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[www.JBiomech.com](http://www.JBiomech.com)Sex differences in leg dexterity are not present in elite athletes<sup>☆</sup>Emily L. Lawrence<sup>a,\*</sup>, Lorenzo Peppoloni<sup>b</sup>, Francisco J. Valero-Cuevas<sup>a,c</sup><sup>a</sup> Department of Biomedical Engineering, University of Southern California, Los Angeles, CA, USA<sup>b</sup> PERCRO Laboratory, TeCIP Institute, Scuola Superiore Sant'Anna, via Alamanni 13b, 56010 Ghezzano, San Giuliano Terme, Pisa, Italy<sup>c</sup> Division of Biokinesiology and Physical Therapy, University of Southern California, Los Angeles, CA, USA

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## ABSTRACT

We studied whether the time-varying forces that control unstable foot–ground interactions provide insight into the neural control of dynamic leg function. Twenty elite (10 F, 26.4 ± 3.5 yrs) and 20 recreational (10 F, 24.8 ± 2.4 yrs) athletes used an isolated leg to maximally compress a slender spring designed to buckle at low forces while seated. The foot forces during the compression at the edge of instability quantify the maximal sensorimotor ability to control dynamic foot–ground interactions. Using the nonlinear analysis technique of attractor reconstruction, we characterized the spatial (interquartile range IQR) and geometric (trajectory length TL, volume V, and sum of edge lengths SE) features of the dynamical behavior of those force time series. ANOVA confirmed the already published effect of sex, and a new effect of athletic ability, respectively, in TL ( $p = 0.014$  and  $p < 0.001$ ), IQR ( $p = 0.008$  and  $p < 0.001$ ), V ( $p = 0.034$  and  $p = 0.002$ ), and SE ( $p = 0.033$  and  $p < 0.001$ ). Further analysis revealed that, for recreational athletes, females exhibited weaker corrective actions and greater stochasticity than males as per their greater mean values of TL ( $p = 0.003$ ), IQR ( $p = 0.018$ ), V ( $p = 0.017$ ), and SE ( $p = 0.025$ ). Importantly, sex differences disappeared in elite athletes. These results provide an empirical link between sex, athletic ability, and nonlinear dynamical control. This is a first step in understanding the sensorimotor mechanisms for control of unstable foot–ground interactions. Given that females suffer a greater incidence of non-contact knee ligament injuries, these non-invasive and practical metrics of leg dexterity may be both indicators of athletic ability, and predictors of risk of injury.

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## 1. Introduction

It is well accepted that female athletes have a four to ten times greater incidence of non-contact knee injury than their male counterparts, particularly in agility-based sports (Hewett, 1999; Huston and Wojtys, 1996; Stanley, 2016; Yoo, 2010). It is speculated that sex differences in anatomical structure and function including joint alignment (Q-angle), ligament laxity, strength, hormonal levels, and more recently, neuromuscular control are major contributors for the disproportionate number of injuries in females (Hewett, 2000; Hewett, 1999; Yoo, 2010). When considering an isolated joint (e.g., knee) during leg function, sensorimotor control is of considerable importance in terms of preventing injuries, particularly anterior cruciate ligament (ACL) tears. Males tend to exhibit muscle-dominant neuromuscular strategies to control joint stabil-

ity, while females display ligament-dominant strategies (Hewett, 2000). This muscle-dominant strategy is described as a protective mechanism to reduce strain on the joint ligaments during dynamic motions. Sex differences in muscle recruitment patterns and synergies are also well reported and speculated to be contributors to the increased injury risk in female athletes (Hewett, 1999; Lephart, 2002; Tsai, 2012).

Neuromuscular and sensorimotor (e.g., plyometric and proprioceptive) training programs have been introduced to athletic training regimens because they have been shown to improve movement biomechanics and joint stability, thus reducing the likelihood of leg injury (Benjaminse, 2015; Hewett, 2000; Hewett, 1999; Mandelbaum, 2005; Myer, 2005; Yoo, 2010). For example, Hewett et al. reported decreased peak landing forces and ab/adduction moments at the knee, increased hamstring-to-quadriceps peak torque ratios, and corrections in hamstring strength imbalances during the landing phases of vertical jumps after a six-week plyometric training program (Hewett, 1996). Another neuromuscular training study showed increased flexion/extension knee range of motion and decreased varus and valgus knee moments during the landing phase of a vertical jump

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(Myer, 2005). While the biomechanical benefits of neuromuscular and sensorimotor training have been extensively documented, to our knowledge, the effect of long-term athletic-based neuromuscular training on sensorimotor processing for leg dexterity has not been investigated. We define “dexterity” as originally described by Valero-Cuevas (Valero-Cuevas, 2003). Namely, it is the ability to use movements and force vectors to stabilize a slender spring prone to buckling. It was originally developed for fingers (Dayanidhi, 2013; Dayanidhi and Valero-Cuevas, 2014; Venkadesan et al., 2007), and then adapted into a lower extremity dexterity test to quantify the dynamical ability to stabilize unstable foot-ground interactions (Lawrence, 2014; Lyle, 2013). We have previously reported sex differences in this leg version in young soccer players (Lyle, 2015) and across the lifespan (Lawrence, 2014) and proposed that may contribute to the disproportionate higher number of non-contact ACL injuries in female athletes compared to males. As such, it is important to understand the influence of athletic ability—likely, in part, a result of long-term exposure to athletic training regimens—on sensorimotor control for leg dexterity.

