moved vertically in the
laboratory space, the mean value of the stick tip position in the V axis was calculated. The angles of deviation of the stick from the vertical in the $V \times ML$ plane (ML angle) and $V \times AP$ plane (AP angle) were calculated. The axial angle of the stick, which represents its rotation about the longitudinal axis, was estimated as described previously (Lee et al. 2012). The velocity and acceleration of these angles were calculated. Root mean squared (RMS) values of these kinematic variables of the stick tip and finger were calculated. To provide a measure of the most common angular displacement of the stick from the vertical, the absolute magnitude of the angle of deviation of the stick from the vertical was calculated for each data point (10 ms interval) from each trial and a histogram normalized to the length of the trial was constructed.

HALF CYCLES OF STICK OSCILLATION. To identify the periodic nature of the stick movement, the average duration of the interval between zero-crossings of the positive and negative angular velocity signals was obtained separately for the ML and AP directions. This duration is equivalent to half the period of the sway cycle of the stick. These cycles indicate the following directions of movement of the stick: toppling to the left for $M\rightarrow L$ toppling cycle, toppling to the right for $M\leftarrow L$ toppling cycle, toppling backwards for $A\rightarrow P$ toppling cycle, and toppling forwards for $A\leftarrow P$ toppling cycle.

RELATIVE COORDINATES. A relative coordinate system that measured the stick angle with reference to the participants’ head was employed in order to gain insight into how the stick moved relative to the visual field. The origin of this relative coordinate system ($ML_{rel}$, $AP_{rel}$ and $V_{rel}$) was the forehead marker. The $ML_{rel}$ axis was aligned with the line between the markers on the left and right zygomatic bone. The orientation of the $V_{rel}$ axis was parallel to that of the $V$ axis of the laboratory coordinate system (and the gravitational field). The $AP_{rel}$
axis was orthogonal to the $ML_{\text{rel}}$ and $V_{\text{rel}}$ axes. Hence, both the $ML_{\text{rel}}$ and $AP_{\text{rel}}$ axes moved with rotations of the head in the horizontal plane. Whilst the head-referenced motion of the stick in the $ML_{\text{rel}}$ axis was not a precise measure of its motion relative to the angle of gaze, substantial coupling of head with eye movements could be assumed to occur during stick balancing. Coupling of head and eye movements occurs in saccades of less than 3° in reading text (Lee 1999) and the contribution of head movements increases as the size of gaze shift increases (Freedman 2008; Guitton and Volle 1987). Furthermore, head movements contribute significantly to predictive gaze shifts (Bizzi, Kalil and Morasso 1972) which could be assumed during stick balancing because the trajectory of motion of the stick when it falls under gravity is familiar and predictable (McIntyre et al. 2001; Senot et al. 2005; Zago et al. 2004; Zago and Lacquaniti 2005; Zago et al. 2008) from the moment the fall begins (only the precise moment and direction of falling are unpredictable). Even for small gaze shifts where the head does not move, the $ML_{\text{rel}}$ position of the head would still be closely aligned with that of the stick tip.

In this relative coordinate system we defined the angle of the stick projected onto the transverse $ML_{\text{rel}} \times AP_{\text{rel}}$ plane as the ‘toppling’ angle. This angle is equivalent to the relative direction of toppling of the stick from the vertical (0–360°) when viewed from above. We examined the amount of time spent at each toppling direction, independent of its magnitude, by constructing a frequency histogram of the toppling angle at each data point (10 ms interval). The frequency count of the toppling direction in each 5° bin was normalized to the trial duration and expressed as a percentage. The pattern of these angle histograms was fitted with an ellipse in order to quantify their shape (see Fig. 4A), using a non-linear fitting method which minimizes the geometric error (Gander et al. 1994). The center coordinate of the ellipse (a measure of whether the toppling was more frequent in one direction or the other), the length of the major and minor axes (a measure of the ratio of the toppling frequency in
one axis versus the other), and the tilt angle of the major axis (a measure of the deviation from the AP_rel axis) were calculated.

KINETIC VARIABLES. The derivations of these variables are described in detail by Lee et al. (2012). The MoI with respect to the pivot point at the base of the stick was derived empirically using the mass of the stick and its oscillation period under gravity (Tipler 1999) and checked theoretically using the equations for composite MoI of hollow cylinders (Halliday et al. 2001). The MoI of axial rotation (MoI_axial) of the stick was obtained by the equation for a hollow cylinder rotating about a longitudinal axis (Halliday et al. 2001). The net torque ($\tau_{\text{net}}$) acting on the stick was computed from the angular acceleration ($\dot{\theta}$) and the MoI in both the V× ML and V × AP planes. Similarly, the axial torque ($\tau_{\text{axial}}$) was calculated from the axial angular acceleration and the MoI_axial. The net torque is the sum of gravitational torque ($\tau_{\text{grav}}$) and active torque ($\tau_{\text{act}}$), where gravitational torque is the torque produced by gravity which rotates the stick about its base and active torque is caused by finger acceleration. The finger reaction force - the translational stick force acting on the fingertip - was calculated in ML, AP and V axes using the acceleration data of the stick CoM. RMS values of the kinetic variables (3-D net torque, 2-D active torque, 2-D gravitational torque and 3-D stick force) of the stick and finger were also calculated.

FREQUENCY DOMAIN ANALYSES. The frequency content of all the kinematic and kinetic variables of the stick and finger were analyzed using fast Fourier transformation with a 512 point Hamming window. The frequency resolution was 0.1 Hz and frequencies up to 5 Hz were examined. The spectrum describes the total power (mean square value) of the signals and its distribution across frequency. It was the distribution across frequency that was of
primary interest here, rather than the absolute power which was already adequately assessed by the magnitude measures of the variables described above. Therefore the power spectral density of each signal was computed. This is the ‘relative power spectrum’, that is, the power at each frequency expressed as a proportion of the total power in the spectrum. Thus, the total area under a spectral density curve is unity. The median power frequency (MPF) for each spectrum was also computed across the trials.

LINEAR SYSTEMS ANALYSES. To investigate the dynamic physical properties of the control of stick translation and rotation, linear systems techniques of cross-correlational and spectrographic analysis (Ada et al. 1993; Bendat and Piersol 1986; Neilson 1972; Winter and Patla 1997) were employed. Coherence, gain, phase frequency response functions were calculated in the ML and AP axes between: finger position and stick tip position, finger position and stick angle, finger reaction force and stick tip position, and net torque and stick angle.

CROSSED AXES ANALYSIS. The relation between the finger position and the stick tip position across the ML and AP axes was analyzed to identify cross-talk between these orthogonal axes (i.e., finger ML position vs. stick tip AP position and finger AP position vs. stick tip ML position). To quantify the degree of cross-talk between these variables, the ‘overall coherence’ (Lay et al. 2002; Oytam et al. 2005; Porges et al. 1980; Smith et al. 2001; Wang et al. 2013) was computed from a cross-correlational and spectrographic analysis. The overall coherence provides a measure across all frequencies of the proportion of the total variance of the output that is linearly related to the input. Thus, the overall coherence provides a single measure of the total variance accounted for by the linear transfer function and in this way is analogous to the square of the Pearson product moment correlation ($r^2$, the coefficient of
determination). Hence, this measure revealed the amount of coupling between medio-lateral and antero-posterior movements and how this coupling changed with practice.

