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RESEARCH ARTICLE

Limb dynamics in agility jumps of beginner and advanced dogs

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ABSTRACT

A considerable body of work has examined the dynamics of different dog gaits, but there are no studies that have focused on limb dynamics in jumping. Jumping is an essential part of dog agility, a dog sport in which handlers direct their dogs through an obstacle course in a limited time. We hypothesized that limb parameters like limb length and stiffness indicate the skill level of dogs. We analyzed global limb parameters in jumping for 10 advanced and 10 beginner dogs. In experiments, we collected 3D kinematics and ground reaction forces during dog jumping at high forward speeds. Our results revealed general strategies of limb control in jumping and highlighted differences between advanced and beginner dogs. In take-off, the spatially leading forelimb was 75% ($P<0.001$) stiffer than the trailing forelimb. In landing, the trailing forelimb was 14% stiffer ($P<0.001$) than the leading forelimb. This indicates a strut-like action of the forelimbs to achieve jumping height in take-off and to transfer vertical velocity into horizontal velocity in landing (with switching roles of the forelimbs). During landing, the more (24%) compliant forelimbs of beginner dogs ($P=0.005$) resulted in 17% ($P=0.017$) higher limb compression during the stance phase. This was associated with a larger amount of eccentric muscle contraction, which might in turn explain the soft tissue injuries that frequently occur in the shoulder region of beginner dogs. For all limbs, limb length at toe-off was greater for advanced dogs. Hence, limb length and stiffness might be used as objective measures of skill.

KEY WORDS: Dog biomechanics, Jumping, Skill, Limb stiffness, Eccentric muscle contraction

INTRODUCTION

Jumping is an important element in the repertoire of movements in many quadrupedal animals. To date, four-legged jumping has mostly been studied in horse steeplechase racing (Deuel and Park, 1993; Leach and Ormrod, 1984) and show jumping (Barrey and Galloux, 1997; Bobbert and Santamaría, 2005; Van den Bogert et al., 1994; Clayton, 1989, 1996; Clayton and Barlow, 1991; Hole et al., 2002; Leach et al., 1984; Powers and Harrison, 2002). A comparatively new and increasingly popular animal sport is dog agility, a dog sport in which handlers direct their dogs quickly through an obstacle course. In agility, dogs exhibit impressive dynamics during the competition, and jumping is a basal part of every course. As they are also easy to handle, agility dogs are highly suited for dynamical studies. Such data are needed for gaining insight into the mechanisms of the dogs' jumping movements, for finding global principles of four-legged jumping and for understanding scaling aspects of jumping dynamics.

In agility, dogs are separated into different categories related to their skill level. Beginner dogs compete in a low-agility grade (A0–A1) while advanced dogs compete in the highest grade (A3). The latter are able to cope with more complex courses. In competition, skill level is solely determined from the ability of the dog to finish a course without faults in a certain time. To the best of our knowledge, there exist no objective dynamical parameters that describe the skill level of an agility dog.

Hurdle height has been shown to affect vertical peak force and landing angle (Pfau et al., 2011) and joint angles of the forelimb and hindlimb at take-off (Birch and Leśniak, 2013). The type of obstacle and the distance between them influences the peak vertical force, the vertical momentum, the accelerating horizontal momentum during landing (Pfau et al., 2011), the speed and the jumping distance (Birch et al., 2015). Furthermore, the peak vertical force depends on the breed of dog (Yanoff et al., 1992). There is only one kinematic study which shows that training level influences speed, take-off and landing distance as well as flexion and extension of the shoulder joint (Birch et al., 2015). Finally, injuries are more common in beginner dogs, and in border collies (Cullen et al., 2013). The reported soft tissue injuries occur mostly in the shoulder region (Cullen et al., 2013; Levy et al., 2009).

As for dog agility, studies on the effects of training/skill level in equestrian jumping are also mostly based on kinematics. Because of the early selection of sport horses, most studies including jumping ability have considered young untrained horses or foals during free jumping before and after a training period (Santamaría et al., 2004, 2005; Bobbert et al., 2005) or related to jumping success (Powers and Harrison, 2000; Wejer et al., 2013). The latter measure has been applied in experienced horses, too (Clayton et al., 1995; Colborne et al., 1995). In the standardized study of Cassiat et al. (2004), differences in competition level of trained horses were visible in back kinematics during free jumping. Cassiat et al. (2004) suggested that the difference is caused by a strut-like effect of the forelimbs, which is more distinct in higher level horses. This indicates that global limb dynamics differ across skill level in forelimbs.

Dynamical parameters based on simple mechanical models can be used to break down the complexity of a system (Blickhan et al., 2018; Full and Koditschek, 1999) and might thus be suited to describe take-off and landing dynamics in a manageable manner. Simple mechanical models have provided deeper insight into the principles of locomotion. Global dynamics of running have been described with the spring-mass model (Blickhan, 1989; McMahon and Cheng, 1990). According to this description, the limbs act like linear springs, repeatedly storing and releasing energy. This simplification reduces all the elements of the musculoskeletal limb, including its control, to an ideal spring with just two parameters: stiffness and angle of attack. The spring (or limb)

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List of symbols and abbreviations

A	advanced dogs
B	beginner dogs
BW	body weight
d	distance to the hurdle
d_x	between-feet distance
FL	forelimbs
F_x	horizontal ground reaction force
F_z	vertical ground reaction force
$F_{z,\max}$	peak vertical ground reaction force
GRF	ground reaction force
HL	hindlimbs
$\hat{k}$	dimensionless limb stiffness
L	landing
l	limb length
l_0	unloaded limb length
l_{TD}	limb length at toe-down
l_{TO}	limb length at toe-off
Ld	leading limb
LdF	leading forelimb
LdH	leading hindlimb
Sync	synchronicity
T	take-off
TD	toe-down
TO	toe-off
Tr	trailing limb
TrF	trailing forelimb
TrH	trailing hindlimb
t_{s}	stance time
v_{TD}	velocity at toe-down
α	angle of attack
Δl	limb compression
$-\Delta p_{x-}$	decelerative impulse
Δp_{x+}	accelerative impulse
Δp_z	vertical impulse

stiffness is an important parameter in locomotion and is typically assessed, experimentally, as the ratio of peak ground reaction force (GRF) and the change in limb length during the stance phase (McMahon and Cheng, 1990; Blickhan and Full, 1993; Farley and González, 1996; Stafilidis and Arampatzis, 2007; Grimmer et al., 2008; Coleman et al., 2012; Liew et al., 2017). Stiffness has also been used as a parameter to characterize human and animal hopping (Farley et al., 1991; Ferris and Farley, 1997; Hobara et al., 2010; Blickhan, 1989), human jumping (Arampatzis et al., 2001; Seyfarth et al., 1999; Laffaye et al., 2005), human running on uneven ground (Ferris et al., 1998), human skipping (Andrada et al., 2016; Müller and Andrada, 2018), and human, avian and macaque locomotion including a trunk (Maus et al., 2010; Andrada et al., 2014; Blickhan et al., 2018). Simple model-based experimental studies exist for human hurdling (Mauroy et al., 2014; Cappa and Behm, 2013). In those studies, leg stiffness did not correlate with skill level. However, quadrupedal locomotion might impose different requirements to global limb control.

We expected skill level in dog jumping to be reflected in global limb dynamics and to find evidence for a strut-like mechanism in dog jumping, similar to that in horses. We hypothesized increased limb stiffness in advanced dogs, as a result of adapted jumping technique and limb coordination. To test this, we analyzed the global limb strategies for jumping in advanced and beginner agility dogs. We investigated kinematics and kinetics during take-off and landing phases of all four limbs individually using force plates in synchrony with marker-based motion capture.