The integration of sensory and motor systems for whole-body dynamic activities is inherently complex. This makes quantification of the functional domain of sensorimotor processing difficult. Traditional measures of leg function during whole-body activity are confounded by the contribution of the functional domains of strength and/or limb coordination—let alone vestibular function, visual acuity, posture control, risk aversion, etc. However, we have shown that different versions of the Valero-Cuevas dexterity test quantify the functional domain of sensorimotor processing, as distinct from the functional domains of strength and limb coordination, in fingers (Dayanidhi, 2013; Dayanidhi and Valero-Cuevas, 2014; Lawrence, 2014; Valero-Cuevas, 2003) and legs (Lawrence, 2015) (Fig. 1). This simple, yet reliable, test requires participants



**Fig. 1.** The lower extremity version of the Valero-Cuevas dexterity test. This test was originally developed for fingers (Dayanidhi, 2013; Dayanidhi and Valero-Cuevas, 2014; Venkadesan et al., 2007), and then adapted into a lower extremity version to quantify the dynamical ability to stabilize unstable foot-ground interactions (Lawrence, 2014; Lyle, 2013).

to compress a slender spring prone to buckling at low forces to a maximal steady state level (Lyle, 2013; Valero-Cuevas, 2003). The spring becomes increasingly unstable as it is compressed (i.e., undergoes a bifurcation in instability (Venkadesan et al., 2007), and one's ability to compress and hold the spring at the edge of instability is a measure of the person's sensorimotor control capabilities (Dayanidhi, 2013; Dayanidhi and Valero-Cuevas, 2014; Lawrence, 2014; Valero-Cuevas, 2003; Venkadesan et al., 2007). Unfortunately, the fact that subjects can reliably control the spring at the edge of instability only for the few seconds produces time series that are not well suited for many classical nonlinear dynamical measures (i.e., maximal Lyapunov Exponent, Correlation Dimension) that require longer time series (Kantz and Schreiber, 2004; Wolf, 1985). We recently showed that a nonlinear dynamical approach to the analysis of the time-varying compression forces at the edge of instability is more robust than traditional linear analyses (e.g., mean compression force, and root-mean square (RMS)) to quantify sensorimotor processing for finger dexterity, and can even distinguish the effects of healthy aging from those of mild-to-moderate degenerative neurologic conditions such as Parkinson's disease (Peppoloni, 2017). Here we extend that work and apply the delayed embedding theorem (Takens' theorem (Takens, 1985), to reconstruct the phase portraits from time series of foot forces collected during the leg dexterity test from both elite (highly-skilled) and recreational (moderately-skilled) athletes. Our goal is to explore the influences of sex and athletic ability on sensorimotor processing for leg dexterity, and its implications for the risk of knee ligament injury.

## 2. Methods

### 2.1. Participant demographics

We applied the nonlinear dynamical analysis of attractor reconstruction to the leg dexterity data from 20 elite (10 F, 10 M,  $26.4 \pm 3.5$  yrs) and 20 recreational athletes (10 F, 10 M,  $24.8 \pm 2.4$  yrs) previously reported in (Lawrence, 2015; Lawrence, 2014), which at the time were analyzed only using linear methods. All participants gave their informed consent prior to participation. The Institutional Review Boards at the University of Southern California (Los Angeles, CA, USA) and the University of Innsbruck (Innsbruck, Tirol, Austria) approved the study protocol. The recreational athletes were students at the University of Southern California who had played high school and/or club sports in college. The elite athletes were student-athletes in Innsbruck, Austria and were in the Austrian National ski team selection pool.

### 2.2. Data collection

All participants performed the leg dexterity test with their self-reported dominant leg. Leg dominance was determined by asking participants which leg they use to kick a ball for distance. Data acquisition hardware (National Instruments, Austin, TX) sampled the signal conditioner of the force sensor measuring the leg dexterity compression force at 400 samp/s in some subjects, and at 2000 samp/s in others, with and custom MATLAB (v2014b, Mathworks, Natick, MA) software. We then downsampled those collected at 2000 samp/s to 400 samp/s to have uniform time series across all subjects. We then bandpass filtered them between 3 Hz and 30 Hz for analysis. The frequency range between 3 and 30 Hz covers (i) fast voluntary action in the 3–6 Hz range, as well as (ii) involuntary responses that are mediated by cortically-controlled reflex gains via the fusimotor ( $\gamma$ ) system (6–15 Hz (Laine et al., 2016)). The spinal and trans-cortical reflex loops that dominate system dynamics in the 6–15 Hz range are potential

neuromechanical mechanisms at work when stabilizing an instability as has been proposed by others (Laine et al., 2016; Proctor and Holmes, 2010; Tsianos et al., 2014). Information in the 15–30 Hz range is advisable, as per the Nyquist criterion, to faithfully capture dynamical behavior in the 3–15 Hz range). Thus, this particular frequency range allowed us to study changes in the short-latency unpredictability, which likely reflects changes in the non-linear behavior/controller in action. Concerns may rise considering the effects that the application of linear filters may have on the analysis of the chaotic behavior of the system, but we feel that our particular interest for higher-frequency behaviors justified the data reduction we applied (Kantz, 2012). We identified the leg dexterity hold phases—defined as the periods of maximal sustained spring compression force with the isolated dominant leg (at least 10 for each participant)—and calculated the mean compression force ( $F_{\text{leg dexterity}}$ ) of each with MATLAB. We considered the three hold phases with the highest mean compression force values held stable for at least 3 s for each participant (120 total hold phases) and reconstructed the phase portraits of the raw force time histories during those hold phases. We compared traditional linear analysis methods (i.e.,  $F_{\text{leg dexterity}}$  and RMS) to a set of spatial features of the reconstructed phase portraits described below.

