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RESEARCH ARTICLE

How innate is locomotion in precocial animals? A study on the early development of spatio-temporal gait variables and gait symmetry in piglets

Charlotte Vanden Hole[1],*, Jana Goyens[2], Sara Prims[1], Erik Fransen[3], Miriam Ayuso Hernando[1], Steven Van Cruchten[1], Peter Aerts[2] and Chris Van Ginneken[1]

ABSTRACT

Locomotion is one of the most important ecological functions in animals. Precocial animals, such as pigs, are capable of independent locomotion shortly after birth. This raises the question whether coordinated movement patterns and the underlying muscular control in these animals is fully innate or whether there still exists a rapid maturation. We addressed this question by studying gait development in neonatal pigs through the analysis of spatio-temporal gait characteristics during locomotion at self-selected speed. To this end, we made video recordings of piglets walking along a corridor at several time points (from 0 h to 96 h). After digitization of the footfalls, we analysed self-selected speed and spatio-temporal characteristics (e.g. stride and step lengths, stride frequency and duty factor) to study dynamic similarity, intralimb coordination and interlimb coordination. To assess the variability of the gait pattern, left–right asymmetry was studied. To distinguish neuromotor maturation from effects caused by growth, both absolute and normalized data (according to the dynamic similarity concept) were included in the analysis. All normalized spatio-temporal variables reached stable values within 4 h of birth, with most of them showing little change after the age of 2 h. Most asymmetry indices showed stable values, hovering around 10%, within 8 h of birth. These results indicate that coordinated movement patterns are not entirely innate, but that a rapid neuromotor maturation, potentially also the result of the rearrangement or recombination of existing motor modules, takes place in these precocial animals.

KEY WORDS: Locomotion, *Sus scrofa*, Spatio-temporal gait characteristics, Neuromotor maturation

INTRODUCTION

Without doubt, locomotion can be considered a key ecological function (e.g. Bertram, 2016). It is important for, among others, finding food, mates and shelter, avoiding predators, and migration. Legged terrestrial locomotion implies cyclical movement patterns characterized by specific interlimb and intralimb coordination patterns (e.g. Alexander, 2003; Bertram, 2016; Biewener, 2003). These patterns emerge from the interaction and feedback between the intrinsic mechanics of the musculoskeletal system and the environment on the one hand and neurological control on the other (e.g. Latash, 2008; Nishikawa et al., 2007). The latter is initiated at the cortical level and signals descend (via lower brain centres) the spinal cord to activate coupled spinal neural networks (central pattern generators, CPGs), which transform the command into coordinated muscle–tendon actions distributed over the limbs and joints (Grillner, 2011; Grillner et al., 2000; Lacquaniti et al., 2012b; Latash, 2008; Orlovsky et al., 1999).

It has been argued that the muscle activity generating the coordinated output at the level of the limb muscle–tendon system is actually accounted for by a combination of a limited number of weighted basic activation patterns. These originate from locomotor modules, which are in turn part of the neuronal networks of the spinal cord (Cappellini et al., 2006; Dominici et al., 2011; Ivanenko et al., 2004b, 2005, 2006; Lacquaniti et al., 2012a,b; Neptune et al., 2009). In humans, two of these basic patterns (essential for support during stance and to drive the limb during swing) are already present in neonates (Dominici et al., 2011; Lacquaniti et al., 2012b). Neonatal rats possess the same two basic patterns (Dominici et al., 2011; Lacquaniti et al., 2012b), and it is suggested that this most probably holds true for other animals as well (Dominici et al., 2011; Grillner, 2011). In some species (such as humans), further development of gait (i.e. inclusion of the remaining basic patterns) takes months to years. In the framework of the 'weighted patterned control', this implies that the additional basic patterns require time to develop and mature.

Despite evidence for evolutionarily conserved timing of locomotor development in mammals, effective postnatal time to onset of independent walking may differ greatly (Garwicz et al., 2009). Humans, rats and mice are altricial and, as such, they are incapable of independent locomotion immediately after birth. But what about precocial mammals (e.g. most ungulates), which are able to move about soon after birth? In the case of wildebeest, for instance, neonates follow the herd in less than 1 h (Pennycuick, 1975; Estes and Estes, 1979). Are the coordinated movement patterns and the underlying muscular control in precocial mammals fully innate or does there still exist (a rapid) maturation? We wanted to address this general question by studying early gait development (between birth and the age of 96 h) of neonatal pigs (*Sus scrofa*). Within a matter of minutes, healthy newborn pigs are able to stand up, after which they quickly (within hours) develop full locomotor capacity (Graves, 1984; Pond and Mersmann, 2001).