MATERIALS AND METHODS

Animals

We obtained kinematic and kinetic data from 20 healthy adult border collies. The dogs were separated into advanced and beginner categories, based on their agility grade. All dogs were categorized as large, with a height at the withers over 43 cm (Table 1).

All animal experiments were in accordance with the national animal protection act. All dogs were healthy, and the experiments reflect the normal training situation but in a different room.

Motion capture

Kinematic data were recorded using an optoelectronic marker-based method. Sixteen infrared cameras (Oqus Series 400, Qualisys, Göteborg, Sweden) were set around the walking track. The animals were recorded at a frequency of 400 Hz, using Qualisys Track Manager® software (QTM, version 2.15). A standard wand-based calibration procedure resulted in a calibrated area of approximately 6×6×1.5 m (length×width×height) with a calibration error (standard deviation of the wand length) of 2 mm (for resulting Cartesian coordinate system, see Fig. 1A). Animals were prepared with 83 passive markers based on methods in Andrada et al. (2017). Markers were attached to the shaved skin with double-sided adhesive tape. Additionally, we used Kinesiotape® to fix the sockets of the markers at the distal ends of the limbs (Fig. 1B). Body markers were secured with a flexible stretch tube, which was drawn along the entire trunk of the dog, to prevent the obscuring of markers by fur (Fig. 1B).

Force data acquisition

We measured 3D GRFs with eight force plates (600 mm×900 mm, 9287 CA, Kistler Instruments AG). Two rows each of four force plates were integrated into the walking track. Each plate was covered with a 3.5 cm Tartan® mat to ensure a slip-proof surface. For the same reason, the floor surrounding the force plate region was fitted with carpet mats. GRF was sampled at 2 kHz, synchronized with the kinematic recording.

Data collection and procedure

Two hurdles in accordance with the agility rules of the Fédération Cynologique Internationale (FCI) were used. In order to ensure comparable conditions for all dogs, hurdle height was set at 90% of the dog's height at the withers. The dogs started 4 m in front of the first hurdle. The distance between the hurdles was 5 m. After the second hurdle, dogs had a minimum of 4 m for runout. The second hurdle was placed over the force plates (Fig. 1A). Because of the long jumping distances, take-off and landing had to be recorded in different trials. The footfall pattern meant we were not able to record forelimbs and hindlimbs in the same trial in most cases.

Each dog was led by its owner, using their preferred technique. The goal was to record three valid trials per pair of limbs and jump phase, depending on the dog's motivation and ability. A jump was considered valid if the dog jumped both hurdles without knocking down the pole and if the dog contacted both hindlimbs or both forelimbs on different force plates during take-off or landing.

Table 1. Classification of 'skill' in experimental setup

	Advanced	Beginner
Grade	A3	A0–A1
Agility experience	>4 years	<4 years
Withers height (cm)	53.6±3.6	51.3±3.7
Mass (kg)	18.7±3.6	17.4±3.2

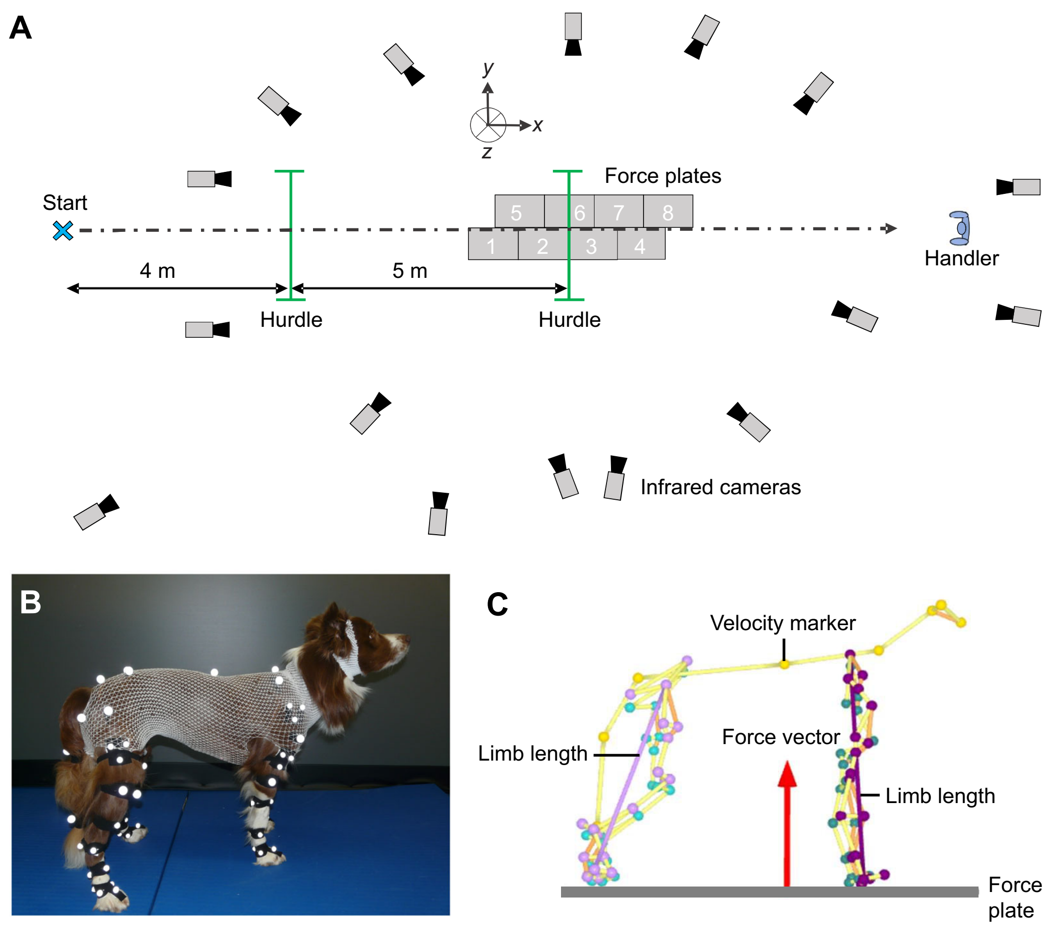

Fig. 1. Experimental setup. (A) Equidistant hurdles were adjusted to enable recording of each limb in a pair on different force plates (numbered 1–8) during take-off and landing (see Materials and Methods, 'Data collection and procedure'). (B) Markers were placed on the shaved skin with double-sided adhesive tape. Body markers were additionally fixed with flexible stretch tube, whereas distal limb markers were additionally fixed with Kinesiotape®. (C) Schematic diagram of a dog standing still on one force plate. The velocity marker, used to determine the running velocity, was aligned with the force vector during stance.

The dog and handler were acquainted with the task. Body weight (BW) was measured while the dog was standing still on one force plate (Fig. 1C). Dogs rested whenever the handler or the experimenter judged it appropriate.

Data analysis

The 'take-off phase' comprised the last four contacts between the limbs and the ground prior to the airborne phase of the jump (Leach et al., 1984; Leach and Ormrod, 1984). Similarly, the 'landing phase' comprised the first four contacts between the limbs and the ground after the airborne phase of the jump. Contact with the ground was made in the following order: trailing forelimb (TrF), leading forelimb (LdF), trailing hindlimb (TrH), leading hindlimb (LdH) (Clayton, 1989). A vertical GRF threshold of 1 N was used to determine the instances of toe-down (TD), toe-off (TO) and thus the stance time (t_s).

