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Single limb dynamics of jumping turns in dogs

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ABSTRACT

Maneuverability is of paramount importance for many animals, e.g., in predator-prey interactions. Despite this fact, quadrupedal limb behavior in complicated maneuvers like simultaneous jumping and turning are not well studied. Twenty adult sport Border Collies were recorded while jumping over an obstacle and simultaneously turning. Kinetic and kinematic data were captured in synchrony using eight force plates and sixteen infrared cameras. These dogs were familiar with the task through regular participation in the dog sport agility. The experiments revealed that during landing, higher lateral forces acting in the forelimbs compared to hindlimbs. During landing, the outer limbs produced about twice the inner limbs' force in both vertical and lateral directions, showing their dominant contribution to turning. Advanced dogs showed significantly higher lateral impulse and stronger inner-outer limb asymmetry regarding lateral impulses than beginner dogs, leading to significantly stronger turning for advanced dogs.

Somewhat unexpected, skill effects rarely explained global limb dynamics, indicating that landing a turn jump is a constrained motion. Constrained motions leave little space for individual techniques suggesting that the results can be generalized to quadrupedal turn jumps in other animals.

1. Introduction

Depending on the task or goal, functional morphology, and skill, quadrupedal animals use different walking, running, and jumping techniques. Complicated tasks such as dynamic predator-prey interactions require sophisticated maneuvers (Wilson et al., 2013; Wilson et al., 2015; Wynn et al., 2015). One example of such a complex maneuver is the rarely investigated combination of turning and simultaneous jumping ('turn jumps'), see Supplementary Videos 1–4. Insights into single limb dynamics during such maneuvers can, e.g. improve our understanding of injury risks or provide valuable information for understanding control using legged robots. In dog sport agility, a sport where dogs overcome different obstacles in a limited time, courses combine turning and jumping. Therefore, in the present study, we investigated dogs' single limb dynamics in complex movements like turn jumps.

Turn jumps are sophisticated maneuvers, and although no studies have investigated this, specific anatomical features may likely play an essential role in the performance. For example, curve negotiation, which, in common with turn jumps, has the simultaneous generation of vertical and inward-directed lateral ground reaction forces (GRF), results in centripetal acceleration (Chateau et al., 2013). Some species lower their speed during curve running, including humans (Qiao et al., 2014; Taboga et al., 2016; Tukuafu, 2010; Usherwood and Wilson, 2006) and horses (Tan and Wilson, 2010). Remarkably, however, running dogs (greyhounds) can maintain their curve running speed compared with straight running, keeping the duty factor constant while increasing limb forces by more than 60% (Usherwood and Wilson, 2005). In horses, the radius and the ulna's fusion prevent the forearm's rotation (Hildebrand, 1987). However, the dog's forearm does allow passive inwards and outwards rotation (Fischer and Lilje, 2011). Hence, dogs can maintain a stable contact point with their forelimb's paws while their body rotates during curve running (Fischer and Lilje, 2011). Additionally, the paws' morphology, with soft pads and claws, increases the friction (Wynn et al., 2015) compared to the horses' hard, stiff hooves. These morphological features might help to explain dogs' high curve running speeds and their use of turn jumps in contrast to horses, which seem to jump only straight. Thus, dogs appear well suited to

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investigate the biomechanics of turn jumps.

Turn jumps likely require different use of the left and right limbs. Different use of the inner and outer limbs occurred in quadrupedal (Chateau et al., 2013; Chateau et al., 2005; Crevier-Denoix et al., 2017) and bipedal curve running (Alt et al., 2015; Chang et al., 2001; Taboga et al., 2016; Tukuafu, 2010). The inner leg stabilizes the frontal plane's movement (the so-called abduction–adduction strategy, Alt et al., 2015). In contrast, the outer leg provides and controls rotation in the horizontal plane (Alt et al., 2015). Additionally, the inner leg shows a longer stance duration (Taboga et al., 2016; Tukuafu, 2010; Chateau et al., 2013; Chateau et al., 2005; Crevier-Denoix et al., 2017) and reduced forces (Chang et al., 2001; Crevier-Denoix et al., 2017) compared with straight running. Finally, curve-running cockroaches show higher lateral forces in outside limbs (Jindrich and Full, 1999). In sum, these findings substantiate the expectation of different functions of inner and outer legs in turn jumps.

The study's first aim is to uncover single limb strategies in jumping turns using agility dogs. We expect that higher lateral forces are exerted in the outer limbs to change the direction in turn jumping, similar to curve running. As a consequence, the inner limbs adopt a more stabilizing role. Based on the literature, we expect an extended stance duration of the inner limbs and higher lateral impulses of the outer limbs. Since turn jumps present a complex motor task, skill can be an essential factor in controlling the movement pattern. The second aim is to uncover the effects of skill on turn jumps. We expect higher lateral force and stronger turning in advanced dogs than beginner dogs, higher stiffness, and less compression of the forelimb for advanced dogs, following previous results on jumping straight (Söhnel et al., 2020). Further, turn jumping is a common but complex movement (superimposing jumping and turning). The first detailed qualitative and quantitative etiology of its kinematics and dynamics represents a valuable database for gaining more insight into the underlying motor patterns.

2. Materials and methods

The turn jump data were recorded as a part of a larger project, part of which, the straight jumps, were presented in Söhnel et al. (2020). All