### 2.3. Attractor reconstruction

The detailed rationale and methodology for this nonlinear analysis are provided in detail elsewhere (Peppoloni, 2017) and in (Fedotenkova, 2013), and therefore, are only described briefly below. It is based on the theory of nonlinear dynamical systems, where the time evolution of a system is defined in a *phase space* or *state space*. Every point in the state space specifies a state of the system, which allows us to study the dynamics of the system through the study of the points it visits in state space. The state variables of dynamical systems with dissipative tendencies evolve asymptotically toward low-dimensional attractors that define their stability properties (Kantz and Schreiber, 2004). These attractors are visually characterized as *m*-dimensional *phase portraits*. Real-world dynamical systems are generally too complex to explicitly or directly quantify these attractors (e.g., by differentiation), especially when in the presence of noise and digitalization/quantization effects (Kantz and Schreiber, 2004). As a result, approximate techniques have been developed to reconstruct the relationship between one-dimensional observed time series data and their corresponding *m*-dimensional attractors. This results in the reconstruction of a phase portrait that preserves the properties of the original, but hidden, system (Stergiou, 2016; Takens, 1985).

A common technique for attractor reconstruction is Takens' theorem, also referred to as the delayed embedding theorem (Takens, 1985), stating that the vector sequence,

$$Y(i) = (y_i, y_{i+\tau}, y_{i+2\tau}, \dots, y_{i+(m-1)\tau}), \quad (1)$$

yields a reconstructed attractor with the same topological and mathematical properties as the original system. Tau ( $\tau$ ) is the embedding delay, *m* is the embedding dimension, and  $y_i$  is the value of the timeseries at time *i*. The embedding parameters  $\tau$  and *m* must be properly chosen to accurately reconstruct the attractor. Several approaches have been proposed to choose the optimal embedding delay, and for this analysis we focus on and employ the first minimum of the mutual information function (Peppoloni, 2017; Stergiou, 2016). The embedding delay  $\tau$  must be large enough so that the information gained from measuring the value of  $y_{i+\tau}$  is significantly different from the information already known from the previous point,  $y_i$ . Furthermore,  $\tau$  should not be so large that memory about the system's initial condition is lost (Peppoloni, 2017; Stergiou, 2016).

We then used the false nearest neighbors method to determine the proper embedding dimension for this analysis (Kennel et al., 1992). Given a time series with a minimal embedding dimension,  $m_0$ , the reconstructed attractor in  $m_0$ -dimensional space is a one-to-one image of the attractor in the original phase space. If the attractor is embedded in an *m*-dimensional space where *m* is greater than  $m_0$ , the topological structure is no longer preserved and points are projected into neighborhoods of other points to which they would not belong in higher dimensions (such points are called false neighbors) (Peppoloni, 2017). For example, if the attractor is a circle, a 1-dimensional (1-D) manifold embedded in 2-D, then points in opposite sides of circle can be seen as adjacent (i.e., false neighbors) if seen sideways in 3-D.

### 2.4. Spatial features of phase portraits and convex hulls

Once the phase portraits were reconstructed, several features were used to characterize the spatial properties of them and their convex hulls (Fedotenkova, 2013; Peppoloni, 2017). Each feature provides a quantitative index of their spatial properties, characterizing information of density, perimeter, area and volume or their combination (Peppoloni, 2017). The first feature is the Length of the Phase Trajectory (TL) and it is defined as,

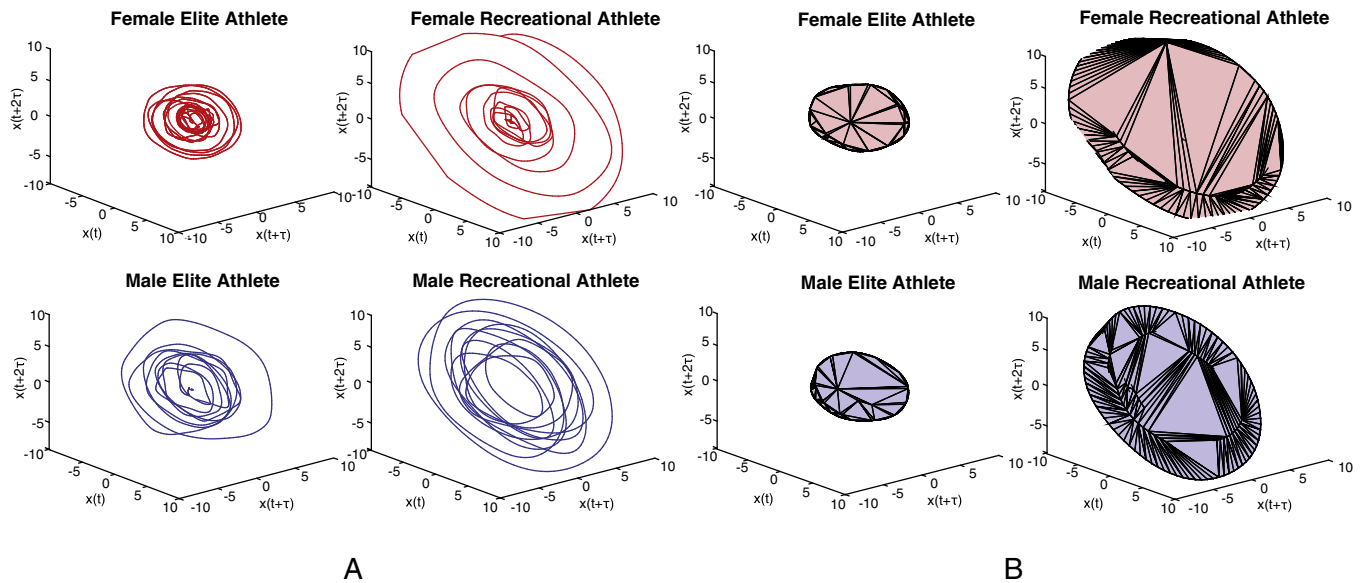
$$TL = \sum_{i=1}^N \|Y_{i+1} - Y_i\|, \quad (2)$$