Here, we focused on the spatio-temporal characteristics (or step-time variables) of the limb movements of piglets during voluntary locomotion at a self-selected speed (*u*; for an overview of all variables see Table 1). According to the 'hybrid' dynamic pattern approach to locomotion (Latash, 2008), these characteristics can be considered the most basic collective output emerging from the entire

[1]Laboratory of Applied Veterinary Morphology, Department of Veterinary Sciences, Faculty of Biomedical, Pharmaceutical and Veterinary Sciences, University of Antwerp, 2610 Wilrijk, Belgium. [2]Laboratory of Functional Morphology, Department of Biology, Faculty of Sciences, University of Antwerp, 2610 Wilrijk, Belgium. [3]StatUa Center for Statistics, University of Antwerp, 2000 Antwerp, Belgium.

*Author for correspondence (charlotte.vandenhole@uantwerpen.be)

C.V., 0000-0001-5341-6518

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Table 1. Summary of all used variables (abbreviations, definitions and formulas), including normalization procedure

Variable	Abbreviation	Definition	Formula	Normalization
Centre of mass	COM	–	–	–
Gravitational acceleration	g	–	–	–
Functional leg height	H	Distance between the most distal part of the distal phalanx and the tail base.		
Self-selected speed	u	The movement of the COM during one cycle divided by the duration of the cycle. Animals are able to move in an unrestrained, voluntary way.	$f\,l_{\text{stride}}$	$\dfrac{u}{\sqrt{H\,g}}$
Stride frequency	f	Inverse of the period between two consecutive footfalls of a particular leg.	$\dfrac{u}{l_{\text{stride}}}$	$f\,\sqrt{H\,g}$
Stride length	l_{stride}	The forward movement during one stride or cycle.	$\dfrac{u}{f}$	$\dfrac{l_{\text{stride}}}{H}$
Stance duration	t_{s}	The period of contact between a limb and the ground.	–	$\dfrac{t_{\text{st}}}{\sqrt{H/g}}$
Swing duration	t_{sw}	The period of limb flight.	–	$\dfrac{t_{\text{sw}}}{\sqrt{H/g}}$
Step length	l_{step}	The movement of the centre of mass during one step (stance phase only).	–	$\dfrac{l_{\text{step}}}{H}$
Duty factor	df	The fraction of the cycle for which the limb is in contact with the ground.	–	–
Front lag	f-lag	The time lag between the two front footfalls as a function of the average cycle duration of the front leg pair (d_{front}). Adapted from Abourachid (2003).	$\dfrac{\text{f-lag}}{d_{\text{front}}}$	–
Hind lag	h-lag	The time lag between the two hind footfalls as a function of the average cycle duration of the hind leg pair (d_{hind}). Adapted from Abourachid (2003).	$\dfrac{\text{h-lag}}{d_{\text{hind}}}$	–
Pair lag	p-lag	The time lag between the two ipsilateral footfalls as a function of the average cycle duration of the ipsilateral leg pair (d_{ipsi}). Adapted from Abourachid (2003).	$\dfrac{\text{p-lag}}{d_{\text{ipsi}}}$	–
Diagonal lag	d-lag	The time lag between the two diagonal footfalls as a function of the average cycle duration of the diagonal leg pair (d_{dia}). Adapted from Abourachid (2003).	$\dfrac{\text{d-lag}}{d_{\text{dia}}}$	–
AI stride frequency	AI_f	Asymmetry index of stride frequency. Adapted from Robinson et al. (1987).	$\dfrac{(f_{\text{R}}-f_{\text{L}})}{0.5(f_{\text{R}}-f_{\text{L}})}100\%$	–
AI stride length	$\text{AI}_{l_{\text{stride}}}$	Asymmetry index of stride length. Adapted from Robinson et al. (1987).	$\dfrac{(l_{\text{stride,R}}-l_{\text{stride,L}})}{0.5(l_{\text{stride,R}}-l_{\text{stride,L}})}100\%$	–
AI stance duration	$\text{AI}_{t_{\text{st}}}$	Asymmetry index of stance duration. Adapted from Robinson et al. (1987).	$\dfrac{(t_{\text{st,R}}-t_{\text{st,L}})}{0.5(t_{\text{st,R}}-t_{\text{st,L}})}100\%$	–
AI swing duration	$\text{AI}_{t_{\text{sw}}}$	Asymmetry index of swing duration. Adapted from Robinson et al. (1987).	$\dfrac{(t_{\text{sw,R}}-t_{\text{sw,L}})}{0.5(t_{\text{sw,R}}-t_{\text{sw,L}})}100\%$	–
AI step length	$\text{AI}_{l_{\text{step}}}$	Asymmetry index of step length. Adapted from Robinson et al. (1987).	$\dfrac{(l_{\text{step,R}}-l_{\text{step,L}})}{0.5(l_{\text{step,R}}-l_{\text{step,L}})}100\%$	–
AI duty factor	AI_{df}	Asymmetry index of duty factor. Adapted from Robinson et al. (1987).	$\dfrac{(\text{df}_{\text{R}}-\text{df}_{\text{L}})}{0.5(\text{df}_{\text{R}}-\text{df}_{\text{L}})}100\%$	–