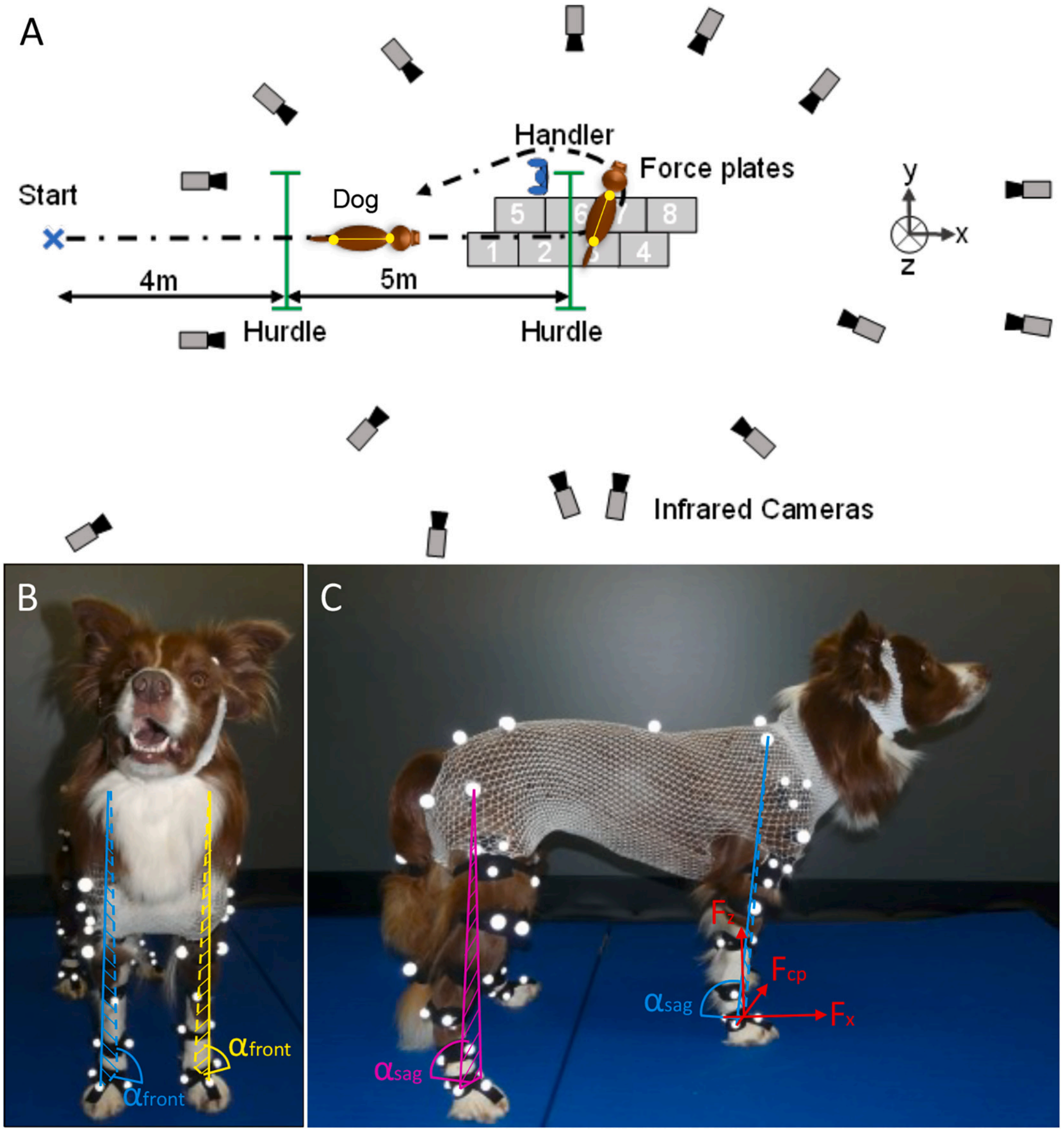

Fig. 1. Experimental setup. A) Top view of the parcours. Hurdles were adjusted to enable the recording of single limbs on different force plates in take-off and landing. B–C) Example of one participant dog fully equipped with passive reflective markers for the 3D kinematic recordings. The turning angle was calculated using two markers on the backline in relation to the global x-axis in top view. B) Definition of limb angle of attack in frontal view using three markers spanning a plane. C) Definition of limb angle of attack in sagittal view using three markers spanning a plane. Force data is rotated along the z-axis using the four markers of each paw.

animal experiments followed the national animal protection act. All dogs were healthy, and the experiments were kept as similar as possible to a regular training situation.

Kinematic and kinetic data were obtained from 20 healthy adult Border Collies. The dogs were separated into advanced ($N = 10$) and beginner ($\mathrm{N} = 10$) categories based on their agility grade. Kinematic data were recorded with sixteen infrared cameras (Oqus Series 400, Qualisys, Göteborg) at 400 Hz using Qualisys Track Manager® software (QTM, Version 2.15, Qualisys, Göteborg). Simultaneously, synchronized three-dimensional ground reaction forces (GRF) were recorded with eight force plates (600 mm × 900 mm, 9287 CA, Kistler Instruments AG) at 2 kHz. The force plates were covered with tartan mats to improve the grip.

2.1. Data collection and procedure

Two hurdles, complying with the Fédération Cynologique Internationale's (FCI) agility rules, were used. Hurdle heights were set to 90% of the dog's height at the withers to achieve comparable conditions for all dogs. The starting position was 4 m in front of the first hurdle. The distance between the hurdles was 5 m. Dogs jumped the second hurdle while turning to the left and then ran back towards the starting point (Fig. 1A). Its owner led each dog to turn as tight and fast as possible. They were acquainted with the task. In the supplemental section, some videos of the turn-jump maneuver are provided. The body weight (BW) was measured while the dog was standing still on one force plate. Dogs rested whenever the handler or the experimenter judged it appropriate.

A jump was valid if the dog jumped across both hurdles without knocking down the poles. A recording was valid if, additionally, single limbs of limb pairs stood on different force plates during take-off or landing. Records for take-off and landing were primarily made in different trials because the four limbs rarely hit individual force plates.

2.2. Data analysis

The take-off phase was defined as the period spanning the last four limb contact phases before the jump's airborne phase. The landing phase was defined as the period spanning the first four limb impact phases after the jump's airborne phase. Pairs of limbs were subdivided into inner (I) and outer (O) limb.

The axial limb function was modeled as parallel spring and damper elements (Andrada et al., 2014) to account for asymmetric limb behavior.

$$F_{Limb} = k(l_0 - l) - c\dot{l}. \tag{1}$$

F_{Limb} is the axial limb force, l_0 is the rest length of the spring (measured five frames before touchdown), l is the instantaneous limb length, $\dot{l}$ is the limb length's rate of change, k is the limb stiffness, and c the damping coefficient. We obtained k and c using the Matlab® function 'lscurvefit' that minimized each trials' sum of squared distances between measured forces and the forces calculated with Eq. (1) (as explained in Andrada et al., 2014). The limb length-time data from experiments were used as input. Hindlimbs span the distance between the femur's greater trochanter and the lateral tarsometatarsal joint (Farley et al., 1993). Forelimbs span the distance between the margo dorsalis of the spina scapulae and the lateral carpometacarpal joint.

A vertical ground reaction force threshold of 1 N determined the instants of toe-down and toe-off, defining the stance time t_s. The orientation of the paw markers (anterior-posterior markers and mediolateral paw markers, respectively, see Fig. 1C) defined the decomposition of forces in the horizontal plane into fore-aft and lateral forces.