where *Y* is the reconstructed phase portrait and *N* is the number of points in the time series (Fedotenkova, 2013). Simply stated, TL is the average distance between consecutive points in the phase portrait that provides an indirect measure of the level of stochasticity of the phase portrait (Fedotenkova, 2013). The next feature, the Interquartile Range of the Euclidean Distance from the Centroid (IQR), provides a measure of the dispersion of the points in the phase portrait. The distance from each point in the phase portrait from the attractor's centroid was calculated and then we studied the statistical distribution of the middle 50% of the values computing the interquartile range. This choice enabled us to be robust against possible outliers, which may derive from artifacts in the analysis (Fedotenkova, 2013; Peppoloni, 2017). Finally, to assess the spatial properties of the reconstructed phase portraits, we computed their convex hulls via MATLAB and considered the Sum of the Length of the Edges (SE) and the Volume (V) as features. The former is an index of the perimeter of the attractor (e.g., the 2-D projection on the plane below, or its shadow), while the latter quantifies the amount of phase space taken up by the phase portrait (Fedotenkova, 2013; Peppoloni, 2017).

### 2.5. Data and statistical analyses

The TISEAN library of functions (v2.1.0, TISEAN, Frankfurt, Germany) was used to calculate the embedding delay and dimension and the resulting delay vectors. Those vectors were then input into MATLAB to plot the reconstructed phase portraits and compute the corresponding convex hulls. We used a single factor analysis of variance (ANOVA, using SPSS (v23, International Business Machines, Armonk, NY)) and repeated measures (number of trials) to compare the attractor features across populations with significance set equal to 0.05. In order to assess the effect of sex, we compared men and women in both athlete groups (elite and recreational). We also compared elite and recreational athletes of both sexes to assess the effect of athletic ability.





**Fig. 2.** A. Representative phase portraits from female elite (top left) and recreational (top right) athletes and male elite (bottom left) and recreational (bottom right) athletes are presented above. TL and IQR were computed from the phase portraits. B. The convex hulls from the phase portraits shown in A are illustrated. V and SE were computed from the convex hulls.

**Table 1**  
Means and standard deviations of all features.

Feature	Elite females	Recreational females	Elite males	Recreational males
$F_{\text{leg dexterity}}$	122.7 ± 13.1	123.4 ± 22.1	136.6 ± 19.4	133.4 ± 31.1
RMS	1.01 ± 0.002	1.02 ± 0.004	1.01 ± 0.002	1.02 ± 0.003
TL	249.9 ± 48.1	520.2 ± 71.5	259.7 ± 51.9	332.9 ± 60.3
IQR	2.4 ± 0.5	4.9 ± 0.4	2.0 ± 0.1	3.2 ± 0.4
V	529 ± 178.3	4709.4 ± 502.8	686.8 ± 191.4	1320.6 ± 801.9
SE	539.2 ± 119.5	1526.6 ± 206.7	533.8 ± 109.2	1074.2 ± 176.3

### 3. Results

#### 3.1. Reconstructed phase portraits and convex hulls

We calculated the embedding delays  $\tau$  for all force time histories while compressing at edge of instability (i.e., hold phases) using the first local minimum of the mutual information function and the mode value was selected as the time delay. Next, to select the appropriate embedding dimension  $m$ , we computed the number of false nearest neighbors for all hold phases. The dimension at which the number of false nearest neighbors reached zero was chosen as optimal, and the mode value was selected as the embedding delay. The values for  $\tau$  and  $m$  for this analysis were 21 data points (i.e., 10.5 ms) and three dimensions, respectively. Representative phase portraits from female and male elite and recreational athletes and the associated convex hulls are illustrated in Fig. 2.