CHARACTERISTIC DYNAMICS OF THE STICK. The movements of the stick tip and finger included both oscillatory movement and translations. In order to reveal the typical oscillatory cycle of the stick unaffected by cycle-to-cycle variations in translation, the stick angle, angular velocity, and active torque in the ML and AP directions were time normalized for each half cycle of oscillation (M→L, M←L, A→P and A←P toppling cycle) and averaged across all trials and participants. For each cycle of oscillation, the mean relation between active torque and angle and between angular velocity and angle was calculated for each participant. The maximum positive and negative value of the average angle from each cycle was defined as the ‘correction’ angle, which represents the angle at which the stick reversed its direction of movement to prevent it from falling.

FREQUENCY HISTOGRAMS OF THE PENDULUM LENGTH. In the descriptive kinematic model of the balanced stick as angular simple harmonic motion of a normal pendulum developed by Lee et al. (2012), an equation was developed using the ratio ($k$) between the magnitudes of the active torque and the gravitational torque to calculate where the pivot point was located. The mean value of this ratio for each toppling direction in each participant was derived from the ratio of the slope of their mean relation between active torque and angle and the slope of the gravitational line. This ratio sets both the pivot point of the pendulum and the sway cycle period of the stick. The length from the pivot point to the base of the stick contacting the finger was termed the pendulum length (PL). Different values of the PL indicated different behaviors of the stick. Three main stick behaviors were operationally defined (see Figure 4 of Lee et al. 2012): (1) pure falling of the stick, when PL ≤ 0 m (the pivot point is at or below
the base of the stick, which shows falling on the finger due to gravitational torque); (2) rotation of the stick, when the PL ranged from 0 m to twice the most frequent PL (the pivot point is located at a point along the stick or up to 30 cm above the tip of the stick, which shows oscillatory movement); (3) pure translation of the stick, when the PL is equal to or greater than twice the most frequent PL (the pivot point is beyond the tip of the stick, and the base and tip travel in parallel). In order to assess changes with skill, frequency histograms of the PL were calculated at 10 ms intervals for collated trials for each participant before and after practice. The frequency values of the histogram were expressed as a percentage of total trial duration and averaged across participants.

STATISTICAL ANALYSES. The effect of practice on the dependent variables was examined using 2 × 2 (Practice [Pre, Post] × Axes [ML, AP]) repeated measures analyses of variance (ANOVA) for stick angle and net torque variables; 2 × 3 (Practice [Pre, Post] × Axes [ML, AP, V]) repeated measures ANOVAs for finger and stick tip range, position, and finger force variables; and t-tests for dependent samples for trial duration, LoP, and axial angle variables (alpha level = .05). The influence of the axes and the sequence of toppling was measured for some variables by 2 × 2 × 2 (Practice [Pre, Post] × Axes [ML, AP] × Toppling Sequence [M→L, M←L or A→P, A←P]) repeated measures ANOVAs. Tukey post-hoc tests were used when significant results were found. All data are presented as means ± standard deviations. Statistical analyses were performed in Statistica 7 software (StatSoft, version 7.1).

RESULTS

Assessment of balance performance

All participants attempted 20 trials of balancing the stick for 20 s in both pre- and post-practice sessions. Five participants could not balance for more than five seconds during
pre-practice trials. They showed a similar pattern whereby, once the stick was released from the left hand, it fell with no more than one oscillatory hand movement. The data from these participants were excluded from further analysis and the number of participants in the statistical analyses was thus reduced to nine. For these nine participants the data from all trials longer than five seconds were averaged and the mean values were used to obtain group mean and standard deviation values.

After practicing for six weeks (~ 5 mins per day, 3.5 hours in total), the participants were able more consistently to balance the stick for a longer duration (Table 1). The average number of successful trials increased with practice from $3.7 \pm 5.5$ to $15.9 \pm 4.0$ (single sided t-test, $P < 0.05$) while the average duration of trials increased from $10.4 \pm 4.2$ s to $17.0 \pm 1.8$ s (single sided t-test, $P < 0.05$).

Sample raw kinematic traces in the ML axis from one participant before and after practice are shown in Fig. 1. It can be seen that the finger and stick tip moved in the same direction for most of the time, with the finger covering a wider range than the tip (Fig. 1, A and C). Most of the movements shown by these traces are slow changes in position that represent translations of varying amplitude of the finger and stick tip in space. Rotation of the stick is not readily apparent in the position traces because rotation occurs only when there is a change in the relative positions of the finger and stick tip. The difference between the positions of the finger and stick tip at each time interval (Fig. 1, A and C) is directly related to the angular deviation from the vertical (Fig. 1, B and D). This is most obvious when the finger and tip move in opposite directions and can be seen more clearly in Fig. 1, C and D where the translations are smaller than in Fig. 1, A and B. A periodicity at approximately 1.7
Hz (~ 0.6 s per cycle) apparent in the rotational displacements coincided with the MPF of stick angular velocity shown by the spectral analyses.

The linear systems analyses indicated that 0.75 Hz was the frequency boundary between translational and rotational motion. Below 0.75 Hz, the finger and stick tip movements were highly coherent and the motion mostly comprised translations where the finger and stick tip moved approximately in parallel. The finger movements and the stick angle were less coherent at low frequency because low-speed finger movement was not effective in producing rotation of the stick. Above 0.75 Hz, the finger movements and the stick angle were highly coherent and the motion mostly comprised rotational movements where the finger and stick tip movements diverged. Hence, the finger and stick tip movements were less coherent because almost all high-speed finger movements were coupled to stick rotation. It can be seen that the trajectory of the stick tip resembled a smoothed version of the trajectory of the finger (Fig. 1, A and C). This was confirmed by filtering the finger trajectory using a low-pass, zero-phase filter (Butterworth 4th-order, dual-pass) with a cut-off frequency of 0.75 Hz. The filtered finger trajectory then very closely matched the trajectory of the stick tip. This result reflects the fact that it was translational motion of the finger that mostly determined both the translational motion of the stick tip and the change in angle of the stick.