Force (F_z vertical GRF, $F_{z,\max}$ peak vertical GRF, F_{fa} fore-aft GRF, F_{lat} the inward-directed lateral GRF, $F_{lat,max}$ peak inward-directed lateral GRF, cf. Fig. 1C) and impulse ($\Delta p = \int_{TD}^{TO} F\, dt$, Δp_z vertical impulse, Δp_a accelerative impulse, Δp_d decelerative impulse, Δp_{lat} lateral impulse) were normalized to BW, and limb length was normalized to l_0. Dimensionless limb stiffness was calculated as (McMahon and Cheng, 1990):

$$\widehat{k} = \frac{k \bullet l_0}{m \bullet g} \tag{2}$$

Furthermore, dimensionless limb damping was calculated as:

$$\widehat{c} = \frac{c}{m} \bullet \sqrt{\frac{\mathrm{l}_0}{\mathrm{g} \bullet}} \tag{3}$$

The angle between the ground and a lateral plane containing the limb (defined by two limb markers and the medial paw marker, see Fig. 1C) defined the angle of attack of the limb in the sagittal plane α_{sag}. The angle between the ground and a fore-aft plane containing the limb (defined by the upper limb marker and the anterior and posterior paw markers, see Fig. 1B) defined the angle of attack of the limb in the frontal plane α_{front}.

A marker was placed at the intersection of the back with the GRF line of action during still standing on one force plate (Söhnel et al., 2020) to assess the dog's velocity at toe-down (v_{TD}). The horizontal velocity of that marker at toe-down of the first limb of the respective pair of limbs (in the respective jump phase) defined v_{TD}. The maximum z-coordinate of the same marker defined jumping height h. For each pair of limbs, the distance between hurdle and limb closest to the hurdle defined the distance to the hurdle d_{hurdle}. The angle between global x-direction and a line through markers at the tail and neck defined the turning angle α_{turn}.

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 were expressed as mean ± standard deviation over all subjects and parameters (Table 1). All data were analyzed using MATLAB® 2017a.

2.3. Statistical analysis

Data was divided into four subsets, containing all parameters for forelimbs (FL) and hindlimbs (HL), respectively of the two phases landing and take-off. Linear mixed-effect models were used to analyze each combination of the parameters predicted by the jumps' categorical descriptors. Models were fitted via a backward selection of the least significant variables until the final minimal adequate model satisfied a minimal Akaike information criterion (Crawley, 2007). The categorical variables 'Skill' (beginner (B) or advanced (A)) and 'Limb' (outer (O) or inner (I) limb), as well as the continuous variables v_{TD}, α_{turn}, and d_{hurdle}, were included as fixed effects in the model. 'Dog,' which contained the individuals, was set as a random effect. Models were fitted using maximum likelihood estimation. Model acquirements and assumptions were fulfilled, as variances were homogeneous and residuals normally distributed. Contrasts analyses of main effects and interaction effects were done comparing the least mean squares with Satterthwaite's degrees of freedom method. Significance was defined for $p \leq 0.01$. All analyses were conducted in R version 3.6.2 (R Core Team (2017)). The package 'lmerTest' (Kuznetsova et al., 2017) was used to analyze the mixed-effect models and perform the post-hoc tests.

3. Results

In total, 262 valid turn jumps were analyzed from 20 subjects. Means and standard deviations are reported in Table 1 for the take-off phase and in Table 2 for the landing phase.

3.1. Hypothesis testing

We hypothesized longer t_s in the inner limbs. In landing, compared with the outer forelimb (OFL), the inner forelimb (IFL) showed significantly increased t_s (23%, $p < 0.001$) but decreased t_s in the take-off phase (12%, $p = 0.004$). HL showed no significant differences for t_s comparing

Table 1
Take-off parameters for advanced (dark) and beginner dogs (bright).

		Forelimbs			**Hindlimbs**	
Skill (N Dogs) =>		**Advanced (7)**	**Beginner (10)**		**Advanced (10)**	**Beginner (10)**
Stance duration	outer	145 ± 23 **a**	144 ± 33 **b**	outer	128 ± 12	133 ± 28
t_s [ms]	inner	121 ± 13 **a**	132 ± 33 **b**	inner	136 ± 20	135 ± 36
	Ratio inner/outer	0.8	0.9	Ratio inner/outer	1.1	1
Max vertical force	outer	1.6 ± 0.26 **a**	1.67 ± 0.44 **b**	outer	1.43 ± 0.25 **c**	1.33 ± 0.25 **d**
$F_{z,max}$ [BW]	inner	1.19 ± 0.26 **a**	1.28 ± 0.23 **b**	inner	1.09 ± 0.15 **c**	1.04 ± 0.16 **d**
	Ratio inner/outer	0.7	0.8	Ratio inner/outer	0.8	0.8
Max lateral force	outer	0.36 ± 0.12 **a**	0.31 ± 0.16 **b**	outer	0.39 ± 0.11 **c**	0.27 ± 0.11 **d**
$F_{lat,max}$ [BW]	inner	0.23 ± 0.13 **a**	0.19 ± 0.11 **b**	inner	0.21 ± 0.09 **c**	0.12 ± 0.06 **d**
	Ratio inner/outer	0.6	0.6	Ratio inner/outer	0.5	0.4
Vertical impulse	outer	0.146 ± 0.016 **a**	0.145 ± 0.022 **b**	outer	0.120 ± 0.010 **c**	0.114 ± 0.016 **d**
Δp_z [BW s]	inner	0.09 ± 0.026 **a**	0.106 ± 0.028 **b**	inner	0.100 ± 0.020 **c**	0.088 ± 0.014 **d**
	Ratio inner/outer	0.6	0.7	Ratio inner/outer	0.8	0.8
Accelerative impulse	outer	0 ± 0	0.001 ± 0.001	outer	0.005 ± 0.003 **a,b**	0.003 ± 0.002 **b**
Δp_a [BW s]	inner	0 ± 0	0.001 ± 0.002	inner	0 ± 0 **a**	0.002 ± 0.002
	Ratio inner/outer	1	1	Ratio inner/outer	0	0.7
Decelerative impulse	outer	0.042 ± 0.010 **a**	0.040 ± 0.014 **b**	outer	0.010 ±0.007 **c**	0.012 ± 0.005
Δp_d [BW s]	inner	0.026 ±0.006 **a**	0.030 ± 0.010 **b**	inner	0.020 ±0.006 **c**	0.016 ± 0.008
	Ratio inner/outer	0.6	0.8	Ratio inner/outer	2	1.3
Lateral impulse	outer	0.028 ± 0.010 **a**	0.023 ± 0.013 **b**	outer	0.029 ± 0.008 **c**	0.020 ± 0.011 **d**
Δp_{lat} [BW s]	inner	0.014 ± 0.009 **a**	0.011 ± 0.008 **b**	inner	0.012 ± 0.009 **c**	0.005 ± 0.004 **d**
	Ratio inner/outer	0.5	0.5	Ratio inner/outer	0.4	0.3
Sagittal angle of attack	outer	60 ± 2	61 ± 5	outer	58 ± 5	59 ± 5
α_{sag} TD [°]	inner	61 ± 3	62 ± 6	inner	58 ± 6	57 ± 6
	Ratio inner/outer	1	1	Ratio inner/outer	1	1
Frontal angle of attack	outer	88 ± 5 **a**	89 ± 6 **b**	outer	86 ± 6 **a**	89 ± 7 **b**
α_{front} TD [°]	inner	76 ± 7 **a**	79 ± 5 **b**	inner	71 ± 6 **a**	77 ± 4 **b**
	Ratio inner/outer	0.9	0.9	Ratio inner/outer	0.8	0.9
Limb length at toe-off	outer	1.01 ± 0.03	0.99 ± 0.05	outer	1.04 ± 0.04	1.02 ± 0.06
l_{TO} [l_0]	inner	1.00 ± 0.08	1.02 ± 0.08	inner	1.01 ± 0.03	1.01 ± 0.05
	Ratio inner/outer	0.9	1	Ratio inner/outer	1	1
Max. limb compression	outer	0.11 ± 0.02 **a**	0.13 ± 0.04 **b**	outer	0.17 ± 0.03	0.17 ± 0.03
Δl [l_0]	inner	0.07 ± 0.06 **a**	0.10 ± 0.06 **b**	inner	0.19 ± 0.02	0.20 ± 0.04
	Ratio inner/outer	0.6	0.8	Ratio inner/outer	1.1	1.2
Time between limb contacts [ms]	front	70 ± 4	56 ± 27	hind	15 ± 7 **a**	23 ±15 **a**
Speed at toe down v_{TD} [m/s]	front	3.7 ± 0.4 **a**	3.9 ± 0.7 **a**	hind	3.1 ± 0.3	3.1 ± 0.7
Orientation at toe-down α_{turn} TD [°]	front	6 ± 4	4 ± 3 **c**	hind	14 ± 8	8 ± 4
Orientation at toe-off α_{turn} TO [°]	front	16 ± 10 **a**	9 ± 6 **a**	hind	24 ± 11 **b**	14 ± 7 **b**
Distance to hurdle d_{hurdle} [m]	front	-0.97 ± 0.32 **a**	-0.78 ± 0.25 **a**	hind	-1.00 ± 0.30 **a**	-0.80 ± 0.20 **a**
Jump height h [withers height]	front	1.55 ± 0.14	1.47 ± 0.11	hind	1.53 ± 0.52	1.47 ± 0.06