Limb stiffness (k) was calculated as the ratio between the maximal axial GRF along the limb and the maximum limb compression: $k = \mathrm{GRF}_{\max}/\Delta l$, where Δl is defined as $l_0 - l_{\mathrm{GRF,max}}$ [limb length five frames before TD (i.e. unloaded limb length) minus limb length at axial $\mathrm{GRF}_{\max}$]. The limb length l of the hindlimbs is defined as the distance between the markers at the greater trochanter of the femur and the lateral tarsometatarsal joint (Farley et al., 1993). For the forelimbs, l is the distance between the markers at the margo dorsalis of the spina scapulae and the lateral carpometacarpal joint. To make data comparable, force (F_z, vertical GRF; F_x, horizontal GRF; $F_{z,\max}$, peak vertical GRF) and impulse ($\Delta p = \int_{\mathrm{TD}}^{\mathrm{TO}} F\mathrm{d}t$; Δp_z, vertical impulse; Δp_{x+}, accelerative impulse; and $-\Delta p_{x-}$, decelerative impulse) parameters were normalized to BW, and limb length was normalized to l_0. Thus, dimensionless limb stiffness was calculated as (McMahon and Cheng, 1990):

$$\hat{k} = \frac{k \cdot l_0}{m \cdot \mathbf{g}}, \tag{1}$$

where m is mass and $\mathbf{g}$ is acceleration due to gravity. The angle of attack α at TD was determined as the angle between the ground and the limb (see Fig. 2 phases I–VIII, colored lines). A representative example of GRFs in take-off and landing phases of an advanced dog is shown in Fig. 2. Means and standard deviations of GRFs, relative limb lengths and limb forces during stance are shown for jumping and landing in Fig. 3. Additionally, we calculated velocity (v_{TD}) from kinematic data using a marker on the dorsal line. The marker was placed in the direction of the force vector whilst the dog was standing still on one force plate (Fig. 1C). Distance to the hurdle d for take-off and landing was defined as the distance between the hurdle and the limb placed closest to the hurdle of each pair of limbs. Jump height was defined as the apex height of the velocity marker divided by the height at the withers. Limb synchronicity (Sync) was measured as the time between the instants of contact with the ground

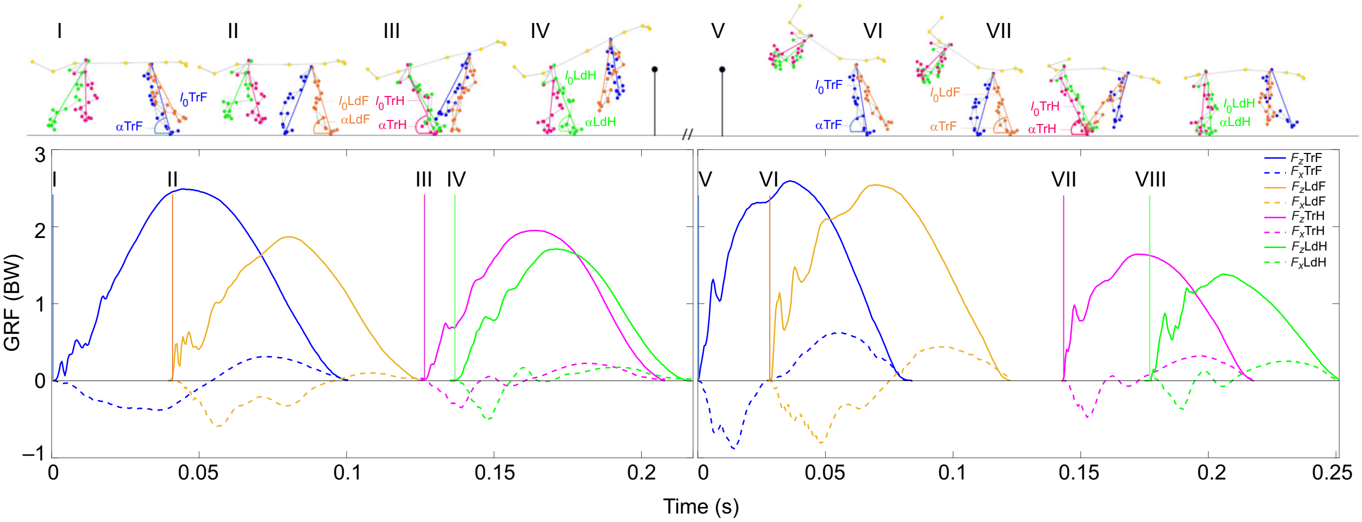

Fig. 2. Schematic drawing of a dog jumping over the hurdle. Top: stick figure with markers. Bottom: vertical (solid) and horizontal (dashed) ground reaction forces (GRFs). Left: take-off of one male dog (body weight, BW 205.7 N). Right: landing of one female dog (BW 146.4 N). Roman numerals indicate consecutive toe-down (TD) events. Blue: trailing forelimb (TrF); orange: leading forelimb (LdF); magenta: trailing hindlimb (TrH); green: leading hindlimb (LdH). α, angle of attack; l_0, unloaded limb length; F_z, vertical force; F_x, horizontal force.

of the two forelimbs or the two hindlimbs. Synchronicity is reported as a percentage of stance time of the trailing limb. Distance between the feet (d_x) was calculated for each pair of limbs as the distance in the x-direction between the feet at toe-down. Raw kinematic data were filtered with a fourth-order zero-lag low-pass Butterworth filter with a cut-off frequency of 20 Hz (Winter, 2005). The results are expressed as means±s.d. over all subjects and parameters (Table 2). All data were analyzed using MATLAB® 2017a.

Statistical analysis

Data were divided into two subsets, one containing all parameters for forelimbs (FL) and another containing all parameters for hindlimbs (HL). Only limb compression and stiffness were additionally analyzed separately for take-off and landing. For statistical analyses, we used a linear mixed effects model approach. To analyze the prediction of parameter variance by the categorical descriptors of the jump, we reduced one-by-one non-significant effects starting with the complete model until the final reduced model satisfied a minimal Akaike information criterion (Crawley, 2007). First, backward random effects elimination was performed, followed by elimination of the fixed effects. From the final reduced model, we calculated P-values using Satterthwaite's approximation for degrees of freedom (Kuznetsova et al., 2017). The categorical parameters 'skill' [beginner (B) or advanced (A)], 'jump' [take-off (T) or landing (L)], 'limb' [trailing (Tr) or leading (Ld)], and real-valued parameters 'velocity at TD' (v_{TD}) and 'distance to hurdle' (d) were included in the model as fixed effects. The full model considered the interactions jump×limb, jump×skill, limb×skill and jump×limb×skill. 'Dog',