Kinematics of finger and stick movement

All of the kinematic measures showed that the magnitude of movement of both the stick and the finger decreased with practice. Reductions in magnitude of one third to a half were observed: the normalized 3-D length of path of the stick and finger (Fig. 2), the RMS
values and range of finger and stick tip movements (Fig. 3A), the RMS values of the angle of
deviation of the stick from the vertical in ML and AP directions (Fig. 3B), the frequency
distribution of the absolute angle of deviation of the stick from the vertical (Fig. 3C), and the
‘correction’ angles at which the stick reversed its direction of movement to prevent it from
falling (Fig. 8). A diagrammatic representation of the 3-D path traveled by the stick tip and
finger during pre- and post-practice trials is depicted of one participant in Fig. 2A. The LoP of
both the stick tip and finger (Fig. 2B) decreased significantly with practice \( [F(1, 8) = 18.74, P
< 0.05] \). Irrespective of practice, however, the LoP for the stick tip was substantially less than
that of the finger \( [F(1, 8) = 49.79, P < 0.05] \) and the ratio between the two did not change
significantly with practice (stick tip LoP / finger LoP: pre-practice = 0.60 ± 0.06 m/s, post-
practice = 0.57 ± 0.06 m/s, single-sided \( t \)-test, \( P = 0.11 \)), confirming that the stick pivoted
more like a normal pendulum than an inverted pendulum. Note that the LoP is normalized by
the total duration of the trial and hence the reduction in LoP corresponds to a reduction
almost by half in the average velocity (m/s) of the stick tip and finger with practice. This
velocity change was supported by a decrease with practice in the MPF for the finger and stick
tip position \( [F(1, 8) = 17.66, P < 0.05] \).

RMS AND RANGE OF FINGER AND STICK TIP MOVEMENTS. Changes in movement amplitude
expressed as RMS displacement in the laboratory space are shown in Fig. 3A. The mean
amplitude of the fingertip and the stick tip movement in all directions decreased significantly
with practice \( [F(1, 8) = 7.24, P < 0.05] \). For both finger and stick tip, the RMS amplitude in
the V direction was on average only 24% of that in the ML and AP directions, and this ratio
did not change with practice (single-sided \( t \)-tests, \( P \geq 0.20 \)). The ranges (maximum-
minimum) of both the finger and stick tip movement also decreased significantly with practice in the ML (finger: 0.58 ± 0.16 m to 0.42 ± 0.17 m; stick tip: 0.47 ± 0.12 m to 0.35 ± 0.15 m), AP (finger: 0.62 ± 0.13 m to 0.49 ± 0.15 m; stick tip: 0.49 ± 0.09 m to 0.41 ± 0.13 m) and V (finger: 0.17 ± 0.04 m to 0.11 ± 0.03 m; stick tip: 0.17 ± 0.05 m to 0.12 ± 0.03 m) directions \[F(1, 8) = 6.58, P < 0.05\]. The decreases in displacement and range of the finger were greater than for the stick tip \[F(1, 8) \geq 6.68, P < 0.05\]. These differences reflect the fact that there was a reduction in the magnitude of the stick angle with practice, as described in the next section.

RMS VALUES OF STICK ANGLES. The RMS value of the stick angle in all directions decreased significantly with practice (Fig. 3B) \[F(1, 8) = 5.77, P < 0.05\]. It can be seen that the amplitude of the axial angle was substantially greater than both the ML and AP angles. Since the stick base contacted firmly with the finger pad, the axial angle reflects the composite rotational movements of the wrist, shoulder, trunk and hips (see Lee et al. 2012), but it contributes minimally to balance of the stick and did not change significantly with practice (single-sided t-tests, \(P = 0.60\)). A comparison of the ML and AP angles showed that the amplitude of the stick angle was greater in the AP compared to the ML direction irrespective of practice \[F(1, 8) = 11.30, P < 0.01\]. Both angles decreased with practice, but the angle in the AP direction decreased more \[F(1, 8) = 6.30, P < 0.05\], so that the ML and AP angles became closer in amplitude.

The angle of deviation of the stick from the vertical indicates the absolute magnitude of deviation without consideration of the direction of toppling. Changes with practice in the time-normalized histograms of the deviation angle are shown in Fig. 3C. The median angle
decreased significantly with practice from $4.6 \pm 1.8^\circ$ to $2.6 \pm 1.2^\circ$ (single sided $t$-test, $P < 0.05$). The distribution pattern narrowed towards $0^\circ$ and the frequency of occurrence of angles greater than $\sim 5^\circ$ was reduced almost by half.

**DURATION OF HALF CYCLE OF STICK OSCILLATION.** Perhaps the most important finding with regard to the characteristic dynamics of the balanced stick was the duration of the stick sway (half) cycles. The zero-crossings of the positive and negative angular velocity signals can be seen as the peaks and troughs of the angle signals in Fig. 1 ($B$ and $D$). The mean intervals between zero-crossings for each toppling cycle are presented in Table 2. This simplest empirical measure showed no evidence of change with practice despite marked reductions in the magnitude of sway (Figs. 1, 3B, 3C) [$F(1, 8) = 0.21, P = 0.66$]. Moreover, despite the clear differences in amplitude of sway between the AP and ML axes, especially before practice (Fig. 3B), the sway durations were very similar for all directions of toppling [$F(1, 8) = 0.00, P = 0.96$]. The mean duration of $0.30 \pm 0.05$ s across all conditions also coincided with the theoretical half cycle time derived from the pendulum model of Lee et al. (2012). As shown by Lee et al. (2012), if this stick were suspended as a physical pendulum at the $r_g$ from its CoM and oscillated under the $4.53$ (mean $k$ ratio) times greater-than-gravity torque exerted by the participants, then the general expression for the period of angular simple harmonic motion of a pendulum predicts a period of $0.60$ s. The corresponding theoretical half cycle duration of $0.30$ s therefore coincides with the measured values. Since a constant period despite varying amplitude of oscillation is one of the fundamental characteristics of a pendulum following simple harmonic motion, the cycle duration employed by the participants was consistent with angular simple harmonic motion of this stick as a physical pendulum operating under greater-than-gravity torque.
Relative coordinates

An example of the time-normalized histogram of the toppling angle in the ML_{rel} AP_{rel} plane from one participant pre- and post-practice is depicted in Fig. 4A. It can be seen from the length of the major and minor axes of the ellipse fitted to each histogram that irrespective of practice, the stick toppled more frequently in the AP_{rel} direction than in the ML_{rel} direction. With practice, a decrease in the frequency of toppling in the AP_{rel} direction can be observed. It can also be seen that the centroid of the ellipse was positioned more posteriorly pre-practice than post-practice, indicating that the stick fell posteriorly more often than anteriorly before practice. After practice, however, a more even distribution in the AP_{rel} direction can be identified from a shift in the centroid (pre-practice: 0.01\% medial, 0.78\% posterior; post-practice: 0.02\% medial, 0.22\% posterior). The group mean and standard deviation of the features of the ellipses are illustrated in Fig. 4B. There was a significant reduction with practice only in the major axis \(F(1, 8) = 5.71, P < 0.05\), while the length of the minor axis did not show any change (Tukey post hoc test: \(P = 0.99\)). The frequency of toppling in the AP_{rel} direction was over three times greater than in the ML_{rel} direction before practice, but after practice it had decreased to about twice the frequency in the ML_{rel} direction. The tilt angle of the major axis of the ellipse and its centroid location in the ML_{rel} direction did not change significantly with practice (single-sided t-tests, \(P \geq 0.29\)). However, the relative frequency of anterior-to-posterior compared to posterior-to-anterior toppling was reduced considerably, as indicated by a shift in the centroid location anteriorly with practice (single-sided t-test, \(P < 0.05\)).