#### 3.2. Comparison of spatial features

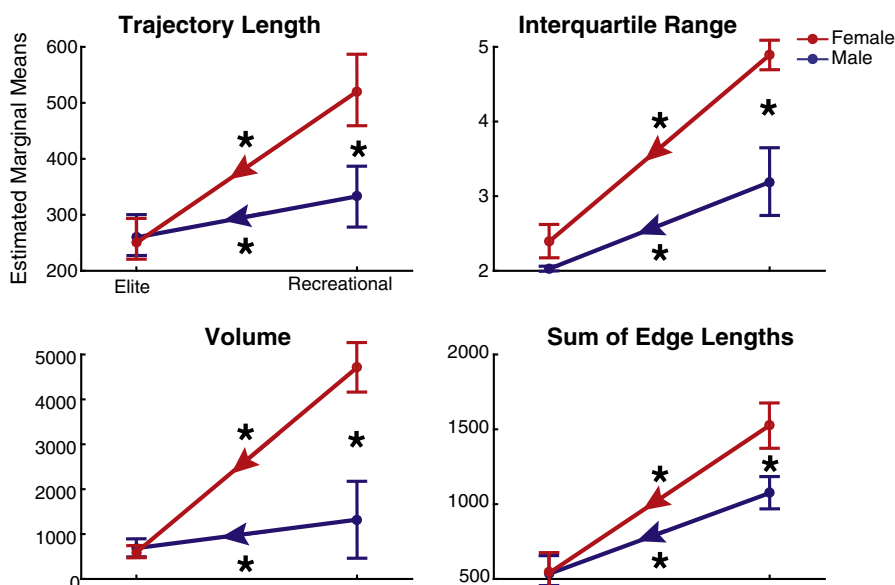
We compared the traditional linear analysis features (e.g., mean compression force ( $F_{\text{leg dexterity}}$ ), RMS) and the spatial features of reconstructed phase portraits elite and recreational athletes of both sexes (Table 1). First, ANOVA results revealed significant sex differences in mean compression force,  $F_{\text{leg dexterity}}$  ( $p = 0.007$ ) with males exhibiting higher mean compression forces than females in both elite ( $p < 0.001$ ) and recreational athletes ( $p = 0.039$ ), but found no effect of sex on either athletic group ( $p = 0.968$ ) (Table 2). The force variability, as per RMS during all hold phases showed significant effects of athletic ability ( $p = 0.041$ ), but not sex

**Table 2**  
ANOVA results among groups. \* indicates significance  $< 0.05$ .

Feature	Sex	Athletic ability	Sex* Athletic ability
$F_{\text{leg dexterity}}$	$p = 0.007^*$	$p = 0.968$	$p = 0.277$
RMS	$p = 0.223$	$p = 0.041^*$	$p = 0.164$
TL	$p = 0.014^*$	$p < 0.001^*$	$p = 0.007^*$
IQR	$p = 0.008^*$	$p < 0.001^*$	$p = 0.088$
V	$p = 0.034^*$	$p = 0.002^*$	$p = 0.01^*$
SE	$p = 0.033^*$	$p < 0.001^*$	$p = 0.046^*$

( $p = 0.223$ ). However, we found significant effects of both sex and athletic ability in the spatial features of the reconstructed phase portraits: TL ( $p = 0.014$  and  $p < 0.001$ ), IQR ( $p = 0.008$  and  $p < 0.001$ ), V ( $p = 0.034$  and  $p = 0.002$ ), and SE ( $p = 0.033$  and  $p < 0.001$ ) (Table 2). Moreover, there are significant interactions between the main effects for three spatial features: TL ( $p = 0.007$ ), V ( $p = 0.01$ ), and SE ( $p = 0.046$ ).

We further examined the estimated marginal mean values (i.e., mean response for each spatial feature of the reconstructed phase portraits, adjusted for any interactions in the model) of all four groups. We find that recreational female athletes have the highest estimated marginal mean values in all four features, followed by male recreational and elite athletes as a combined group (Fig. 3). Considering the effects of sex, we report that female recreational athletes have significantly greater estimated marginal mean values of TL ( $p = 0.003$ ), IQR ( $p = 0.018$ ), V ( $p = 0.017$ ), and SE ( $p = 0.025$ ) than male recreational athletes. Interestingly, however, these sex differences are not present in elite athletes (TL:  $p = 0.975$ ; IQR:



**Fig. 3.** ANOVA results. The significant main effects of sex and athletic ability and their interactions for TL (top left), IQR (top right), V (bottom left), and SE (bottom right) are illustrated above. \*indicates significance level  $<0.05$ .

$p = 0.664$ ; V:  $p = 0.755$ ; SE:  $p = 0.842$ ). In terms of the effects of athletic ability, we find that recreational male and female athletes have significantly greater estimated marginal mean values than their elite counterparts in all four spatial features (TL:  $p < 0.001$  and  $p = 0.005$ ; IQR:  $p < 0.001$  and  $p < 0.001$ ; V:  $p = 0.002$  and  $p < 0.001$ ; SE:  $p < 0.001$  and  $p = 0.002$ ).

#### 4. Discussion

Several studies employ kinematic and biomechanical analyses to understand the effects of sex and athletic training on leg function, and their implications for injury risk (Hewett, 1999; Huston and Wojtys, 1996; Yoo, 2010). Here we present a nonlinear dynamical approach (i.e., attractor reconstruction) that successfully quantified the effects of both sex and athletic ability on sensorimotor processing for leg dexterity in young adults. Leg dexterity is defined here as the ability to control dynamic interactions at the edge of instability. We examined four spatial features of the reconstructed phase portraits and found increased overall size and variability in the phase portraits of recreational athletes compared to elite athletes, with female recreational athletes demonstrating the largest, most variable phase portraits of the four groups. We further showed that the strong sex differences in recreational were not present in elite athletes.