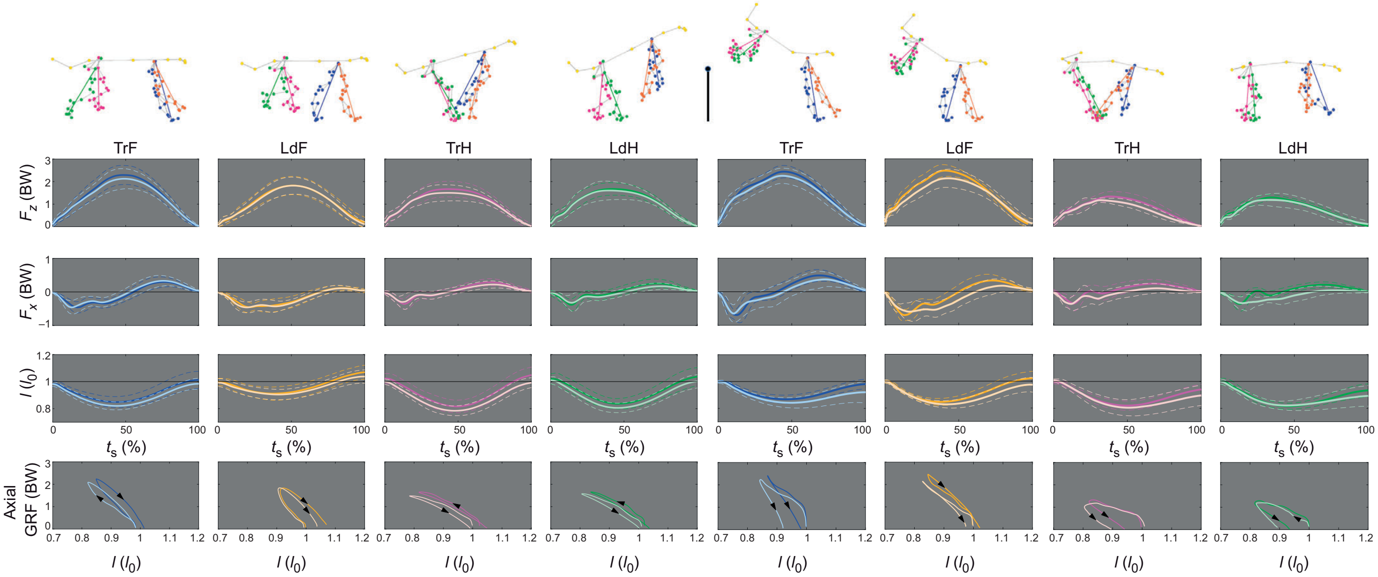

Fig. 3. Mean curves of GRFs and limb lengths of advanced (dark colors) and beginner (light colors) dogs. Solid line: averaged mean, dashed line: standard deviation. Blue: trailing forelimb (TrF); orange: leading forelimb (LdF); magenta: trailing hindlimb (TrH); green: leading hindlimb (LdH). First row: vertical force (F_z) over stance duration (t_s); second row: horizontal force (F_x) over t_s; third row: limb length (l; as a proportion of unloaded limb length, l_0) over t_s: fourth row: axial GRF–l curve.

Table 2. Take-off and landing parameters for advanced (dark gray) and beginner (light gray) dogs

	Forelimb pair				Hindlimb pair			
	Take-off		Landing		Take-off		Landing	
	Advanced	Beginner	Advanced	Beginner	Advanced	Beginner	Advanced	Beginner
Trailing limb								
t_s (ms)	104±14	118±22	87±7	102±21	91±15	98±22	88±9	106±16
$F_{z,max}$ (BW)	2.15±0.48	2.05±0.42	2.46±0.23	2.3±0.36	1.68±0.33	1.57±0.24	1.42±0.23	1.26±0.27
Δp_z (BW s)	0.128±0.015	0.141±0.011	0.131±0.01	0.138±0.008	0.097±0.01	0.099±0.01	0.075±0.013	0.076±0.012
Δp_{x+} (BW s)	0.007±0.004	0.01±0.004	0.016±0.006	0.013±0.008	0.01±0.004	0.008±0.003	0.01±0.007	0.006±0.005
$-\Delta p_{x-}$ (BW s)	0.016±0.005	0.019±0.005	0.012±0.006	0.015±0.011	0.006±0.002	0.006±0.003	0.005±0.003	0.010±0.012
$\hat{k}$	16±5	12±3	19±4	15±3	11±6	8±2	8±2	8±3
α at TD (deg)	65±3	63±4	77±4	76±7	61±3	61±4	70±5	70±11
l at TD (l_0)	0.99±0.01	0.98±0.01	1.0±0.01	1.0±0.01	1.02±0.02	1.0±0.01	0.99±0.01	1.01±0.01
l at TO (l_0)	1.01±0.06	0.98±0.03	0.98±0.04	0.9±0.08	1.05±0.05	0.98±0.03	0.95±0.03	0.91±0.08
Δl (l_0)	0.15±0.04	0.18±0.02	0.13±0.02	0.16±0.03	0.17±0.04	0.2±0.03	0.18±0.03	0.18±0.05
Leading limb								
t_s (ms)	94±28	100±13	100±7	123±28	86±13	95±20	89±12	115±36
$F_{z,max}$ (BW)	1.85±0.26	1.82±0.31	2.5±0.21	2.06±0.45	1.7±0.2	1.68±0.36	1.27±0.12	1.14±0.23
Δp_z (BW s)	0.102±0.03	0.106±0.018	0.15±0.008	0.153±0.027	0.093±0.012	0.097±0.008	0.069±0.01	0.074±0.018
Δp_{x+} (BW s)	0.002±0.001	0.002±0.001	0.011±0.005	0.005±0.003	0.009±0.005	0.005±0.002	0.008±0.004	0.003±0.003
$-\Delta p_{x-}$ (BW s)	0.019±0.009	0.022±0.005	0.021±0.007	0.032±0.019	0.006±0.004	0.007±0.003	0.004±0.004	0.012±0.005
$\hat{k}$	25±6	23±6	17±4	13±3	10±2	9±2	8±1	7±2
α at TD (deg)	62±5	60±2	66±4	64±4	59±4	58±2	60±3	58±3
l at TD (l_0)	1.0±0.02	1.0±0.03	1.0±0.01	1.0±0.01	1.01±0.03	1.01±0.02	1.0±0.02	1.0±0.02
l at TO (l_0)	1.06±0.05	1.04±0.05	1.02±0.05	0.96±0.05	1.03±0.04	1.0±0.04	0.93±0.03	0.91±0.07
Δl (l_0)	0.09±0.03	0.09±0.03	0.15±0.03	0.17±0.02	0.16±0.02	0.19±0.02	0.17±0.02	0.17±0.03
Synchronism (% of t_s, Tr)	41.8±5.2^{a,c}	56.7±5.2^{b,c}	37.2±6.9^{a}	33.1±10.8^{b}	13.5±7.2^{d}	17±8.9^{e}	45.5±9.5^{d}	42.7±19.2^{e}
v_{TD} (m s^{-1})	5.9±0.5^{a}	5.5±1.0^{c}	6.3±0.4^{a,b}	5.2±1.2^{b,c}	5.4±0.6^{d}	4.7±0.9	6.0±0.5^{d,e}	4.7±1.0^{e}
d_x (cm)	23.6±6.8^{b}	35.0±5.9^{a}	19.2±8.8	18.4±10.1^{a,b}	6.9±3.5^{c}	9.7±5.4^{d}	26.7±5.3^{c}	23.5±13.5^{d}
d (m)	2.06±0.5^{a,b}	1.39±0.32^{b,c}	1.2±0.7^{a,d}	1.2±0.3^{c,d}	1.95±0.43^{e,f}	1.3±0.39^{e}	1.4±0.2^{f,g}	1.3±0.4^{g}
n	8	9	10	10	10	10	7	8

Data are means±s.d. Dark and light gray shading indicate advanced and beginner, respectively, to aid comparison. White cells are parameters that were not measured per limb. Superscript letters indicate means that are significantly (P<0.05) different using backward reduction of mixed effect models.

t_s, stance time; $F_{z,max}$, peak vertical force; Δp_z, vertical impulse; Δp_{x+}, accelerative impulse; $-\Delta p_{x-}$, decelerative impulse; $\hat{k}$, limb stiffness; α, angle of attack; TD, toe-down; TO, toe-off; l, limb length; l_0, unloaded limb length; Δl, maximum limb compression; Tr, trailing; v_{TD}, speed at TD; d_x, between-feet distance; d, distance to hurdle; n, number of dogs.

which contained the individuals, was set as a random effect. Although obstacle height was the same for all dogs, we checked whether jumping height was significantly different between the two groups of skill. Therefore, we used a model containing the whole dataset and included 'skill', 'velocity at TD' (v_{TD}) and 'distance to hurdle' (d) as fixed effects. Parameters calculated for each pair of limbs (Sync, v_{TD}, d, d_x) did not include 'limb' as a fixed effect.