<Insert Fig. 4 near here>
Kinetics of finger and stick movement

In parallel with the kinematic changes, the kinetic measures showed corresponding reductions in the forces and torques applied between the finger and stick (Fig. 5).

NET TORQUE AND FINGER REACTION FORCE. The average amplitude of net torque in the three planes of motion (Fig. 5) reduced significantly with practice \( F(1, 8) = 17.53, P < 0.05 \). Similar to the results for the amplitude of the stick angle, the net torque was greater in the AP compared to the ML direction irrespective of practice \( F(1, 8) = 6.24, P < 0.05 \) and the torque in the AP direction decreased more with practice \( F(1, 8) = 5.52, P < 0.05 \). Although the amplitude of the axial torque was extremely small compared to the ML and AP torques, it also decreased significantly with practice (single-sided \( t \)-test, \( P < 0.05 \)). The average amplitude of the finger reaction force also decreased with practice in all three directions \( F(1, 8) = 16.27, P < 0.05 \). Post-hoc Tukey tests of a significant difference across the three axes \( F(1, 8) = 6.77, P < 0.05 \) revealed a significantly greater force in the AP compared to the ML direction in pre-practice but not post-practice trials.

Frequency domain analyses

CROSSED AXES ANALYSIS: FINGER POSITION (INPUT) AND STICK TIP (OUTPUT). The overall coherence between crossed axes decreased with practice (Fig. 6) \( F(1, 8) = 13.74, P < 0.05 \). There was no difference between the two directions of the cross-talk between axes (finger ML vs. stick tip AP and finger AP vs. stick tip ML values) \( F(1, 8) = 0.02, P = 0.88 \). The change in coupling between axes with practice represented a one third reduction in
movements of the finger which produced erroneous off-axis movements of the stick rather
than correcting the stick angle.

Characteristic dynamics of the stick

The performance improvement with practice did not result from changes in the
dynamics between the finger and stick movement because there was no change in the
characteristic dynamics of the stick oscillations, as shown by the mean torque-angle relations
(Fig. 7) and the phase portrait of the rotational dynamics (Fig. 8). These findings again
support the model of the observed balancing behavior of the stick as consistent with angular
simple harmonic motion of a physical pendulum (Lee et al. 2012).

TORQUE-ANGLE RELATIONSHIP. The characteristic oscillatory cycle of the stick, unaffected
by cycle-to-cycle variations in translation, is shown by the mean relationship between active
torque and angle for each toppling cycle (Fig. 7). The additive inverse of the gravitational
torque indicates the minimum magnitude of active torque that the participant must generate in
order to prevent the stick from falling under gravity. The ratio between the magnitude of the
active torque and the gravitational torque is termed the ‘k ratio’ (Lee et al. 2012), which
represents the participant’s strategy to control the rotational dynamics of the stick. The mean
ratios ranged from 4.3 (± 0.4) to 4.8 (± 0.5) and did not vary significantly either with practice
\[F(1, 8) = 2.70, P = 0.14\] or toppling direction (e.g., M→L vs. M←L) \[F(1, 8) = 1.84, P =
0.21\] (Table 2). Hence, the participants utilized only a narrow range of (greater-than-gravity)
torques to rotate the stick. On the other hand, the ratio for the ML axis (4.64 ± 0.45) was
slightly greater than that for the AP axis (4.43 ± 0.47) irrespective of practice \[F(1, 8) = 5.55,
It can be seen that the excursion of the torque and angle traces was reduced after practice, reflecting smaller oscillations of the stick, and was slightly more linear and closely centered about the origin (0, 0). Regardless of these changes with practice, however, the slopes of the torque-angle lines remained almost constant and indicate that the stick behavior was similar to a mass-spring system where the displacement of the spring is proportional to the magnitude of the force applied in the opposite direction.

PHASE PORTRAIT OF THE ROTATIONAL DYNAMICS. The phase portraits similarly decreased their excursion but showed little qualitative change with practice other than the trajectories becoming more symmetrical and more congruent with the theoretical pendulum model. Time-normalized and averaged relationships between angular velocity and angle are depicted in Fig. 8 to generate an average phase portrait of the stick dynamics in both the ML and AP axes. The direction of the arrow for each trajectory indicates the toppling cycle direction. Similar to normal pendulum dynamics, when the angular velocity reaches its peak, the stick becomes upright (i.e., its toppling angle reaches zero) and when the magnitude of the stick angle becomes maximum, as indicated by the vertical dashed lines in the figure, the stick stops rotating (i.e., its angular velocity reaches zero). These maximum values of the angles in the cycle are defined as the ‘correction angles’ where the stick trajectory away from the vertical is halted and reversed. The dark dashed lines in Fig. 8 show the theoretical pendulum dynamics from Lee et al. (2012) for the stick pivoting at the \( r_g \) from the CoM for the mean pre- and post-practice correction angles. The background grey dashed lines show these theoretical phase portraits for a range of correction angles larger and smaller than those observed. The observed mean trajectories decreased their size with practice and became more
congruent with the model. The trajectories were also shifted laterally (ML) and posteriorly (AP) before practice but became symmetrical with practice.

Both the ML and AP correction angles decreased significantly with practice \(F(1, 8) = 5.55, P < 0.05\) (Fig. 8B). The AP correction angles were larger than the ML angles irrespective of practice \(F(1, 8) = 6.32, P < 0.05\) but reduced more with practice \(F(1, 8) = 5.49, P < 0.05\) as confirmed by a post-hoc Tukey test, so that the angles became closer in amplitude. There were also greater reductions with practice in M→L than M←L toppling, and in A→P than A←P toppling \(F(1, 8) = 22.32, P < 0.05\), as confirmed by post-hoc Tukey tests. These effects are in accordance with the improvements in symmetry in the phase portraits.

PENDULUM LENGTH (PL). Support for the pendulum model was also provided by the PLs. Using the mean \(k\) ratios measured for each participant for each toppling direction, the PLs before and after practice were calculated via the model of the balanced stick as angular simple harmonic motion of a normal pendulum (Lee et al. 2012). The notable finding here again was the lack of change with practice in the PLs, with mean (± standard deviation) pre- and post-practice values for the four directions of stick toppling all within a very narrow range of 0.40 - 0.42 (± 0.01 – 0.02) \(F(1, 8) = 2.70, P = 0.14\). Moreover, a PL of 0.41 m placed the pivot point of the pendulum at the \(r_g\) from the CoM of the stick.