Data are means ± s.d. Parameters for advanced dogs (dark) and beginner dogs (bright). Blue: outer forelimb; orange: inner forelimb; magenta: outer hindlimb; green: inner hindlimb. White cells are parameters that were not measured per limb. Same bold letters per Parameter and Limbpair indicate means that are significantly ($p < 0.05$) different using backward reduction of mixed effect models; N: number of dogs.

Table 2
Landing parameters for advanced (dark) and beginner dogs (bright).

		Forelimbs			**Hindlimbs**	
Skill (N Dogs) =>		**Advanced (9)**	**Beginner (10)**		**Advanced (7)**	**Beginner (7)**
Stance duration	outer	160 ± 21 **a**	138 ± 16 **b**	outer	198 ± 13 **c**	153 ± 13 **c**
t_s [ms]	inner	188 ± 35 **a**	179 ± 37 **b**	inner	174 ± 33 **d**	148 ± 29 **d**
	Ratio inner/outer	1.2	1.3	Ratio inner/outer	0.9	1
Max vertical force	outer	2.00 ± 0.26 **a**	1.91 ± 0.25 **b**	outer	1.20 ± 0.25 **c**	1.16 ± 0.31**d**
$F_{z,max}$ [BW]	inner	1.04 ± 0.24 **a**	1.30 ± 0.28 **b**	inner	0.65 ± 0.15 **c**	0.83 ± 0.29 **d**
	Ratio inner/outer	0.5	0.7	Ratio inner/outer	0.5	0.7
Max lateral force	outer	0.98 ± 0.13 **a**	0.75 ± 0.23 **b**	outer	0.68 ± 0.15 **c**	0.56 ± 0.26 **d**
$F_{lat,max}$ [BW]	inner	0.54 ± 0.17 **a**	0.53 ± 0.16 **b**	inner	0.34 ± 0.13 **c**	0.30 ± 0.08 **d**
	Ratio inner/outer	0.6	0.7	Ratio inner/outer	0.5	0.5
Vertical impulse	outer	0.199 ± 0.030 **a**	0.159 ± 0.021	outer	0.147 ± 0.035 **b**	0.107 ± 0.030
Δp_z [BW s]	inner	0.128 ± 0.033 **a**	0.148 ± 0.028	inner	0.060 ± 0.030 **b**	0.067 ± 0.024
	Ratio inner/outer	0.6	0.9	Ratio inner/outer	0.4	0.6
Accelerative impulse	outer	0.003 ± 0.003	0.009 ± 0.009	outer	0.021 ± 0.013	0.011 ± 0.011
Δp_a [BW s]	inner	0.004 ± 0.009	0.003 ± 0.003	inner	0.023 ± 0.004	0.019 ± 0.009
	Ratio inner/outer	1.3	0.3	Ratio inner/outer	1.1	1.7
Decelerative impulse	outer	0.027 ± 0.013	0.021 ± 0.019	outer	0.006 ± 0.004 **a**	0.007 ± 0.006 **b**
Δp_d [BW s]	inner	0.020 ± 0.010	0.023 ± 0.013	inner	0 ± 0 **a**	0.001 ± 0.002 **b**
	Ratio inner/outer	0.7	1.1	Ratio inner/outer	0	0.1
Lateral impulse	outer	0.096 ± 0.018 **a,b**	0.060 ± 0.023 **b**	outer	0.077 ± 0.022 **c,d**	0.046 ± 0.023 **d,e**
Δp_{lat} [BW s]	inner	0.059 ± 0.013 **a**	0.055 ± 0.014	inner	0.024 ± 0.012 **c**	0.020 ± 0.005 **e**
	Ratio inner/outer	0.6	0.9	Ratio inner/outer	0.3	0.4
Sagittal angle of attack	outer	75 ± 6	80 ± 5	outer	77 ± 5 **a**	72 ± 5 **b**
α_{sag} TD [°]	inner	73 ± 10	70 ± 8	inner	84 ± 4 **a**	84 ± 11 **b**
	Ratio inner/outer	1	0.9	Ratio inner/outer	1.1	1.2
Frontal angle of attack	outer	74 ± 3 **a**	78 ± 5 **b**	outer	70 ± 4 **c**	74 ± 6 **d**
α_{front} TD [°]	inner	65 ± 3 **a**	70 ± 4 **b**	inner	59 ± 4 **c**	59 ± 6 **d**
	Ratio inner/outer	0.9	0.9	Ratio inner/outer	0.8	0.8
Limb length at toe-off	outer	0.92 ± 0.05	0.90 ± 0.02	outer	0.90 ± 0.05	0.91 ± 0.07
l_{TO} [l_0]	inner	0.92 ± 0.08	0.95 ± 0.07	inner	0.83 ± 0.06	0.85 ± 0.09
	Ratio inner/outer	1	1.1	Ratio inner/outer	0.9	0.9
Max. limb compression	outer	0.14 ± 0.02	0.15 ± 0.02	outer	0.14 ± 0.04	0.14 ± 0.03
Δl [$\mathrm{l_0}$]	inner	0.14 ± 0.06	0.16 ± 0.02	inner	0.14 ± 0.03	0.18 ± 0.04
	Ratio inner/outer	1	1.1	Ratio inner/outer	1	1.3
Time between limb contacts [ms]	front	27 ± 30	21 ± 8	hind	16 ± 13	37 ± 29
Speed at toe down v_{TD} [m/s]	front	2.8 ± 0.5	2.9 ± 0.4	hind	2.2 ± 0.4 **a**	2.6 ± 0.5 **a**
Orientation at toe-down α_{turn} TD [°]	front	33 ± 11 **a**	20 ± 10 **a**	hind	75 ± 14 **b**	50 ± 18 **b**
Jump height h [m]	front	1.50 ± 0.13	1.48 ± 0.09	hind	1.49 ± 0.11	1.46 ± 0.08