Normalized variables are indicated with primes. L, left; R, right.

underlying neuromotor and biomechanical (i.e. neuro-mechanical) system (Aerts et al., 2000; Nishikawa et al., 2007; Segers et al., 2006). As such, relative phasing of the limbs reveals interlimb coordination, while single limb behaviour (during stance and swing) is a collective measure of intralimb coordination. The above-mentioned general question can thus be reformulated as follows: is the spatio-temporal behaviour constant during early development in piglets, indicating fully innate control in this precocial species? Or does the spatio-temporal behaviour rapidly change over time anyway, as is suggested for neonate altricial species (Dominici et al., 2011; Grillner, 2011; Lacquaniti et al., 2012b)?

In order to assess changes or constancy in the spatio-temporal behaviour during early development, the potential growth and eventual postural changes of the piglets should be taken into account. With the change of inertia, the dynamics of kinematically identical locomotor tasks will change as well. Alexander and Jayes (1983) argue that two motions are dynamically similar if they could be made identical by applying uniform scaling factors for linear dimensions, time and forces (see also Alexander, 1977). Therefore,

in order to answer the above general question, the spatio-temporal behaviour at voluntary u was normalized according to the dynamical similarity concept for terrestrial locomotion (e.g. Alexander, 2003; Hof, 1996). This results in the dimensionless spatio-temporal variables presented in Table 1 [note that u' is equal to the square root of the Froude number as mostly used in locomotor studies; identical u' (or u'^2) values mean dynamically equivalent (dimensionless) locomotor speeds].

More specifically we aimed to answer the following questions. (1) Is voluntary locomotion at u' dynamically similar during early gait development? We hypothesize that this is the case, implying that the dynamical task for the motor system does not change during this early developmental period. For this purpose, we compared u' between developmental stages and how this u' is established [in terms of normalized stride frequency (f') and normalized stride length (l_{stride}')]. If u', f' and l_{stride}' do not change, the hypothesis will be confirmed. (2) Does interlimb coordination change during early gait development? We hypothesize that this is not the case, implying established innate interlimb coordination. For this purpose, we

compared the relative phasing of the limbs between developmental stages. Relative phasing includes the front lag (f-lag), hind lag (h-lag), pair lags (p-lag) and diagonal lags (d-lag). If these relative timings of the footfalls do not change, the hypothesis will be confirmed. (3) Does the individual limb behaviour (intralimb coordination) change during early gait development? We hypothesize that this is not the case, implying established innate intralimb coordination. For this purpose, we compared the normalized swing (t_{sw}') and stance durations (t_{st}') and the normalized step lengths (l_{step}') between developmental stages, as these three variables determine to a large extent the limb configuration. If per limb these variables do not change, the hypothesis will be confirmed. However, we also hypothesize that, given the body build, a difference between front and hind limbs will be present. To this end, we compared duty factor (df) between leg pairs. (4) Does the variability of the gait pattern change during early gait development? We hypothesize this is the case and gait variability decreases rapidly during early development, leading to a stable gait pattern. We compared left–right asymmetries within the locomotor cycles between developmental stages to assess this variability.

Confirmation of all these hypotheses will support the assumption of complete innate locomotor control in pigs and possibly in other precocial mammals.