<Insert Fig. 8 near here>
As the $k$ ratio increases, the stick pivots closer to its CoM, whereas when the $k$ ratio decreases, the pivot point is located further up the stick, even above the tip, creating translational movement where the finger and stick tip move in parallel. Based on the PL calculated at 10 ms intervals for collated trials for each participant, the most frequently used PL was found to range between 0.38 and 0.42 m for both axes and for both pre- and post-practice trials (Fig. 9). Closely overlapping values between the pre- and post-practice histograms indicated that the pattern of PL distribution did not change with practice. Moreover, the occurrence of pure falling, where the stick pivots at or below its base (when the PL was $\leq 0$; $\sim 10\%$ of the time) and pure translation of the stick (when the PL was equal to or greater than twice the most frequent PL; $\sim 10\%$ of the time) did not change with practice for either the ML or AP axes [$F(1, 8) = 0.73, P = 0.42$]. For over half of the time (53–55%), however, the stick behaved like a normal pendulum with PLs from 0.29–0.5 m in both ML and AP axes. These findings empirically validated the participants’ preference for the distinctive location of the pivot point to be at the $r_g$ from the CoM of the stick. Lee et al. (2012) proposed that pivoting the stick at this location could provide the participants with optimal capability to perceive the motion of the stick under gravity and predict its future path, because the stick is most responsive and a transfer of energy to or from the stick may have the maximum effect on stick rotation at this point.

DISCUSSION

The results for the characteristic dynamics of the stick oscillations and the pendulum model indicate that the participants were already attuned to the physical properties of the stick under gravity before our data collection began. Since they were given 10 minutes of familiarization with the task immediately before data collection, we missed this acquisition of the pendulum model by the participants. Our guess is, however, that they ‘learned’ the
gravitational dynamics and mass distribution of the stick within the first moments of wielding it through ‘dynamic touch’ (Solomon and Turvey 1988; Turvey 1996). The sensitivity of humans to the physics of manipulated objects has been noted previously (Lee et al. 2012; Mah and Mussa-Ivaldi 2003; Zatsiorsky et al. 2005) and it seems likely that the participants here quickly learned a predictive internal model of the torque-angle (Fig. 7) and mass distribution (Fig. 9) characteristics of the stick which did not change with practice. This appears to be consistent with the finding that in novel object-manipulation tasks, people may learn to predict the behavior of the object before they can master its control (Flanagan et al. 2003). Even before attempting the novel task, however, it is likely that the ability to predict the timing of a falling stick on the fingertip was already familiar to the participants because a putative internal model in the vestibular cortex is involved in processing visual motion when it is coherent with natural gravity (Zago and Lacquaniti 2005) and such a gravity model (internalized Newton’s laws) would operate from the earliest stages of learning. Miller et al. (2008) have proposed that an early stage of integration of high-level visual analysis with gravity-related motion information occurs in the vestibular nuclei and posterior cerebellar vermis regions, which are reciprocally connected with the vestibular cortex.

Notwithstanding these issues of how and when they learned the physics of the stick, however, it is clear from the initial recorded trials that the pendulum model, though presumably necessary, was not sufficient to enable the participants to balance the stick (see Table 1). This suggests, in line with the findings of Flanagan et al. (2003), that the participants took much longer to fine-tune the inverse dynamics model that is required to stabilize and control the stick. The question then arises, how did they learn to stabilize the stick and reduce its motion? The mechanisms underlying this acquisition of skill will now be explored.
Mechanisms of learning

The trajectory of motion of the stick when it falls under gravity is familiar and predictable from the moment the motion begins, but the precise moment and direction of falling are unpredictable. Oscillating the stick like a pendulum following simple harmonic motion imposes a significant degree of predictability on its rotational trajectory, even despite the superimposed translations of varying magnitude and direction. This oscillatory strategy, evident from the first trials, maintained the same duration (0.605 s) and periodicity (1.65 Hz) of the sway cycle throughout practice as the magnitude of stick motion decreased, thereby almost halving the average velocity of stick motion (Fig. 2B). A more slowly translating stick is easier to stabilize, as evidenced after practice by the much smaller correction angles, which identify where the stick trajectory away from the vertical was halted and reversed (Fig. 8). Slower movements are likely to reduce the uncertainty in signals of motor output, efference copy and afferent feedback compared with fast movements, because of the effects of fixed feedback delays in afferent input, slower changes of signals with time, and lower signal-dependent noise (Gritsenko et al. 2007). Combined with the constant rotational period, this slowing of the translational motion may explain why no change was necessary - or detected - in the timing relations between movement of the finger and the stick in order to improve balancing skill. Hence no direct evidence of a change in ability to predict the motion of the stick was observed. Again, however, it begs the question of how the participants learned to slow and stabilize the motion of the stick.

The motion of the stick is determined by the active torque applied by the participant and the torque due to gravity. The magnitude ratio between these torques - the $k$ ratio - sets the sway cycle period, as well as the pivot point of the pendulum (Lee et al. 2012). Greater-than-gravity torque reduces the period of a pendulum relative to that under gravitational torque alone. Any increase or decrease in active torque applied by the participants, and hence
in the value of $k$, would respectively decrease or increase the period, and shift the most
frequent pivot point away from its location at the $r_g$ from the CoM. This underscores the
importance of the sensitivity to the torque due to gravity (Zatsiorsky et al. 2005) in balancing
the stick. Consequently, Lee et al. (2012) proposed that the $k$ ratio is the major control input
parameter in this task. The three parameters - $k$ ratio, cycle period and pivot point location -
were held constant irrespective of practice. This was the most surprising finding of the study,
raising the question of how did the subjects improve their skill without a change in the
rotational dynamics? The answer lies in the finding that although the slope of the torque-angle relation was unchanged, the amplitude of the signals was substantially reduced (Figs. 7, 8). So the torque-angle gain was unchanged, but the torque and angle signals were smaller.
This demonstrates that the motor commands changed with practice. Smaller torques will
mean lower signal-dependent noise (Harris and Wolpert 1998; Meyer et al. 1988; Schmidt et
al. 1979), while smaller and slower movements point to more precise perceptual signals
(Gritsenko et al. 2007). From this starting point, two factors of perception and action can be
identified that were correlated with increased balancing skill.

Perceptual factors

The toppling angle of the stick as measured with respect to the markers on the
participants’ forehead provides an indication of how the stick moved relative to the
participants’ visual field. The time-normalized histograms of this toppling angle show the
relative amount of time spent at each toppling direction, independent of its magnitude (Fig.
4). The histograms revealed that before practice, the stick toppled three times more frequently
in the $AP_{rel}$ direction than the $ML_{rel}$ direction. Since the precision of human detection of
motion in depth (the AP direction) is about half of that in the medio-lateral (ML) direction
(Sumnall and Harris 2002; Tyler 1971; Westheimer 1990), the participants could be expected
to make more errors and spend more time correcting errors in the less accurately perceived direction, thereby creating the pattern before practice shown in Fig. 4.