Data are means ± s.d. Parameters for advanced dogs (dark) and beginner dogs (bright). Blue: outer forelimb; orange: inner forelimb; magenta: outer hindlimb; green: inner hindlimb. White cells are parameters that were not measured per limb. Same bold letters per parameter and limb pair indicate means that are significantly ($p < 0.05$) different using backward reduction of mixed effect models; N: number of dogs.

inner hindlimb (IHL) and outer hindlimb (OHL). Thus, our hypothesis is only valid for the IFL in landing.

We hypothesized higher $F_{lat,\max}$ and Δp_{lat} in the outer limbs to achieve the dog's change in direction. In the take-off phase, the OFL showed increased $F_{lat,\max.}$ and increased Δp_{lat} than the IFL (58%, $p = 0.0037$; 100%, $p < 0.001$, respectively). During the take-off phase, the OHL showed a much higher $F_{lat,max}$ and Δp_{lat} than the IHL (97%, $p < 0.0001$; 193%, $p < 0.001$, respectively). During the landing phase, the OFL showed a higher $F_{lat,max}$ again compared to the IFL (61%, $p < 0.0001$) and higher Δp_{lat}, but this was only significant for advanced dogs (170%, $p < 0.0001$). The OHL showed a more than doubled Δp_{lat} compared to the IHL (162%, $p < 0.001$) and a higher $F_{lat,\max}$ (61%, $p < 0.0001$). These results confirm our hypothesis that the outer limbs mainly contribute to turning for both limb pairs.

Advanced dogs reached significantly higher turning compared to beginner dogs in all jumping phases (α_{turn}: FL-TO: 441%, $p < 0.001$, HL-TO: 69%, $p = 0.0051$, FL-L: 36%, $p = 0.0003$, HL-L: 36%, $p = 0.0002$). We additionally expected that advanced jumpers show higher limb stiffness and less damping. This hypothesis is not confirmed. There were no statistically significant differences in global single limb parameters between advanced and beginner dogs (Fig. 3).

3.2. General description

3.2.1. Take-off phase

The take-off phase started with the ground contact by the OFL (advanced dogs 87.5%, beginner dogs 78.9%). The forelimbs displayed a strut-like function typical of jumping, as shown by the decelerating and upward forces and impulses (Table 1). The Δp_d was significantly higher in OFL than IFL (46%, $p = 0.0009$). The OFL had a significantly longer t_s (13%, $p = 0.0039$), higher $F_{z,max}$ (32%, $p < 0.0001$) and Δp_z (47%, $p < 0.0001$) than IFL.

At the end of the forelimb's stance phase, both hindlimbs touched the ground nearly synchronously, especially in advanced dogs. Advanced dogs made the first contact with the OHL in 54% of the trials, beginner dogs in 46%. The highest forces and impulses were typically found in the OHL, especially for $F_{z,\max}$ and Δp_z compared to the IHL (30%, $p < 0.0001$; 26%, $p < 0.0001$, respectively). The lateral impulse was mainly provided by the OHL, as hypothesized. The limb stiffness ($\widehat{k}$) of the OHL was 70% higher ($p < 0.0001$) compared to the IHL. Advanced dogs showed a higher Δp_a and a reduced Δp_d in the OHL than IHL (844%, $p < 0.0001$; 51%, $p < 0.0001$, respectively). This asymmetry was not significant for beginner dogs.

Concerning the dogs' skill, beginner dogs generally exhibited lower inner-outer leg asymmetry and less rotation than advanced ones. The distance to the hurdle at take-off was more considerable for both front- and hind limbs in the skilled dogs (d_{hurdle} FL: 50%, $p < 0.0001$ HL: 22%, $p = 0.0089$).

During the take-off phase of the jump, the vertical and lateral impulses were nearly the same for advanced dogs in FL and HL ($\Delta p_{z:}$ FL: 52%, HL: 48%; Δp_{lat}: FL: 51%, HL: 49%). Beginner dogs showed a shift of vertical and lateral impulses to the FL ($\Delta p_{z:}$ FL: 54%, HL: 46%; Δp_{lat}: FL: 58%, HL: 42%). The HL provided the accelerative impulse. Only beginner dogs showed a small contribution of the FL to the accelerative impulse (FL: 29%, HL: 71%). The FL contributed majorly to a decelerative impulse (FL: 69%, HL:31%).

3.2.2. Landing phase

Forelimbs were placed nearly in synchrony. Initially, the forelimbs exerted a deceleration and lateral force (Fig. 2), while the turn around the vertical axis continued (Table 2). In the landing phase, compared with the IFL, the OFL reached higher $F_{z,\max}$ (67%, $p < 0.0001$) and Δp_z (55%, $p < 0.0001$) in advanced dogs. Limb stiffness and damping were higher in OFL compared to IFL ($\widehat{k}$: 56%, $p < 0.0001$; $\widehat{c}$: 200%, $p < 0.0001$). Both forelimbs were highly compressed until the end of the stance phase. The IFL showed a significantly longer t_s than the OFL (24%, $p < 0.0001$).