These results, from a nonlinear dynamical systems viewpoint, suggest an empirical relationship between the structure of reconstructed phase portraits and sensorimotor ability. It is critical to mention that attractor reconstruction of experimental data from biological (or other high-order or “complex”) systems is an exercise in logical inference to extract an empirical approximation to their stability characteristics (Peppoloni, 2017; Perc, 2005; Perc, 2005). In the case of dexterity, we study the stability characteristics of a nonlinear, stochastic, delayed neural controller working at the edge of instability (Venkadesan et al., 2007). While it is undeniable that passive structures and the viscoelastic properties of muscles contribute to the stabilization task, we also propose the presence of a neural controller as per (Venkadesan et al., 2007), as well subsequent work that rejects the null-hypothesis that such stabilizing behavior could emerge from purely passive mechanisms. In (Venkadesan et al., 2007) we find that tactile and sensory occlusions degrade performance, as would be expected

in a delayed neural controller. Subsequent fMRI and corticospinal coherence studies (Holmstrom, 2011; Mosier, 2011; Nagamori et al., 2016; Pavlova, 2015; Reyes, 2017) further confirm a strong likelihood that neural processing of sensory information is necessary for the motor action of stabilizing the spring with the fingers or legs. At this point, however, we cannot propose a definitive mechanistic link between the properties of the attractors and nature or structure of specific neuroanatomical structures or neural controllers. Future work is necessary to interpret these empirical results about leg dexterity in a mechanistic way (e.g., (Nagamori et al., 2016), as we have begun to do for finger dexterity (e.g., (Dayanidhi et al., 2013; Ko, 2015; Mosier, 2011; Reyes, 2017).

Being mindful of the limitations of empirical observations, we believe we can nevertheless interpret key features of the statistically significant results from attractor reconstruction. We do so because it is self-evident that elite athletes—by virtue of their longer and greater exposure to training, competitive selection into elite teams, and physical accomplishments—are better than recreational athletes at controlling their bodies in dynamical and unstable situations. This provides an interpretation for sex differences; the statistical differences seen between the groups of athletes can be considered to reflect differences in the sensorimotor ability to control unstable foot-ground interactions (Fig. 3).

##### 4.1. Effects of sex and athletic ability

Our prior work on sensorimotor function shows strong sex differences in hand and leg dexterity across the lifespan (Lawrence, 2014). A separate study showed that female athletes exhibit reduced leg dexterity compression force and higher limb stiffness during landing compared to male athletes, which may contribute to the higher incidence of ACL tears in females (Lyle, 2014). Sensorimotor processing to dynamically regulate foot-ground interactions with the isolated leg seems to also be predictive of athletic ability. For example, the leg dexterity test is predictive of agility, the ability to quickly and efficiently change direction, in young soccer players (Lyle, 2015). Similarly, it is indicative of skill in cross-country skiing given that single-leg gliding distance correlates well with leg dexterity, but whole-body single-leg postural stability does not (Krenn, 2015).

In this study, we find that the mean sustained compression force at the edge of instability ( $F_{\text{leg dexterity}}$ ) was significantly affected by sex ( $p = 0.007$ , with both elite,  $p < 0.001$ , and recreational,  $p = 0.039$ , males exhibiting greater compression force values than their female counterparts), but not by athletic ability ( $p = 0.968$ ) (Table 2). In terms of compression force variability during the hold phases, however, we report no sex effects on RMS ( $p = 0.223$ ). Interestingly, when we employed the nonlinear analysis of attractor reconstruction, we found significant effects of both sex and athletic ability on four spatial features of the phase portraits and their convex hulls (Table 2, Figs. 2 and 3).

Both sex ( $p = 0.014$ ) and athletic ability ( $p < 0.001$ ) had an effect on the trajectory length (TL) of the phase portraits—defined as the distance between consecutive points, giving a graphical representation of the dynamics of system's behavior independently of time (Fedotenkova, 2013). TL can provide insight into structure of the stability of the system of interest. As a signal becomes more stochastic, its trajectories in the phase space also become more variable, with initially close states that can follow very different trajectories over time (Fedotenkova, 2013; Peppoloni, 2017). The longer TL values observed in female recreational athletes indicates they have the more stochastic, and perhaps weaker, sensorimotor control of all groups, since we can hypothesize that they are less capable of organizing the available degrees of freedom towards a stable attractor.

A denser phase portrait can be interpreted as exhibiting more sustained corrective actions (i.e., on average, the system will be closer to the attractor)—which can imply a more active sensorimotor control because the probability that the trajectories remain close to the attractor is higher (Peppoloni, 2017). This density can be quantified by the spatial probability distribution of points in the phase portraits (IQR), which we found is affected by both sex ( $p = 0.008$ ) and athletic ability ( $p < 0.001$ ) (Table 2). We next compared properties of the convex hulls of each phase portrait, and also found volume (V) and sum of the edge lengths (SE) of the respective convex hulls for the phase portraits were significantly affected by sex ( $p = 0.034$  and  $p = 0.033$ , respectively) and athletic ability ( $p = 0.002$  and  $p < 0.001$ , respectively) (Table 2). These results are shown graphically in Fig. 2. A larger phase portrait could be an indicator for a stronger attractor, since points belonging to further portions of the phase space are still pulled towards the attractor's center. However, the phase portraits associated with recreational athletes, particularly females, are larger. But the points composing the phase portrait trajectories are more scattered (greater TL) and show more dispersion in the distribution (greater IQR), which, again, are indicators of a weakening of the associated attractor.

Moreover, we report significant interactions between the main effects of sex and athletic ability for the features TL ( $p = 0.007$ ), V ( $p = 0.01$ ), and SE ( $p = 0.046$ ) (Table 2), indicating that the effect of athletic ability depends on the sex of the participant. The ANOVA results revealed a strong sex difference in recreational athletes in the estimated marginal means of TL ( $p = 0.003$ ), IQR ( $p = 0.018$ ), V ( $p = 0.017$ ), and SE ( $p = 0.025$ ), but not in elite athletes (TL:  $p = 0.975$ ; IQR:  $p = 0.664$ ; V:  $p = 0.755$ ; SE:  $p = 0.842$ ). Furthermore, recreational male and female athletes have significantly greater estimated marginal mean values than their elite counterparts in all four spatial features (TL:  $p < 0.001$  and  $p = 0.005$ ; IQR:  $p < 0.001$  and  $p < 0.001$ ; V:  $p = 0.002$  and  $p < 0.001$ ; SE:  $p < 0.001$  and  $p = 0.002$ ) (Fig. 3).