MATERIALS AND METHODS
Selection of piglets
Institutional and national guidelines for the care and use of animals were followed and all experimental procedures involving animals were approved by the Ethical Committee of Animal Experimentation, University of Antwerp, Belgium (approval number 2015-26). The data were collected from 14 domestic piglets (*Sus scrofa*, Topigs×Belgian Piètrain) between 12 February and 11 May 2015 on a local farm. Seven litters were monitored, with 1–3 healthy piglets selected per litter. Upon selection, the piglets were ear notched. The average number of piglets born alive within these litters was 15.71±4.39 (mean±s.d., here and throughout). Sex was not used as a selection criterion (although 7 females and 7 males were included). Piglets were chosen based on their body mass at birth and vitality score. Each piglet was weighed at birth and its vitality was scored (0–4, dead to normal vitality), based on respiration (0–2, no to regular respiration) and movement (0–2, no movement to taking a few steps). This way of scoring is based on the Apgar score of human neonates, but has been modified for piglets (Zaleski and Hacker, 1993; Randall, 1971). Animals that scored 3 or 4 out of 4 were considered to have a normal vitality. Piglets with a birth mass that was within the limits of the average birth mass in the litter ±1 s.d. were classified as normal birth mass piglets. Only piglets that were classified as being of normal birth mass with normal vitality were used. The mean birth mass of the piglets was 1.19±0.23 kg. The piglets that were included in the study were also weighed at each walking session. All relevant data for included piglets are listed in Tables S1–S7.

Video sequences
Lateral view video recordings were made of the animals when walking through a corridor, perpendicular to the camera (3.3 megapixel, 50 Hz deinterlaced, JVC GZ-V515, JVC Kenwood Corporation, Kanagawa, Japan), provided with a reference grid (see Fig. 1). The corridor was 0.2 m in width, 1.5 m in length with a polymethyl methacrylate (Plexiglas®) wall on one side. The surface of the corridor was covered with anti-skid material (rubber) for
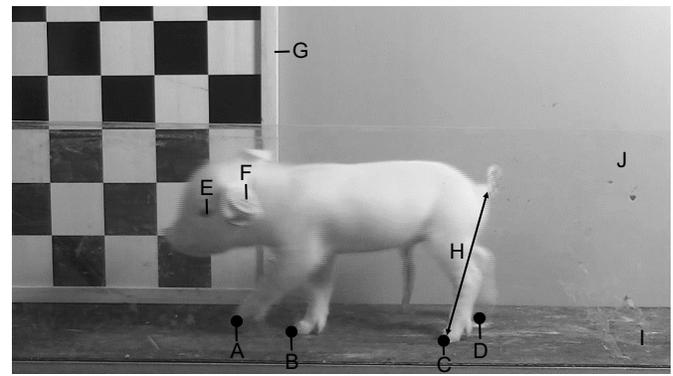

Fig. 1. Lateral view of the recording set-up (video still image). A: digitized point on left front leg; B: digitized point on right front leg; C: digitized point on left hind leg; D: digitized point on right hind leg; E: eye; F: ear-notch; G: reference grid; H: functional hind limb length at midstance; I: corridor with anti-skid material; J: Plexiglas® wall.

optimal grip. Ten time points (0, 1, 2, 4, 6, 8, 24, 26, 28 and 96 h after birth) were chosen. To study the maturation of locomotion, it was necessary to choose a control age to which all other ages were compared. Initially, in view of our hypotheses regarding the innateness of locomotion, 0 h was considered as a control age. However, the variation at this age was considerable, in comparison to the other ages. Additionally, this way of working would have provided us with no information regarding the exact timing of maturation. Keeping this in mind, we opted to use age 96 h, a time point with minimal variation that was still within the frame of early development (see above). Furthermore, age 96 h, later referred to as control age 96 h (CA 96 h), is an exceptionally relevant age in early piglet development, because mortality is highest during the first 3 postnatal days (Quiniou et al., 2002; Tuchscherer et al., 2000).

Piglets were gently encouraged to walk at voluntary u through the corridor. To avoid fatigue, only three successive trials were recorded at each time point per piglet. From these trials, we aimed at retaining two sequences in which the piglets completed at least one entire cycle (stride) without pausing or falling for further analysis. One animal died just prior to CA 96 h and 12 trials (from 9 piglets at four developmental points) were discarded because of the lack of a complete stride. As such, 266 (out of 280) trials were included in the analysis.