Both hindlimbs contacted the ground nearly synchronously, with the OHL mostly slightly earlier than the IHL. The hindlimbs exerted a high Δp_a, especially in advanced dogs. $F_{z,max}$ was significantly larger in the OHL than in the IHL (57%, $p < 0.0001$). In advanced dogs, the vertical impulse was higher in OHL than IHL (143%, $p < 0.0001$). Like the forelimbs, the hindlimbs showed a high compression until the end of the stance phase. The OHL showed higher $\widehat{k}$ and higher $\widehat{c}$ compared to the IHL (135%, $p < 0.0001$; 46%, $p = 0.0398$, respectively).

During the jump's landing phase, two-thirds of the vertical and lateral impulses were provided by the FL, respectively. The HL majorly contributed to acceleration and the forelimbs to deceleration (Advanced dogs: Δp_a: FL: 14%, HL: 86%, Δp_d: FL: 89%, HL:11%; Beginner dogs: Δp_a: FL: 29%, HL: 71%, Δp_d: FL: 85%, HL:15%).

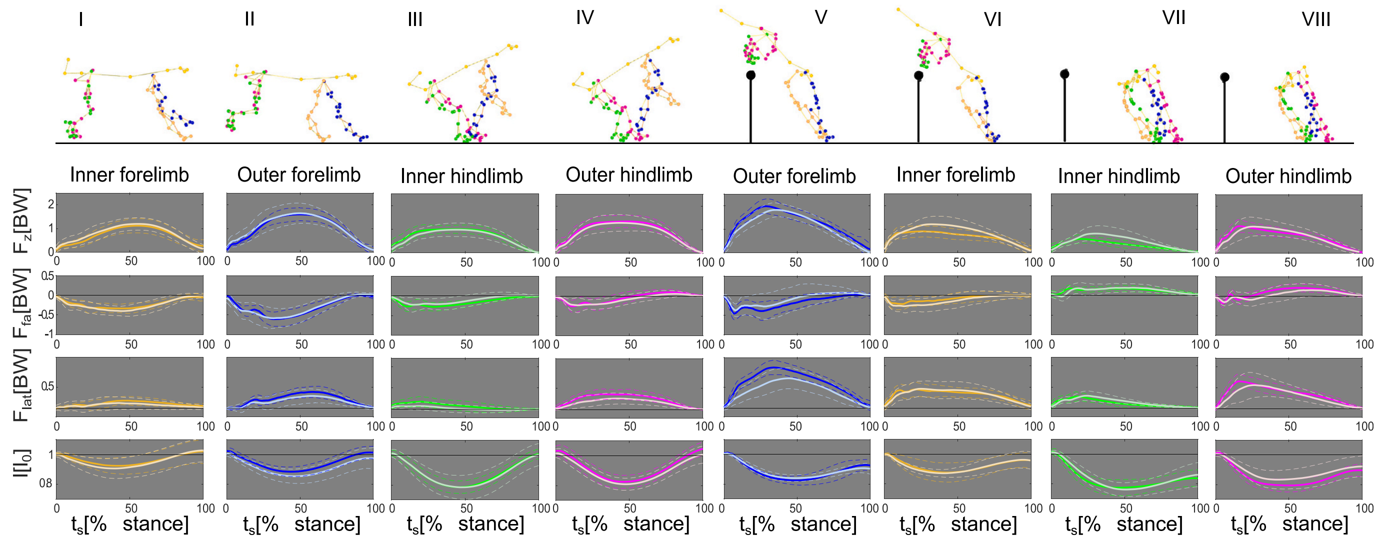

Fig. 2. Mean curves of GRF and limb length; solid line: averaged mean, dashed line: standard deviation blue: outer forelimb; orange: inner forelimb; magenta: outer hindlimb; green: inner hindlimb; dark colors advanced dogs; bright colors: beginner dogs; first row: vertical force over stance duration; second row: horizontal force over stance duration; third row: lateral force over stance duration; fourth row: limb length over stance duration. Column 1–4: take-off; Column 5–8: landing. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Agility, speed, and flexibility is a hallmark of quadrupedal mammalian locomotion. A central feature of agility is transition between and superposition of stationary locomotion forms. Such intricate movement patterns are common, e.g., in predator and prey interactions and sports. Turn jumps represent a common motorically complex maneuver.

The data confirmed our hypotheses that higher lateral impulses are exerted in the outer limbs than the inner ones. In advanced dogs, the OFL lateral impulse in landing was almost four times that during take-off (Tables 1 and 2, Fig. 4), resulting in dominant turning during the landing phase. The lateral impulse by forelimbs was overall higher than hindlimbs'. During landing, outer limbs generated about twice the inner limbs' force in vertical and lateral directions (Table 2, Fig. 4), showing their major contribution to turning and landing.

Advanced dogs reach a significantly higher turning angle during all jump phases than beginner dogs, caused by higher inner-outer limb asymmetries regarding GRF and impulses. Clayton and Hobbs (2019) suggested that with the increasing diameter of a circle, the degree of asymmetry increased. This is in accordance with our findings, concluding that advanced dogs reach significantly greater turnings due to increasing the asymmetry between the outer and inner limbs. Additionally, we did not examine the kinematics during the flight phase. Aerial righting effects (Jusufi et al., 2011) could lead to a higher inside leaning of the trunk, which is related to circle radius.

Somewhat unexpected, skill effects rarely explained global limb dynamics, especially for landing (Table 2), indicating that landing a turn jump is a highly constrained motion leaving little space for individual technique. The turn-jump technique applied by dogs involved a sharp 90° turn during landing. The turn prohibits taking advantage of converting vertical velocity into horizontal velocity via a strut-like mechanism because the dog would not be able to complete the turn but would have to travel around a curve with a larger radius. Dogs realized turning