To summarize, we find that phase portraits of recreational athletes are larger, more disperse and stochastic than those of elite athletes; and that a sex difference exists in recreational athletes. Biologically speaking, this strongly suggests that recreational athletes, particularly females, have reduced sensorimotor control for leg dexterity compared to their elite counterparts of either sex. Future work could use state-dependent perturbations as a means

to probe such dynamical attractors (Revzen, 2013). Another is to probe the involvement of different parts of the nervous system as the level of instability is changed. A recent study finds this to be a promising future direction (Reyes, 2017).

#### 4.2. Clinical implications

We have previously speculated that reduced sensorimotor control for leg dexterity may also be a risk factor for knee ligament injuries (Lawrence, 2014; Lyle, 2014). Our  $2 \times 2$  factorial design now allows us to more confidently say, in light of the ground truth of athletic ability, that sex differences in leg dexterity may explain the higher risk of injury in females as a reduced sensorimotor ability to dynamically control unstable foot-ground interactions. We find it particularly noteworthy that the sex differences we reported in prior work (Lyle, 2015; Wolf, 1985) was only found in recreational athletes given that female athletes without neuromuscular training are known to have the greatest risk for non-contact knee ligament injuries (Cammarata and Dhaher, 2008; Hewett, 1999; Mandelbaum, 2005; Taylor, 2015; Yoo, 2010).

While our results indicate that athletic ability is associated with better neuromuscular control for leg dexterity, it is unclear if these improvements arise from genetic predisposition, extensive exposure to athletic training regimens, or their combination. Nevertheless, we now provide a crucial empirical link between athletic ability, sex differences, and the properties of reconstructed portraits. They represent an important first step in designing future clinical and basic science studies to understand the neuromuscular mechanisms responsible for sensorimotor control at the edge of instability. We conclude that a nonlinear dynamical approach to analysis of leg dexterity may, upon further study, become a simple and useful indicator of athletic ability and a predictor of risk for non-contact knee ligament injury.

#### Conflict of interest statement

FVC holds US Patent No. 6,537,075 on some of the technology used in this study that is commercialized by Neuromuscular Dynamics, LLC. ELL and LP have no financial or personal relationships with other people or organizations that could inappropriately influence this work.

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#### References

- Benjaminse, A. et al., 2015. Optimization of the anterior cruciate ligament injury prevention paradigm: novel feedback techniques to enhance motor learning and reduce injury risk. *J. Orthop. Sports Phys. Ther.* 45 (3), 170–182.
- Cammarata, M.L., Dhaher, Y.Y., 2008. The differential effects of gender, anthropometry, and prior hormonal state on frontal plane knee joint stiffness. *Clin. Biomech. (Bristol, Avon)* 23 (7), 937–945.
- Dayanidhi, S. et al., 2013. Developmental improvements in dynamic control of fingertip forces last throughout childhood and into adolescence. *J. Neurophysiol.* 110 (7), 1583–1592.
- Dayanidhi, S., Kutch, J.J., Valero-Cuevas, F.J., 2013. Decrease in muscle contraction time complements neural maturation in the development of dynamic manipulation. *J. Neurosci.* 33 (38), 15050–15055.