A substantial decrease with practice was observed in the length of the major axis of the ellipse fitted to the histograms of the stick toppling angle, so that the frequency of toppling in the $\text{AP}_{\text{rel}}$ direction was then only about twice that in the $\text{ML}_{\text{rel}}$ direction. This ratio after practice matches the reported relative precision of human detection of motion in depth versus the medio-lateral direction (Sumnall and Harris 2002; Tyler 1971; Westheimer 1990). The reduction in the length of the major axis, therefore, is consistent with perceptual learning of depth discrimination and it has been shown that learning of depth perception can indeed occur with practice (Gantz et al. 2007; O'Toole and Kersten 1992; Ramachandran 1976). Furthermore, approximately 50% of the variance of the measures of balancing performance could be accounted for by their correlation with this perceptual measure (Table 3). Hence, better visual discrimination of depth was associated with more skilled balancing performance. The corollary of this association is that less sensitive visual perception of the stick toppling in depth is likely to be a primary deficit in the unskilled balancer.

Another significant change in the time-normalized histogram of the toppling angle was the shift in the centroid location of the ellipse in the $\text{AP}_{\text{rel}}$ direction (Fig. 4B). Whilst the frequency of $\text{M}\rightarrow\text{L}_{\text{rel}}$ and $\text{M}\leftarrow\text{L}_{\text{rel}}$ stick toppling was symmetrical irrespective of practice, $\text{A}\rightarrow\text{P}_{\text{rel}}$ toppling occurred significantly more often than $\text{A}\leftarrow\text{P}_{\text{rel}}$ toppling before practice. This change could have been due to the proprioceptive localization ability of the hand in the depth direction. Van Beers et al. (1998) studied the precision of proprioceptive position sense and found that as the hand moved further away from the shoulder, their participants’
localization ability decreased accordingly (i.e., the ability to pinpoint the location of the hand in space without the aid of vision). Since the finger is further away from the body during A→P\textsubscript{rel} stick toppling (and the visual attention of the participant is focused primarily on the tip of the stick so that they cannot simultaneously see the finger), it would therefore be expected that the movement would not be as accurate as during A←P\textsubscript{rel} toppling, when the finger is closer to the body. The reduced proprioceptive accuracy in depth would contribute to more errors in the A→P\textsubscript{rel} toppling direction, resulting in the stick toppling in that direction more often and leading to the pattern of asymmetry seen in Fig. 4B. With practice, the toppling frequency in the AP\textsubscript{rel} direction became far more symmetrical, though a slight degree of asymmetry remained. As with visual discrimination of depth, therefore, proprioceptive localization in depth may have improved with practice, consistent with the observed reduction in asymmetry. Furthermore, the centroid location in the AP axis was correlated with both the duration of successful trials and the 3-D length of path of the finger (Table 3). Hence, more skilled balancing performance also appeared to be associated with better proprioceptive discrimination of depth. The importance of proprioceptive learning in stick balancing similarly was emphasized by Cabrera and Milton (2012) who noted that the observation that expert stick balancers adopt a characteristic posture, namely elbow held in flexion with wrist and index finger extended in line with the forearm, suggests that proprioceptive information from the shoulder contributes to skill.

The question whether perceptual learning also occurred in the ML axis with practice must be considered. The histograms of the toppling angles in the relative coordinate space (Fig. 4) were time normalized and so provided information on relative rather than absolute frequency of the directions of stick toppling. The lack of change in the minor axis of the fitted ellipse therefore does not necessarily mean that there was no reduction in stick toppling in the ML axis with practice. In fact, the correction angle in the ML axis reduced by close to a half
with practice (Fig. 8B). That perceptual learning is likely to have contributed to this reduction is shown by recent demonstrations of perceptual learning in vision, audition, somatosensation and olfaction (see Fahle 2005 for review). In vision, perceptual features of widely differing complexity can be learned, ranging from straightforward orientation discrimination to detecting complex patterns (Fahle 2005; Fine and Jacobs 2002). Furthermore, even early sensory cortices, conventionally considered as hard wired, can be involved in the underlying changes of the central nervous system (Fahle 2005; Paz et al. 2004). Perceptual learning improves performance in nearly all tasks investigated so far, is often quite specific for the exact task trained and does not lead to conscious insights that can be easily communicated; hence, it is of the procedural or implicit type (Fahle, 2005), consistent with the phenomenology of stick balancing. In light of this research, it seems likely that perceptual learning did also occur in the ML axis.

Motor factors

Cross-talk between the orthogonal ML and AP axes of finger and stick tip movements (finger ML vs. stick tip AP, finger ML vs. stick tip AP) represents an important source of error in control of the stick (Fig. 6). Consider for instance what happens if the stick topples towards the participant in the A→P direction and the participant produces an opposing movement that is not wholly within the V × AP plane of movement that would return the stick directly to the vertical, but instead deviates slightly from the AP direction. The inaccurate opposing movement will oppose toppling in the direction of the opposing movement, and this may return the stick partially towards the vertical, but it will now deviate from the vertical in a new direction due to the out-of-plane or ‘off-axis’ error. This deviation must then be corrected, and if further error is not to be created, the corrective movement again must remain wholly within the plane that returns the stick to the vertical. Hence,
skillful balancing depends on precisely accurate stick movements that do not cause the stick to move in off-axis directions between the ML and AP axes of finger and stick tip movement. Conversely, the process of unskilled balancing can be viewed as a vicious cycle where cross-talk between orthogonal axes of finger and stick tip movement result in an accumulation of errors, causing a progressive increase in the toppling angle which leads to increased movement, at increased speed, of the finger and stick. Since a larger toppling angle entails both a larger gravitational torque on the stick and less time to avert a fall, the participants must generate more torque, more rapidly on the stick in order to maintain balance. These factors will amplify the inaccuracy of corrective movements due to signal-dependent noise and exacerbate the error in accordance with the speed-accuracy trade-off (Carlton and Newell 1993; Fitts 1954; Harris and Wolpert 1998; Meyer et al. 1988; Schmidt et al. 1979), hence the vicious cycle of unskilled balancing.

The reductions with practice in overall coherence between orthogonal axes of finger and stick tip movements (Fig. 6) therefore reflect a reduction in movement error, such that the ML direction of finger movement became less coupled with the AP direction of the stick tip movement, and vice versa. Moreover, this measure of cross-talk between orthogonal axes was highly correlated with both the duration of successful trials and the 3-D length of path of the finger (Table 3). These correlations show that this source of error was closely linked to successful balancing performance and suggest that reduced cross-talk contributed to increased balancing skill.