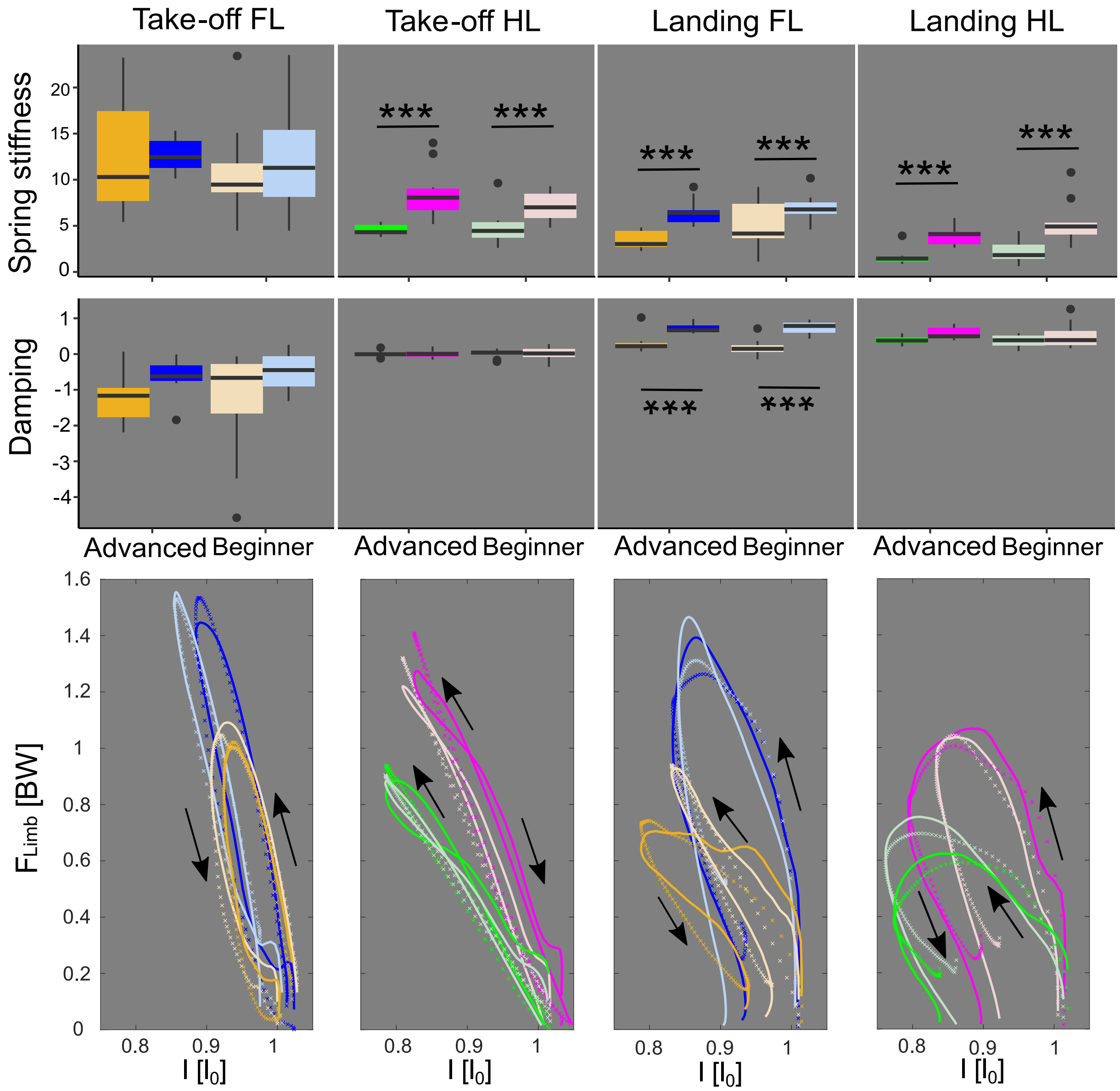

Fig. 3. Fit of parallel spring-damper model. Left to right: jumping phases forelimb take-off, hindlimb take-off, forelimb landing, and hindlimb landing. Top: boxplots of dimensionless spring stiffness, middle: boxplots of dimensionless damping; bottom: mean axial force-limb length curve of experimental data (solid) and fitted data (marker x), showing the change in axial limb force over the change in limb length. Dark colors: advanced dogs; bright colors: beginner dogs; orange: inner forelimb; blue: outer forelimb; green: inner hindlimb; magenta: outer hindlimb. Significant differences *: $p < 0.01$; ** $p < 0.001$; ***$p < 0.0001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

during landing by absorbing energy from jumping and changing their direction on the spot. All limbs' stiffness is much lower and damping higher than in take-off, leading to low limb length at toe-off after landing (Fig. 2, Fig. 3). The crouched posture resulting from dealing with the vertical energy during landing is at the same time suitable to apply horizontal force during an extended stance duration for accelerating again horizontally after landing (Biewener, 1983).

Dogs abolish nearly all translational speed during the turn and start from an almost still position. Given these constraints, their best option seems to orient the upper body in the desired direction to achieve a fast running initiation where the hindlimbs can push forward. However, they do not overextend their hindlimbs when initiating running as they do from still standing (Walter and Carrier, 2009).

When landing after a straight jump, advanced dogs achieved an efficient technique by strutting forelimbs (higher stiffness and lower limb compression than beginner dogs) to translate vertical velocity quickly into forward speed (Söhnel et al., 2020). The skill effect indicates that jumping straight can improve through training. In contrast to jumping straight, we found only very few differences between advanced and beginner dogs while landing a turn-jump. Moreover, during straight jumps, the random effect dog explained approximately 40% of the data's variation (Söhnel et al., 2020), indicating a range of possible realizations of the technique. In contrast, dogs' random effect in turn jumps was not significant. These findings suggest that landing after a turn-jump is a strongly constrained motion that leaves not much room for individual technique.

4.1. Hindlimbs functions in turn jumps

In the take-off phase of turn-jumps, hindlimbs touched the ground nearly synchronously. However, the IHL mechanical function differed from the OHL. The IHL showed increased Δp_d despite low axial stiffness and almost exclusively braking force. In contrast, the OHL showed (smaller) braking forces only for the first half of the contact period and then changed to accelerative forces (Fig. 2). Thus both legs generate a torque that causes turning around the vertical axis.

In the hindlimbs' landing phase, hindlimbs' main task is generating propulsion in the new direction (Δp_a, Table 2, Fig. 2, Fig. 4). The hindlimbs provide the same amount of acceleration impulse after landing like dogs during the first two steps starting rapidly from still standing (Walter and Carrier, 2009).

4.2. Forelimb function in jumping turns

In the take-off, forelimbs displayed a strut-like function (Fig. 4) typical of jumping, as shown by the decelerating and upward forces and