All models were fitted using maximum likelihood estimation. Model acquirements and assumptions were fulfilled, as variances were homogeneous and residuals normally distributed. *Post hoc* analyses of main effects and interaction effects were carried out using comparison of least mean squares of group means. The approximation for degrees of freedom is Satterthwaite's (Kuznetsova et al., 2017). Significance was defined for P≤0.05. All analyses were conducted in R version 3.4.2 (http://www.R-project.org/). The package 'lmerTest' (Kuznetsova et al., 2017) was used to analyze the mixed-effect models and perform the *post hoc* tests.

An overview of the main effects and interactions of 'skill', 'jump', 'limb', 'velocity at TD' and 'distance to hurdle', as well as the variance caused by the random effect is shown in Table 3. Significant differences of parameters calculated for each pair of limbs (Sync, v_{TD}, d, d_x) are reported in Table 2 (see superscripts).

RESULTS

In total, 271 valid jumping trials were analyzed from 20 subjects. Over the whole dataset, jumping height did not differ significantly between skill levels. Skill effect was not included in the final reduced model for jumping height (P=0.915). Jump height increased significantly with higher velocity and greater distance to the hurdle (P=0.023, P<0.001, respectively).

Main effects of skill, jump, limb, velocity and distance in dog jumping

In the following, all differences were significant. Overall, the compared parameters were more often significantly different for the forelimbs than for the hindlimbs (Table 3). If both group-wise comparisons were significantly different in the same direction, then the main effect was regarded as relevant. Other main effects were interaction driven and are reported with asterisks.

Skill

Beginner dogs showed shorter hindlimb stance duration than advanced dogs and shorter limb length at toe-down (7%, P=0.032; 2%, P=0.009). Their limb stiffness in the forelimbs was lower (19%, P=0.009). For both pairs of limbs, limb length at toe-off was lower in beginner dogs (FL: 5%, P=0.005; HL: 4%, P=0.009). Additionally, beginner dogs showed larger limb compression than advanced dogs (FL: 21%, P=0.004; HL: 15%, P=0.047).

Jump

Comparing landing with take-off, limb length at toe-off was shorter in the forelimbs (6%, P<0.001) and hindlimbs (8%, P<0.001).

Table 3. Main effects and interactions of final reduced mixed models

	t_s	$F_{z,\max}$	Δp_z	Δp_{x+}	$-\Delta p_{x-}$	$\hat{k}$	α	l_{TD}	Δl	l_{TO}
Forelimb										
Random effect										
Dog	45%	20%		46%	41%	27%	59%		33%	35%
Fixed effects										
v_{TD}	↓ ***	↑ ***						↓ *		
d							↓ **		↑ **	
Skill B:A				↓ ‡,*		↓ **	↓ ‡		↑ **	↓ **
Jump L:T	↑ ‡,***	↑ ***	↑ ‡,***	↑ ‡,***	↑ ‡,**	↓ ‡,***	↑ ‡	↑ ‡	↑ ‡,***	↓ ***
Limb Ld:Tr	↑ ‡,***	↓ **	↓ ‡	↓ ***	↑ ‡,***	↑ ‡,*	↓ ‡,***	↑ ‡	↓ ‡,**	↑ ***
Interaction effects										
Skill × Jump										
BL:AL				↓ *			↓			
AL:AT				↑ ***			↑ **			
BL:BT				↑ **			↑ ***			
BT:AT				↑			↓ **			
Jump × Limb										
LLd:TLd	↑ ***		↑ ***		↑ *	↓ ***	↑	↓	↑ ***	
LLd:LTr	↑ ***		↑ *		↑ ***	↓ *	↓ ***	↓	↑ **	
TLd:TTr	↓ ***		↓ ***		↑	↑ ***	↓ **	↑ *	↓ ***	
LTr:TTr	↓ ***		↓		↓	↑ **	↑ ***	↑ *	↓	
Hindlimb										
Random effect										
Dog				56%	38%	32%	40%	32%	38%	41%
Fixed effects										
v_{TD}	↓ ***	↑ ***	↓ ***	↓ *				↓	↑ *	
d			↑ **	↑ ***		↑ ***			↓ *	
Skill B:A	↓ *		↓ ‡,*	↓ ‡,**	↑ ‡,**			↓ **	↑ *	↓ **
Jump L:T	↑ ***	↓ ***	↓ ‡	↑ ‡,*	↑ ‡	↓ *	↑ ‡		↓ **	↓ ***
Limb Ld:Tr				↓ ***			↓ ‡,***			
Interaction effects										
Skill × Jump										
BL:AL			↓	↓ **	↑ **					
AL:AT			↓	↑ *	↓					
BL:BT			↓ ***	↓	↑ **					
BT:AT			↑	↓	↑					
Jump × Limb										
LLd:TLd							↑			
LLd:LTr							↓ ***			
TLd:TTr							↓ *			
LTr:TTr							↑ ***			

Arrows show the direction of the effect or comparison. For example, peak vertical force in forelimbs becomes higher with increasing velocity and was higher during landing compared to take-off and was lower in the leading limb compared to the trailing limb. Asterisks indicate significant effects of final reduced model and *post hoc* analyses of interaction effects (*$P<0.05$, **$P<0.01$, ***$P<0.001$). Random effect (Dog) values are shown as individual variance (%). Empty fields indicate the effect was not included in the final model. The final reduced model for each parameter can be obtained from the non-empty fields in the corresponding table column. For example, the final reduced model for stance duration *t*s contains velocity v_{TD}, jump and limb as main effects, jump×limb interaction as well as the random effect dog [$ts \sim v_{TD}$+Jump+Limb+Jump:Limb+(1|Dog)].

‡ Interaction-driven main effects. t_s, stance time; F_z,max, peak vertical force; Δp_z, vertical impulse; Δp_{x+}, accelerative impulse; $-\Delta p_{x-}$, decelerative impulse; $\hat{k}$, limb stiffness; α, angle of attack; l, limb length; TD, toe-down; TO, toe-off; Δl, maximum limb compression; v_{TD}, velocity at TD; d, distance to hurdle; skill: B – beginner, A – advanced; limb Ld – leading, Tr – trailing; jump T – take-off, L – landing.

Moreover, peak vertical force was higher in the forelimbs and lower in the hindlimbs (FL: 18%, $P<0.001$; HL: 26%, $P<0.001$). For the hindlimbs, stance duration was longer, limb stiffness was lower and limb compression was lower in the landing phase when compared with the take-off phase (15%, $P<0.001$; 14%, $P=0.018$; 10%, $P=0.006$, respectively). In the hindlimbs, distance between the feet was greater in landing and therefore limb feet were placed with less synchronicity (200%, $P<0.001$; 164%, $P<0.001$, respectively).

Limb

In the forelimbs, peak vertical force was smaller (8%, $P<0.001$) and limb length at toe-off was longer (6%, $P<0.001$) in the leading limb compared with the trailing limb. For both pair of limbs, the leading limb showed a lower accelerative impulse compared with the trailing limb (FL: 56%, $P<0.001$; HL: 25%, $P<0.001$).

Velocity

With increasing velocity, for both pairs of limbs, distance to the hurdle increased, peak vertical force increased and stance duration decreased (all: $P<0.001$). Additionally, limb length at toe-down decreased (FL: $P=0.025$; HL: $P=0.001$). The hindlimbs showed increased limb compression and decreased vertical and accelerative impulse with increasing velocity ($P=0.022$, $P<0.001$, $P=0.023$, respectively).