**Perceptual-motor interactions**

We propose therefore that the mechanisms underlying the acquisition of skill in balancing a stick comprise firstly, perceptual learning which provides the participant with more accurate visual localization of the stick and proprioceptive localization of the finger;
and secondly, motor learning of the directional accuracy of finger movements which reduces off-axis errors in finger movements. Perceptual learning and motor learning alike will improve both the precision and direction of movement, leading to more accurate action matched to more accurate perception, the major benefit of which is the avoidance of accumulating errors that lead to loss of stability. This proposal is supported by recent evidence that motor learning and perceptual learning are linearly correlated (Vahdat et al. 2011). Vahdat and colleagues identified a network involving second somatosensory cortex, ventral premotor cortex, and supplementary motor cortex whose activation was specifically related to perceptual learning; and a network comprising cerebellar cortex, primary motor cortex, and dorsal premotor cortex that was linked to motor learning. Subjects who showed greater changes in functional resting-state connectivity related to motor learning showed greater changes related to perceptual learning.

Successful balancing is determined by motion of the stick in both the ML and AP directions (Fig. 10A). Therefore, measures of perception of stick motion in the AP direction alone would not be expected to account for all of the variance in performance measures (cf., Table 3). However, the potential for interaction between the ML and AP axes in balancing makes the contribution to performance from perception of depth difficult to estimate. Errors in perception create inaccurate estimates of the location of the hand or stick tip in space. Such inaccurate estimates will often result in off-axis errors in the corrective finger movements, thereby affecting movement in both axes, as illustrated in Fig. 10 (B, D, E, F). Similarly, motor execution errors will often result in off-axis errors, thereby affecting movement in both axes, as illustrated in Fig. 10 (C, D, E, F). Hence, perceptual (visual and proprioceptive) and motor errors interact in their effect on balancing performance and so both types of error contribute to cross-talk between orthogonal axes of finger and stick tip movement. A similar situation applies in control of human standing, where a majority of studies have shown that
sensorimotor noise or inappropriate torque modulation is the primary source of standing sway (Kiemel et al. 2011; Loram et al. 2001; Loram and Lakie 2002; Maurer and Peterka 2005; Mergner et al. 2002). Increased skill in stick balancing therefore depends on both perceptual and motor learning, and recent research suggests that similar neuronal mechanisms may govern learning across sensory and motor domains (Paz et al. 2004; Poggio and Bizzi 2004). As noted by Paz et al. (2004), improved encoding of information is equally important for motor and sensory systems, because the signals generated from both systems must be shared with other brain areas in controlling movement. In the present study, it was not the internal model of the rotational dynamics that changed with practice but the precision of the signals flowing through the model. The model was not sufficient without precisely accurate sensory and motor signals, which depend on learning.

Finally, it should be noted that the findings of the present study regarding perceptual learning of depth discrimination cannot be applied where the stick balancing tasks employed are in one (medio-lateral) dimension (e.g., Foo et al. 2000; Reeves et al. 2013; Treffner and Kelso, 1999) or virtual (e.g., Mehta and Schaal, 2002). Since visual and proprioceptive signals of depth are not available to the participant in such approaches, they can have no role in the acquisition of balancing skill.
Acknowledgment

This work was supported in part by Sport Knowledge Australia.

REFERENCES


PERCEPTUAL AND MOTOR LEARNING IN HUMAN STICK BALANCING


FIGURE CAPTIONS

Fig. 1. A 15s sample of raw kinematic data in the ML axis from one participant. A, C: Finger (dark line) and stick tip (grey line) position in laboratory coordinate system pre- and post-practice, respectively. B, D: Stick angle pre- and post-practice, respectively.

Fig. 2. A: 3-D movement traces of the stick and fingertip for 10 seconds from one participant. The total distances traveled by each of the stick and the finger markers represent the length of path (LoP) values. B: Group mean and standard deviation of the normalized (Norm.) LoP values (m/s) for the fingertip (Fing) and stick tip (S-Tip) pre- and post-practice. Note that the normalized LoP also corresponds to the average velocity of the stick tip and finger. *: indicates significant difference ($P < 0.05$) with practice, †: indicates significant difference ($P < 0.05$) between the finger and stick tip.

Fig. 3. A: Group mean and standard deviation of the fingertip (Fing) and stick tip (S-Tip) root-mean-squared (RMS) displacement in the ML (medio-lateral), AP (antero-posterior) and V (vertical) axes pre- and post-practice. B: Group mean and standard deviation of the RMS stick angle values pre- and post-practice. ML and AP angle (left). Axial angle (right). Note that the axial angle could be related to rotations of the wrist, shoulder, trunk and/or hips. *: indicates significant difference ($P < 0.05$) with practice, †: indicates significant difference ($P < 0.05$) between ML and AP angles. C: Group mean (thick lines) ± standard deviation (thin lines) of the time-normalized histogram of the angle of deviation of the stick from the vertical in the laboratory space before and after practice. Pre- and post-practice median angles are indicated in boxes next to the vertical lines. *: indicates significant difference ($P < 0.05$).
Fig. 4. A: Time-normalized histograms of the toppling angle in the relative coordinate space with the ellipse fitted to the pre- and post-practice histograms from one participant. Major: length of major axis of the ellipse, Minor: length of minor axis of the ellipse, and $\alpha$: tilt angle of the major axis of the ellipse in reference to the $\text{AP}_{\text{rel}}$ axis (positive values indicate clockwise direction). The coordinates and direction of the centroid of the ellipse are shown in square brackets. B: Group mean and standard deviation of the features of the ellipses fitted to the time-normalized histograms of the toppling angle. Left: length of semi-axes. $\text{M}_j = \text{Major}$; $\text{M}_n = \text{Minor}$. Middle: tilt angle of the major axis in relation to the $\text{AP}_{\text{rel}}$ axis. Right: location of the centroid. (M): medial, (L): lateral, (A): anterior, (P): posterior. *: indicates significant difference ($P < 0.05$).

Fig. 5. Group mean and standard deviation of the RMS net and axial torque (left) and finger reaction force (right) in all directions. Note the difference in scale for axial torque. *: indicates significant difference ($P < 0.05$). †: indicates significant difference ($P < 0.05$) between ML and AP torque.

Fig. 6. Changes with practice in group mean overall coherence between crossed axes of the finger and the stick tip movement. Left: ML finger position (input) and AP stick tip position (output). Right: AP finger position (input) and ML stick tip position (output). *: indicates significant difference ($P < 0.05$).

Fig. 7. Time-normalized pre-practice (grey) and post-practice (black) active torque vs. angle relationships for $\text{M} \rightarrow \text{L}$ and $\text{M} \leftarrow \text{L}$, and $\text{A} \rightarrow \text{P}$ and $\text{A} \leftarrow \text{P}$ toppling cycles, averaged across participants for all trials. The straight grey lines show the gravitational torque line, while the
straight dashed black lines show its additive inverse. Lateral and posterior angles are positive; medial and anterior angles are negative.

Fig. 8. A: Angular velocity vs. angle relationship for the ML and AP axes for pre-practice (large continuous curves) and post-practice (small continuous curves) balancing, averaged across participants for all trials. The black curves indicate M→L and A→P toppling while the grey curves indicate M←L and A←P toppling. The negative and positive correction angles are indicated by the vertical dashed lines. The dark dashed ellipses in each plot show the phase portrait of the stick pivoting at the rg from the CoM for the observed mean correction angles. The background grey dashed lines show these phase portraits for a range of different values of the correction angle. B: Group mean and standard deviation of the negative and positive correction angles pre- and post-practice. M: medial, L: lateral, A: anterior, P: posterior. *: indicates significant difference (P < 0.05).