- Dayanidhi, S., Valero-Cuevas, F.J., 2014. Dexterous manipulation is poorer at older ages and is dissociated from decline of hand strength. *J. Gerontol. A Biol. Sci. Med. Sci.* 69 (9), 1139–1145.
- Fedotenkova, M., 2013. Mathematical modeling of level of anaesthesia from EEG measurements.
- Hewett, T.E., 2000. Neuromuscular and hormonal factors associated with knee injuries in female athletes. Strategies for intervention. *Sports Med.* 29 (5), 313–327.
- Hewett, T.E. et al., 1999. The effect of neuromuscular training on the incidence of knee injury in female athletes. A prospective study. *Am. J. Sports Med.* 27 (6), 699–706.
- Hewett, T.E. et al., 1996. Plyometric training in female athletes. Decreased impact forces and increased hamstring torques. *Am. J. Sports Med.* 24 (6), 765–773.
- Holmstrom, L. et al., 2011. Dissociation of brain areas associated with force production and stabilization during manipulation of unstable objects. *Exp. Brain Res.* 215 (3–4), 359–367.
- Huston, L.J., Wojtys, E.M., 1996. Neuromuscular performance characteristics in elite female athletes. *Am. J. Sports Med.* 24 (4), 427–436.
- Kantz, H., 2012. *Nonlinear Analysis of Physiological Data*. Springer Science & Business Media.
- Kantz, H., Schreiber, T., 2004. *Nonlinear Time Series Analysis*. Cambridge University Press.
- Kennel, M.B., Brown, R., Abarbanel, H.D., 1992. Determining embedding dimension for phase-space reconstruction using a geometrical construction. *Phys. Rev. A* 45 (6), 3403–3411.
- Ko, N.H. et al., 2015. Force variability during dexterous manipulation in individuals with mild to moderate Parkinson's disease. *Front Aging Neurosci.* 7, 151.
- Krenn, O. et al., 2015. The lower extremity dexterity test quantifies sensorimotor control for cross-country skiing. *Sci. Skiing VI*, 439–445.
- Laine, C.M., Nagamori, A., Valero-Cuevas, F.J., 2016. The dynamics of voluntary force production in afferented muscle influence involuntary tremor. *Front Comput. Neurosci.* 10, 86.
- Lawrence, E.L. et al., 2015. Strength, multijoint coordination, and sensorimotor processing are independent contributors to overall balance ability. *Biomed. Res. Int.* 2015, 561243.
- Lawrence, E.L. et al., 2014. Quantification of dexterity as the dynamical regulation of instabilities: comparisons across gender, age, and disease. *Front Neurol.* 5, 53.
- Lephart, S.M. et al., 2002. Gender differences in strength and lower extremity kinematics during landing. *Clin. Orthop. Relat. Res.* 401, 162–169.
- Lyle, M.A. et al., 2014. Control of dynamic foot-ground interactions in male and female soccer athletes: females exhibit reduced dexterity and higher limb stiffness during landing. *J. Biomech.* 47 (2), 512–517.
- Lyle, M.A. et al., 2015. Lower extremity dexterity is associated with agility in adolescent soccer athletes. *Scand. J. Med. Sci. Sports* 25 (1), 81–88.
- Lyle, M.A. et al., 2013. The lower extremity dexterity test as a measure of lower extremity dynamical capability. *J. Biomech.* 46 (5), 998–1002.
- Mandelbaum, B.R. et al., 2005. Effectiveness of a neuromuscular and proprioceptive training program in preventing anterior cruciate ligament injuries in female athletes: 2-year follow-up. *Am. J. Sports Med.* 33 (7), 1003–1010.
- Mosier, K. et al., 2011. Controlling instabilities in manipulation requires specific cortical-striatal-cerebellar networks. *J. Neurophysiol.* 105 (3), 1295–1305.
- Myer, G.D. et al., 2005. Neuromuscular training improves performance and lower-extremity biomechanics in female athletes. *J. Strength Cond. Res.* 19 (1), 51–60.
- Nagamori, A., Valero-Cuevas, F.J., Finley, J.M., 2016. Unilateral eccentric contraction of the plantarflexors leads to bilateral alterations in leg dexterity. *Front Physiol.* 7, 582.
- Pavlova, E. et al., 2015. Activity in the brain network for dynamic manipulation of unstable objects is robust to acute tactile nerve block: an fMRI study. *Brain Res.* 1620, 98–106.
- Peppoloni, L. et al., 2017. Characterization of the disruption of neural control strategies for dynamic fingertip forces from attractor reconstruction. *PLoS One* 12 (2), e0172025.
- Perc, M., 2005. The dynamics of human gait. *Eur. J. Phys.* 26 (3), 525.
- Perc, M., 2005. Nonlinear time series analysis of the human electrocardiogram. *Eur. J. Phys.* 26 (5), 757.
- Proctor, J., Holmes, P., 2010. Reflexes and preflexes: on the role of sensory feedback on rhythmic patterns in insect locomotion. *Biol. Cybern.* 102 (6), 513–531.
- Revzen, S. et al., 2013. Instantaneous kinematic phase reflects neuromechanical response to lateral perturbations of running cockroaches. *Biol. Cybern.* 107 (2), 179–200.
- Reyes, A. et al., 2017. Beta band corticomuscular drive reflects muscle coordination strategies. *Front Comput. Neurosci.* 11, 17.
- Stanley, L.E. et al., 2016. Sex differences in the incidence of anterior cruciate ligament, medial collateral ligament, and meniscal injuries in collegiate and high school sports: 2009–2010 through 2013–2014. *Am. J. Sports Med.* 44 (6), 1565–1572.
- Stergiou, N., 2016. *Nonlinear analysis for human movement variability*, xiii, 394 pages.
- Takens, F., 1985. On the numerical determination of the dimension of an attractor. In: *Dynamical Systems and Bifurcations*, Springer. pp. 99–106.
- Taylor, J.B. et al., 2015. Evaluation of the effectiveness of anterior cruciate ligament injury prevention programme training components: a systematic review and meta-analysis. *Br. J. Sports Med.* 49 (2), 79–87.
- Tsai, L.C. et al., 2012. Greater muscle co-contraction results in increased tibiofemoral compressive forces in females who have undergone anterior cruciate ligament reconstruction. *J. Orthop. Res.* 30 (12), 2007–2014.
- Tsianos, G.A., Goodner, J., Loeb, G.E., 2014. Useful properties of spinal circuits for learning and performing planar reaches. *J. Neural Eng.* 11 (5), 056006.
- Valero-Cuevas, F.J. et al., 2003. The strength-dexterity test as a measure of dynamic pinch performance. *J. Biomech.* 36 (2), 265–270.
- Venkadesan, M., Guckenheimer, J., Valero-Cuevas, F.J., 2007. Manipulating the edge of instability. *J. Biomech.* 40 (8), 1653–1661.
- Wolf, A. et al., 1985. Determining Lyapunov exponents from a time series. *Physica D: Nonlinear Phenomena* 16 (3), 285–317.
- Yoo, J.H. et al., 2010. A meta-analysis of the effect of neuromuscular training on the prevention of the anterior cruciate ligament injury in female athletes. *Knee Surg. Sports Traumatol. Arthrosc.* 18 (6), 824–830.