Distance to the hurdle

For both pairs of limbs, the distance to the hurdle effected the maximum limb compression. With increasing distance to the hurdle, limb compression increased in the forelimbs, while it decreased in the hindlimbs ($P=0.02$, $P=0.018$, respectively). Further, the angle of attack decreased and the distance between the feet increased in the forelimbs (*P*=0.002, *P*=0.009, respectively). For the hindlimbs, limb stiffness as well as vertical and accelerative impulses increased (*P*<0.001, *P*=0.008, *P*<0.001, respectively). Both pairs of limbs showed increasing velocity with increasing hurdle distance (all *P*<0.001).

Interactions of skill, jump and limb in dog jumping

We observed nine interactions in the forelimbs and only four in the hindlimbs.

Skill and jump

During landing, the accelerative impulse was higher for advanced dogs than in take-off, for both pairs of limbs (FL: 176%, *P*<0.001; HL: 48%, *P*=0.013). Beginner dogs showed a smaller accelerative impulse than advanced dogs during landing, for both pairs of limbs (FL: 31%, *P*=0.021; HL: 56%, *P*=0.002). In the forelimbs, beginner dogs showed a larger accelerative impulse in landing in comparison to take-off (52%, *P*=0.009). Further, the angle of attack was steeper in landing for advanced and beginner dogs in comparison to take-off in the forelimbs (7%, *P*=0.005; 13%, *P*<0.001, respectively). Additionally, during take-off, beginner dogs showed a shallower angle of attack compared with advanced dogs (8%, *P*=0.008). The forelimbs of beginner dogs showed higher synchronicity and decreased distance between the feet during landing compared with take-off (40%, *P*<0.001; 41%, *P*<0.001, respectively). Additionally, beginner dogs showed less synchronicity and more spread feet placement during take-off compared with advanced dogs (33%, *P*<0.001; 89%, *P*<0.001, respectively).

For the hindlimbs, the decelerative impulse during landing was larger, not only for beginner dogs compared with advanced dogs (131%, *P*=0.004) but also for beginner dogs compared with beginner dogs in take-off (59%, *P*=0.003). Additionally, in the hindlimbs, vertical impulse was only lower for beginner dogs during landing, in comparison to take-off (25%, *P*<0.001).

For both pairs of limbs, velocity at toe-down for advanced dogs was higher and distance to the hurdle decreased in landing compared with take-off (FL: 17%, 47%; HL: 18%, 38%; *P*<0.001 for all). Only in the forelimbs of beginner dogs did both parameters decrease in landing compared with take-off (4%, *P*=0.019; 10%, *P*=0.024, respectively). During landing, advanced dogs showed faster velocity and decreased distance to the hurdle compared with beginner dogs (FL: 16%, *P*=0.003; 25%, *P*=0.007; HL: 21%, *P*<0.001; 30%, *P*=0.009, respectively). During take-off, beginner dogs reached a shorter distance to the hurdle compared with advanced dogs (FL: 27%, *P*<0.001; HL: 21%, *P*<0.001, respectively).

Jump and limb

We found increased values in leading versus trailing forelimbs during landing for stance duration (18%, *P*<0.001), vertical impulse (12%, *P*=0.014) and maximum limb compression (12%, *P*=0.005). Conversely, during take-off, all three parameters were lower in leading versus trailing forelimbs (14%, *P*<0.001; 23%, *P*<0.001; 48%, *P*<0.001, respectively). Limb stiffness was lower in landing and higher in take-off in leading versus trailing forelimbs (14%, *P*=0.034; 75%, *P*<0.001). Limb length at toe-down during take-off was longer in the leading forelimb than in the trailing forelimb, and the trailing forelimb showed longer limb length at toe-down during landing in comparison to take-off (2%, *P*=0.01 for both). In both jump phases, braking impulse was higher and angle of attack was lower in leading versus trailing forelimbs (landing: 101%, *P*<0.001; 15%, *P*<0.001; take-off: 23%, *P*=0.136; 4%, *P*=0.003, respectively). The leading forelimb showed higher values for stance duration, vertical impulse, decelerative impulse and maximum limb compression (18%, *P*<0.001; 45%, *P*<0.001; 32%, *P*=0.009; 101%, *P*<0.001, respectively) during landing compared with take-off. Conversely, stance duration decreased during landing in the trailing limb (14%, *P*<0.001). Compared with take-off, limb stiffness during landing was lower in the leading forelimb and higher in the trailing forelimb (38%, *P*<0.001; 26%, *P*=0.004).

The angle of attack was steeper in landing versus take-off in the trailing forelimb, as well as in the trailing hindlimb (FL: 16%, *P*<0.001; HL: 14%, *P*<0.001). Additionally, the leading hindlimb showed a shallower angle of attack than the trailing hindlimb in both jump phases (take-off: 4%, *P*=0.024; landing: 15%, *P*<0.001).

Analysis of limb compression and stiffness in take-off and landing

During take-off, the leading forelimb showed higher limb stiffness and lower limb compression in comparison to the trailing forelimb (75%, *P*<0.001; 46%, *P*<0.001, respectively). Beginner dogs showed larger compression of the hindlimbs in comparison to advanced dogs (20%, *P*=0.008). During landing, forelimb stiffness was lower, and compression of the forelimbs was larger in beginner dogs in comparison to advanced dogs (24%, *P*=0.005; 17%, *P*=0.017, respectively). During landing, the leading forelimb showed lower stiffness and larger compression in comparison to the trailing forelimb (14%, *P*<0.001; 13%, *P*=0.002, respectively). Statistical results are provided in Tables S1–S4.

DISCUSSION

This study is the first to present single limb global dynamics during take-off and landing in agility jumping and to compare limb dynamics of dogs with different skill levels. Skill effects were visible at the level of limb global kinetics and kinematics. Advanced dogs showed higher limb stiffness, decreased limb compression and higher limb length in take-off and landing in their forelimbs (Tables 2 and 3). Their hindlimbs acted almost simultaneously during take-off. The forelimbs of dogs acted differently, especially during landing.

Role-switching of trailing and leading forelimbs in take-off versus landing

For all dogs, our results show that forelimb dynamics differ between limbs during take-off. The angle of attack in the leading limb is shallower and its stiffness is higher than that of the trailing limb. This leading limb configuration leads to a strut-like action that helps to translate horizontal motion into vertical motion as hypothesized for jumping horses (Clayton and Barlow, 1991).

During landing, strut-like limb action is used conversely to translate vertical motion into horizontal motion. Here, the trailing forelimb takes the role of the strut. The angle of attack in the trailing forelimb is steeper than that in the leading limb and its stiffness is higher. The fact that the vaulting role alternates between trailing and leading limbs is a key mechanism to redirect the impulse and is reflected in the increased number of interaction effects between limb and jump in forelimbs compared with hindlimbs (7 versus 1, Table 3). Evidence for the same angle of attack strategy of the forelimbs in take-off and landing has been observed in horses (Clayton and Barlow, 1991).

How level of skill is reflected in jumping technique

For beginner dogs, there was a longer time between toe-down of the trailing and leading forelimb during the take-off phase of the jump

(Table 2). In other words, the dogs showed a reduced stride frequency. Likewise, in horses, Barrey and Galloux (1997) found that 'poor' jumpers used lower stride frequencies. This suggests that beginner dogs lack the prerequisites to jump at higher speed.

Separate statistics for the forelimbs in take-off revealed a non-significant, more pronounced strut-like action in advanced dogs (tendency towards higher stiffness and lower compression; Table 2; Tables S2 and S4). Similarly, differences in trunk rotation in advanced versus beginner horses were attributed to a more pronounced strut-like effect in advanced horses (Cassiat et al., 2004). Moreover, lengthening of the forelimbs was more pronounced in advanced dogs (Table 2).