Fig. 9. Group mean (continuous lines) and standard deviation (broken lines) of frequency distribution of the PLs in the ML and AP axes for pre- and post-practice trials. Pure falling (PL ≤ 0 m) is shown in the bars on the left and pure translation (PL ≥ twice the most frequent PL) is shown in the bars on the right, with error bars showing standard deviations.

Fig. 10. Schematic illustration of hypothetical perceptual and motor errors. All panels depict motion relative to the finger. A: Stick tip falls in M→L and A←P directions – actual plane of falling shown by shaded semicircle in A, B and C. Accurate corrective action of finger (filled arrow) will result in corrective motion of stick tip (open arrow) within plane of falling. B: Hypothetical inaccurate perception of location of stick tip results in corrective action of finger (filled arrow) in M→L direction only. C: Hypothetical accurate perception but
inaccurate movement execution results in corrective action of finger (filled arrow) in M→L direction only. D: From B and/or C, action of finger in M→L direction only will result in motion of stick tip in M←L direction only (open arrow). E: From B and/or C, stick motion in A←P direction is uncorrected and hence stick tip will fall further in A←P direction (open arrow). F: Resultant motion of stick tip (open arrow) is outside plane of falling (shown by open semicircle outlined with continuous lines) and creates cross-coupling between ML and AP axes.
Table 1. Number of analyzable trials (> 5 s duration) and mean duration per trial in seconds pre- and post-practice for each participant.

<table>
<thead>
<tr>
<th>Participant</th>
<th>Number of trials</th>
<th>Mean duration (s)</th>
<th>Number of trials</th>
<th>Mean duration (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0</td>
<td>-</td>
<td>20</td>
<td>17.6</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>8.9</td>
<td>20</td>
<td>19.1</td>
</tr>
<tr>
<td>3</td>
<td>14</td>
<td>9.3</td>
<td>20</td>
<td>14.9</td>
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<tr>
<td>4</td>
<td>0</td>
<td>-</td>
<td>14</td>
<td>16.4</td>
</tr>
<tr>
<td>5</td>
<td>3</td>
<td>6.2</td>
<td>18</td>
<td>15.8</td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td>-</td>
<td>18</td>
<td>16.1</td>
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<tr>
<td>7</td>
<td>8</td>
<td>7.9</td>
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<td>15.6</td>
</tr>
<tr>
<td>8</td>
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<td>17.2</td>
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<td>17.8</td>
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<tr>
<td>9</td>
<td>6</td>
<td>8.7</td>
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<td>19.5</td>
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<tr>
<td>10</td>
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<td>13.4</td>
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<td>18.7</td>
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<tr>
<td>14</td>
<td>0</td>
<td>-</td>
<td>16</td>
<td>16.0</td>
</tr>
</tbody>
</table>

*Note.* The duration of post-practice trials was less than 20 s in most cases due to the data trimming process (mean duration of data trimmed = 3.4 s). Only the 9 participants who had more than 3 analyzable trials in the pre-practice session were included in further analyses. Participants 8 and 11 were already successful in many pre-practice trials and so showed no improvement on these measures, but were included in further analyses because they showed improvement on other measures of balancing.
Table 2. Group mean (± standard deviation) sway half cycle duration and $k$ ratios* of the magnitudes of the active torque applied by the participants and the torque on the stick due to the gravity, for $M\rightarrow L$, $M\leftarrow L$, $A\rightarrow P$, and $A\leftarrow P$ toppling directions pre- and post-practice. The theoretical sway half cycle duration derived from the pendulum model of Lee et al. (2012) is also shown below.

<table>
<thead>
<tr>
<th>Toppling cycles</th>
<th>Sway duration (s)</th>
<th>$k$ ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pre-practice</td>
<td>Post-practice</td>
</tr>
<tr>
<td>$M\rightarrow L$ topl</td>
<td>0.31 ± 0.06</td>
<td>0.29 ± 0.04</td>
</tr>
<tr>
<td>$M\leftarrow L$ topl</td>
<td>0.29 ± 0.05</td>
<td>0.32 ± 0.05</td>
</tr>
<tr>
<td>$A\rightarrow P$ topl</td>
<td>0.31 ± 0.03</td>
<td>0.30 ± 0.07</td>
</tr>
<tr>
<td>$A\leftarrow P$ topl</td>
<td>0.29 ± 0.06</td>
<td>0.31 ± 0.03</td>
</tr>
</tbody>
</table>

Theoretical duration from mean $k$ ratio: 0.30

* The ratio ($k$) between the magnitudes of the active torque and the gravitational torque determines both the sway cycle period and the pivot point of the pendulum. The ratio for each participant was calculated from the slope of their mean torque-angle line for each toppling direction relative to the slope of additive inverse of the gravitational torque-angle line.

Table 3. Variance ($r^2$)* of pre- and post-practice measures of stick balancing performance (duration, normalized length of finger path) accounted for by their relation with perceptual measures (length of $AP_{rel}$ axis, centroid location in $AP_{rel}$ axis) and motor measures (crosstalk†).

<table>
<thead>
<tr>
<th></th>
<th>Length of $AP_{rel}$ axis of ellipse</th>
<th>Centroid location in $AP_{rel}$ axis</th>
<th>Crosstalk between ML and AP axes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balancing duration</td>
<td>0.44</td>
<td>0.44</td>
<td>0.72</td>
</tr>
<tr>
<td>3-D finger LoP</td>
<td>0.54</td>
<td>0.58</td>
<td>0.54</td>
</tr>
</tbody>
</table>

* $F(1, 14) \geq 10.68, P < 0.05$. † Mean of coherences for finger ML vs. stick tip AP and finger AP vs. stick tip ML. Note that an ellipse could not be fitted to the toppling angle data for participant 5 due to the small number and short duration of successful pre-practice trials and so the participant number is reduced to 8, pre and post combined = 16, for these analyses.
A

PRE

Major: 2.4 %, Minor: 0.9 %
α: 2.4°, [M: 0.01 %, P: 0.78 %]

POST

Major: 1.7 %, Minor: 1.0 %
α: 14.9°, [M: 0.02 %, P: 0.22 %]

B

Length of Semi-axes (%)

Mj Mn

Tilt Angle of Ellipse (deg)

Centroid Location of Ellipse (%)

PRE
POST
A. Finger action in the correct plane

B. Inaccurate perception of stick tip location and its coupled finger action

C. Inaccurate action of the finger with correct perception of stick tip location

D. Motion of stick tip in ML axis

E. Motion of stick tip in AP axis

F. Resultant motion of stick tip due to inaccurate perception or action of the finger