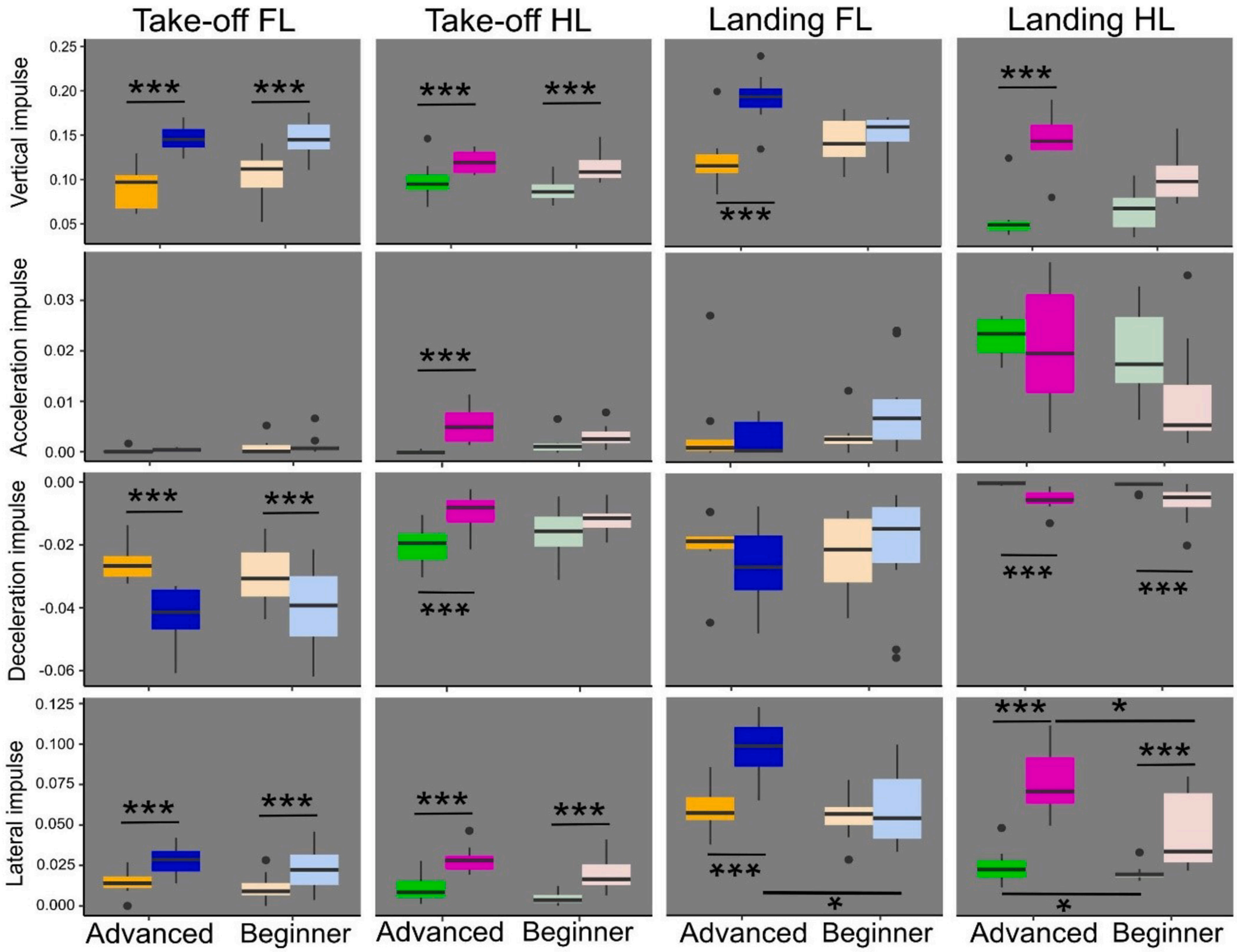

Fig. 4. Boxplot of measured impulses. Jump phases left to right take-off forelimbs, take-off hindlimbs, landing forelimbs, landing hindlimbs. Top: accelerative impulses, middle decelerative impulses, bottom lateral impulses. Orange: inner forelimb; blue: outer forelimb; green: inner hindlimb; magenta: outer hindlimb; advanced dogs: dark colors; beginner dogs: bright colors. Significant differences *: $p < 0.01$; ** $p < 0.001$; ***$p < 0.0001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

impulses (Table 1). High decelerative impulses are necessary to change the momentum from horizontal to vertical. The braking impulses are higher compared to straight jumping (Söhnel et al., 2020), dogs anticipate the turn and slow down as seen in quadruped curve movement (Walter, 2003; Wynn et al., 2015; Tan and Wilson, 2010). Therefore take-off distance is shortened. Forelimbs produced net breaking impulses only, which is higher in the OFL (Table 1). Because they place the OFL at a higher frontal angle (i.e., more below the body), the force might pass through the dog's center of mass in the x-y-plane, not producing outward rotation. The peak forces produced by OFL were about twice as high as those exerted by the IFL (Table 1, Fig. 2).

During landing, both forelimbs touch down almost synchronously, but OFL exhibits a shorter stance duration, higher forces, and higher impulses than IFL. These characteristics are similar to the reported inner-outer leg asymmetries of circling horses (Chateau et al., 2013; Chateau et al., 2005; Crevier-Denoix et al., 2017) and human curve running (Taboga et al., 2016; Tukuafu, 2010; Chang and Kram, 2007). Further, the inner forelimb was placed close to the center of mass and showed a longer stance duration (Table 2) to provide a stable point for turning, which is possible because of the dog's anatomical ability of passive rotation between ulna and radius (Fischer and Lilje, 2011). The dog is leaning inward, the IFL is adducted, and the OFL abducted (Table 2) to align the force vector with the limb axes, which generates a high lateral impulse of OFL as in circling horses (Clayton and Hobbs, 2019). Concluding from its high lateral force and impulse, the OFL drives the turning. Thus, comparable to human curved running (Alt et al., 2015), where the inside limb stabilizes the turn, and the outside limb drives the motion.

The forelimbs shift the body in the new heading direction with a high lateral force and impulse that is higher than hindlimbs, in accordance with reports from circling horses (Clayton and Hobbs, 2019; Clayton et al., 2014), resulted in higher turning during forelimb landing. In contrast to hindlimbs, forelimbs produced zero net forward acceleration in the landing phase (Fig. 2), similar running initiation from standing still (Walter and Carrier, 2009). However, after landing, they still need to generate considerable vertical force during this period because the upper body is already in a low position due to weight capturing. Thus, it seems that the forelimbs support turning and provide a suitable initial body configuration for initiating running by providing breaking and lateral forces.

5. Conclusion

This study presents the first examination of quadruped limb dynamics during jumping and simultaneous turning. Dog's hindlimbs accelerate and forelimbs decelerate horizontally in jumping and landing phases. Moreover, fore- and hindlimbs contribute equally to the vertical impulse in jumping. During landing, however, forelimbs produce two-third of the vertical and lateral impulses and thus compensate for the landing impact and steer the body in the desired direction while the hindlimbs accelerate the body. In addition, we found strong inner-outer limb asymmetries, especially for the lateral forces and impulses in all four limbs in both jumping phases, indicating that the outer limbs drive the turning motion. Advanced dogs achieve tighter turns due to higher lateral force and impulse and a more present inner-outer limb asymmetry. In contrast to previously investigated straight jumping, the dog's skill did not affect global limb dynamics in landing. Therefore, landing a turn jump seems to be a highly constrained motion, and we assume a general pattern for terrestrial mammals in this maneuver.

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Declaration of Competing Interest

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