Bobbert and Santamaria (2005) found that in horses the process of lengthening the hindlimbs from toe-down to toe-off leads to a positive work contribution. In our study, advanced dogs overextended their hindlimbs at toe-off, while beginner dogs merely reached initial limb length, suggesting that the hindlimbs of advanced dogs contribute more work than those of beginners. Hindlimb extension was nearly in phase with the change from the horizontal braking to propulsion phase (Fig. 2). Overextending the limb increases the time over which acceleration can be applied, as seen in hopping and jumping wallabies (McGowan et al., 2005). In advanced dogs, the averaged acceleration impulse of the hindlimbs was twice the deceleration impulse of the hindlimbs, which again is in accordance with hopping wallabies. In contrast, beginner dog's acceleration and deceleration impulses were equal (Table 2). Beginner dogs might lack the muscular strength to overextend the hindlimbs during stance.

In take-off, advanced dogs placed their hindlimbs almost simultaneously and parallel to each other, as in a half-bound. The tendency for spatial and temporal synchronization of the hindlimbs during take-off, even using low obstacles, was also seen in cats, dogs and horses (Abourachid et al., 2007; Alexander, 1974; Leach et al., 1984). This technique allows them to attain a long and balanced aerial phase, as described for bipedal hopping (Blickhan and Full, 1993). Beginner dogs did not achieve the same level of synchronicity of the hindlimbs during the take-off phase, although this was not significant. They showed longer time differences and distances between toe-down of hindlimbs (Table 2). Similarly, the effect of training was visible in horses in the reduced distance between hindlimbs (Wejer et al., 2013). It seems that beginner dogs lack the speedy coordination that is required to switch within one step from an alternating galloping mode to a synchronous jumping mode.

For an efficient hurdling technique, the landing phase is equally important. Spatial and temporal foot placement during landing is less synchronized compared with that during take-off. During landing, the hindlimbs show a significantly longer time and distance between both toe-downs (Table 2). These differences are larger for the hindlimbs than for the forelimbs. This is in accordance with cats and dogs jumping over small obstacles (Abourachid et al., 2007). However, Abourachid et al. (2007) found equal timing of the forelimbs comparing the take-off and landing phase, which is different from our results. We found decreased time of forelimb contacts during landing in comparison to take-off. This could be related to the higher obstacles used in our study. Additionally, we found that beginner dogs showed more synchronized forelimbs in landing than advanced dogs, which indicates that they had to deal with impact with a limited ability to quickly roll over, using the strut-like effect of the forelimbs, as described above. During the landing phase, the change from breaking to propulsion occurred later in beginner dogs than in advanced dogs in all four limbs (Fig. 3, second row). Beginner dogs exhibited a poor landing technique, with a reduced accelerative impulse in comparison with advanced dogs (Table 2).

Beginner dogs were less effective in re-establishing horizontal speed after landing. For all four limbs, limb length at toe-off was shorter compared with that of advanced dogs, resulting in reduced horizontal acceleration impulses (Table 2). Further, beginner dogs showed a higher percentage of breaking time (Fig. 3, second row). This is like in human hurdling, where poor technique has been characterized by a long contact time and a large percentage of breaking time, resulting in a loss of horizontal velocity (Coh et al., 2000; Dapena, 1991; La Fortune, 1988). We can conclude that beginner dogs still had to deal with the impact from landing while advanced dogs re-established their gallop pattern in the phase of hindlimb landing, with only slight differences compared with normal gallop reported by Walter and Carrier (2007).

Brazier et al. (2014; 2003) assumed that limb stiffness relates to performance and injuries. If limb stiffness becomes too high, bone injuries can occur. Conversely, low limb stiffness can result in soft tissue injuries (Brazier et al., 2014; Butler et al., 2003), as a result of excessive joint motion. During landing, beginner dogs showed a less pronounced strut-like effect (lower limb stiffness and higher limb compression; Table 2; Tables S1 and S2). This limited their ability to convert vertical motion into horizontal motion. Consequently, beginner dogs showed larger compression of their limbs in dealing with landing impact (Table 2; Tables S3 and S4). Stiffness depends on pre-activation of the muscles to resist flexion of joints during the subsequent stance phase. Possibly, beginner dogs did not activate antigravity muscles early enough. The flexion of joints is associated with a decreased mechanical advantage (Biewener et al., 2004) that must be compensated by increased muscular activity. Further, excessive joint flexion is associated with extensive eccentric contractions that, in turn, are associated with increased muscle forces (e.g. Tomalka et al., 2017). It follows that beginner dogs tire more quickly and are at a greater risk of soft tissue injuries, especially in the shoulder region (Cullen et al., 2013).

Higher forelimb stiffness in advanced dogs can be caused by a more extended limb configuration (segment arrangement) or higher muscle forces. We found no differences between advanced and beginner dogs with respect to forelimb length and angle of attack at toe-down, during landing (Table 2). This means that leg segments are similarly arranged. Thus, it seems that muscle forces in advanced dogs are higher. This could be caused by higher muscle activity or deviating muscle properties. For example, muscle force in advanced dogs could be enhanced by a passive spring that is recruited upon activation (Lindstedt et al., 2002; Rode et al., 2009).

We conclude that level of skill in dog jumping is reflected in global limb dynamics. We found significantly higher values of forelimb stiffness in advanced jumpers during landing; additionally, greater limb length at toe-off in all limbs in take-off and landing phase was observed in advanced jumpers. Therefore, we suggest that these limb parameters during jumping could be used as an objective measure of jumping skill and possibly to monitor training progress. Greater risk of soft tissue injuries in beginner dogs could be caused by higher limb compression in the forelimbs that is associated with extensive eccentric muscle contractions.

Limitations of the chosen limb model

The chosen parameterization of limbs as linear springs stems from model-based descriptions of animals during periodic locomotion (e.g. Blickhan and Full, 1993). Nonetheless, the spring-like leg model has been successfully applied, in studies of non-conservative human jumping (Seyfarth et al., 1999; Laffaye et al., 2005; Mauroy et al., 2013, 2014), human perturbed locomotion (Ernst et al., 2012; Müller et al., 2016; Grimmer et al., 2008) and comparison of human and bird locomotion (Ernst et al., 2012; Müller et al., 2016). Not unexpectedly, some of the dog limbs in our study showed a non-conservative function (Fig. 3, fourth row). In particular, beginner dogs during landing of the trailing forelimb and hindlimb exhibited a limb function that deviated from pure spring-like behavior. However, the hindlimbs and trailing forelimb in take-off, and the leading forelimb in landing approximate spring-like leg behavior. Our goal was to use a model with a manageable number of parameters and to calculate parameters from experimental data, for each limb in take-off and landing phase, which could then be compared between dogs with different levels of skill. Even with this approach, we found differences that could not only be used as objective parameters for training aspects of dogs but also be used for future bioinspired robot developments and their validation (e.g. Buehler, 2002; Lakatos et al., 2018; Eckert et al., 2019).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: K.S., H.W., M.S.F., E.A.; Methodology: K.S., H.W., M.S.F., E.A.; Software: K.S.; Validation: K.S., C.R.; Formal analysis: K.S.; Investigation: K.S., M.H.E.d.L.; Resources: K.S., M.H.E.d.L., H.W.; Data curation: K.S.; Writing - original draft: K.S., C.R.; Writing - review & editing: C.R., M.H.E.d.L., H.W., M.S.F., E.A.; Visualization: K.S.; Supervision: K.S., M.S.F.; Project administration: K.S.; Funding acquisition: K.S., M.S.F.

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Supplementary information

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Supplements

Table S1: Separated statistics for parameter limb stiffness. Type III Analysis of Variance Table with Satterthwaite's method (complete model)

Pair of Legs	Jump	Fixed effects	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Forelimb	**Take-off**	**Skill**	20.4159785	20.4159785	1	13	0.99075063	0.33772598
		Limb	872.5635	872.5635	1	15	42.3439337	**9.91E-06**
		v	14.5889969	14.5889969	1	13	0.70797772	0.41532598
		d	1.39543837	1.39543837	1	13	0.06771811	0.79876482
		Skill:Limb	11.4640889	11.4640889	1	15	0.55633157	0.46727086
	Landing	**Skill**	23.1713809	23.1713809	1	16	6.17126318	**0.02443809**
		Limb	58.5683561	58.5683561	1	18	15.5985843	**0.00093982**
		v	0.49347959	0.49347959	1	16	0.13142904	0.72169924
		d	5.49866288	5.49866288	1	16	1.46446583	0.24379642
		Skill:Limb	0.27698945	0.27698945	1	18	0.07377095	0.78901402
Hindlimb	**Take-off**	**Skill**	0.45217677	0.45217677	1	16	0.07006544	0.79462116
		Limb	0.17601329	0.17601329	1	18	0.02727351	0.87066891
		v	2.91927136	2.91927136	1	16	0.45234527	0.51082049
		d	8.04643023	8.04643023	1	16	1.24680587	0.28065187
		Skill:Limb	11.6191153	11.6191153	1	18	1.80039852	0.19634722
	Landing	**Skill**	0.03403203	0.03403203	1	11	0.01372403	0.90885312
		Limb	3.55827561	3.55827561	1	13	1.43493899	0.25234461
		v	0.33859678	0.33859678	1	11	0.13654528	0.71875493
		d	0.00054915	0.00054915	1	11	0.00022146	0.98839328
		Skill:Limb	0.13060834	0.13060834	1	13	0.05267017	0.82205181

Table S2: Separated statistics for parameter limb stiffness. Backward reduced fixed-effect table with order of elimination.

Pair of Legs	Jump	Fixed effects	eliminated	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Forelimb	**Take-off**	**v**	1	14.5889965	14.5889965	1	13	0.70797771	0.41532598
		d	2	3.81970316	3.81970316	1	14	0.18536331	0.67335832
		Condition:Limb	3	11.4640889	11.4640889	1	15	0.55634171	0.46726662
		Condition	4	40.6457944	40.6457944	1	15	2.02869291	0.17482444
		Limb	0	887.440453	887.440453	1	16	44.2941297	**5.53E-06**
	Landing	**Condition:Limb**	1	0.27698945	0.27698945	1	18	0.07377095	0.78901402
		v	2	0.469423	0.469423	1	16	0.13142904	0.72169924
		d	3	9.93660072	9.93660072	1	17	2.78204927	0.11363927
		Condition	0	36.3494554	36.3494554	1	18	10.1771198	**0.00507098**
		Limb	0	58.5683561	58.5683561	1	19	16.3979671	**0.00068437**
Hindlimb	**Take-off**	**v**	1	2.91927136	2.91927136	1	16	0.45234527	0.51082049
		Condition:Limb	2	11.6191153	11.6191153	1	18	1.80039852	0.19634722
		Limb	3	0.17601329	0.17601329	1	19	0.02617102	0.87319129
		Condition	4	0.1726857	0.1726857	1	17	0.02699046	0.87144217
		d	0	72.6006702	72.6006702	1	18	11.3473509	**0.00342137**
	Landing	**d**	1	0.00054915	0.00054915	1	11	0.00022146	0.98839329
		Condition:Limb	2	0.13060834	0.13060834	1	13	0.05267017	0.82205181
		Condition	3	0.04873774	0.04873774	1	12	0.02108084	0.88696915
		v	4	1.76636382	1.76636382	1	13	0.76401641	0.39793462
		Limb	5	3.66604546	3.66604546	1	14	1.58569776	0.22853284

Table S3: Separated statistics for parameter limb compression. Type III Analysis of Variance Table with Satterthwaite's method (complete model)

Pair of Legs	Jump	Fixed effects	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Forelimb	**Take-off**	**Skill**	0.0011471	0.0011471	1	13	2.39673432	0.14558125
		Limb	0.04734782	0.04734782	1	15	98.9278014	**5.36E-08**
		v	2.99E-05	2.99E-05	1	13	0.06255239	0.80641523
		d	0.00016962	0.00016962	1	13	0.35440027	0.56185339
		Skill:Limb	0.00121956	0.00121956	1	15	2.54812971	0.1312734
	Landing	**Skill**	0.00315388	0.00315388	1	16	12.5248418	**0.00272894**
		Limb	0.00339543	0.00339543	1	18	13.484128	**0.0017438**
		v	0.0011667	0.0011667	1	16	4.63324979	**0.04696571**
		d	0.0005742	0.0005742	1	16	2.28029341	0.15052222
		Skill:Limb	0.00036526	0.00036526	1	18	1.45055277	0.24403763
Hindlimb	**Take-off**	**Skill**	0.00101187	0.00101187	1	16	1.83157407	0.1947543
		Limb	0.00068061	0.00068061	1	18	1.23195919	0.2816349
		v	0.00093876	0.00093876	1	16	1.69923215	0.21083405
		d	0.00184297	0.00184297	1	16	3.33592367	0.08649951
		Skill:Limb	0.00027062	0.00027062	1	18	0.48984237	0.49294473
	Landing	**Skill**	5.12E-05	5.12E-05	1	11	0.0612346	0.80911323
		Limb	0.00056426	0.00056426	1	13	0.67472585	0.42621689
		v	1.48E-06	1.48E-06	1	11	0.0017709	0.96718737
		d	0.00054604	0.00054604	1	11	0.65294357	0.43618881
		Skill:Limb	1.88E-05	1.88E-05	1	13	0.02248335	0.88310982

Table S4: Separated statistics for parameter limb compression. Backward reduced fixed-effect table with order of elimination

Pair of Legs	Jump	Fixed effects	eliminated	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Forelimb	**Take-off**	**v**	1	2.99E-05	2.99E-05	1	13	0.06255239	0.80641523
		d	2	0.00055959	0.00055959	1	14	1.16919043	0.29784222
		Condition:Limb	3	0.00121956	0.00121956	1	15	2.54813381	0.13127309
		Condition	4	0.0010296	0.0010296	1	15	1.96143513	0.18170558
		Limb	0	0.04841355	0.04841355	1	16	92.2304846	**4.81E-08**
	Landing	**Condition:Limb**	1	0.00036526	0.00036526	1	18	1.45055286	0.24403761
		d	2	0.00058782	0.00058782	1	16	2.28029301	0.15052225
		v	3	0.0006212	0.0006212	1	17	2.40978616	0.13899598
		Condition	0	0.00178518	0.00178518	1	18	6.92517013	**0.01693515**
		Limb	0	0.00339543	0.00339543	1	19	13.1717809	**0.00178536**
Hindlimb	**Take-off**	**Condition:Limb**	1	0.00027062	0.00027062	1	18	0.48984239	0.49294472
		Limb	2	0.00068061	0.00068061	1	19	1.26595049	0.27454085
		v	3	0.0009257	0.0009257	1	16	1.69923208	0.21083406
		d	4	0.00085846	0.00085846	1	17	1.57579621	0.22634902
		Condition	0	0.00486521	0.00486521	1	18	8.93066613	**0.00788129**
	Landing	**Condition:Limb**	1	1.88E-05	1.88E-05	1	13	0.02248335	0.88310982
		v	2	1.38E-06	1.38E-06	1	11	0.0017709	0.96718737
		Condition	3	8.52E-05	8.52E-05	1	12	0.10947459	0.74644895
		Limb	4	0.00055307	0.00055307	1	14	0.71098554	0.41329177
		d	5	0.00124214	0.00124214	1	13	1.62817924	0.2242823