Gait analysis
In all video sequences, five body points were digitized field-by-field using Matlab (Mathworks, Natick, MA, USA), using a free work package written by Ty Hedrick (University of North Carolina, USA; http://www.unc.edu/~thedrick/software1.html): the most distal point of the distal phalanx of each leg and either the eye or the ear notch. As no information on the exact position of the centre of mass (COM) was available, the displacements of the eye or the ear notch were used as a proxy for overall forward displacement of the body throughout the stride. The choice of either eye or ear notch was determined for each sequence separately and preliminary tests showed the forward displacement was correctly represented by both. Our preference was the ear notch, the landmark that was most easily traceable throughout an entire sequence. The ear in these young piglets is a rigid structure that moves with the head. As there were no conspicuous head movements throughout a stride, it is assumed to represent the forward movement of the body accurately. However, for some sequences, it was not possible to use the ear notch. To encourage voluntary locomotion, the piglets were able to choose the

direction of movement (left to right or right to left). As such, the ear notch was sometimes located on the side of the animal that was invisible to the camera. When this was the case, we opted to use the eye as a proxy for COM. However, it was not feasible to use the eye for all movies throughout the analysis, for practical reasons. All movies were made at close range to provide enough detail for subsequent analysis. As such, the eye was sometimes no longer visible in the frame, while the stride was still ongoing. In these cases, the ear notch was still visible, because of its more caudal location. In addition, some animals only opened their eyes after a few hours, making it a hard landmark to trace.

Additionally, a locomotion-related linear dimension needed to be digitized for normalization purposes (see below). Traditionally, hip height is used for normalization, according to the dynamic similarity principle (Alexander, 1992b). However, for these young piglets it was impractical to measure hip height. Newborn pigs typically have very loose skin, which not only makes the hip joint very difficult to localize and mark correctly but also results in large marker displacements during locomotion as a result of skin movement. As such, we opted to use the functional leg length/ height (H), i.e. the distance between the most distal part of the distal phalanx and a fixed point on the pelvis, i.e. the tail base. These landmarks can be digitized unequivocally, which minimizes the measurement error (and hence the non-biological variation in our data). H was determined for each sequence, in the frame coinciding with midstance of the hind limb closest to the camera. Two points of the reference grid were digitized for scaling purposes.

From the digitizations of these five body points, 19 gait-related variables were calculated using a custom-written Matlab script (J.G.). An overview of these variables, including definitions and formulas, can be found in Table 1. Variables were calculated per piglet (u, u' and time lags), per leg pair (asymmetry indices, AIs) or per leg (spatio-temporal gait variables). AIs were used

as a proxy for variability. According to Meijer et al. (2014), absolute AI values can range from 200% to 0%, the latter being indicative of perfect contralateral symmetry. In accordance with the dynamical similarity (Alexander and Jayes, 1983), u and all spatio-temporal gait variables were normalized to H. All formulas used for normalization of the parameters can also be found in Table 1.

Statistics

Linear mixed models were fitted to evaluate the effect of age and leg on the outcome variables. Fixed factors included age and leg (if relevant for the parameter in question), and sex was included as a covariate. To account for the dependence between observations on littermates or within the same animal, random factors were included for sow and piglet (nested in sow), plus random slopes for age, leg and piglet (nested in sow). The starting model was simplified using stepwise backwards modelling. Some outcome variables required no transformations (u', df, l_{stride}', l_{step}' and p-lag); others were either log-transformed [t_{st}', f', AI stride length (AI$_{l_{stride}}$), AI step length (AI$_{l_{step}}$), AI duty factor (AI$_{df}$), f-lag, h-lag, d-lag] or square-root transformed [t_{sw}', AI stride frequency (AI$_f$), AI stance duration (AI$_{t_{st}}$), AI swing duration (AI$_{t_{sw}}$)] to meet normality and/or homoscedasticity assumptions. Models were fitted using JMP® Pro 12 (SAS Institute Inc., Cary, NC, USA). An effect was considered to be statistically significant if $P \leq 0.05$. *Post hoc* analysis with Dunnett's correction was used for comparing the different age groups to CA 96 h for u', f', l_{stride}', t_{sw}', t_{st}', l_{step}' and AIs. *Post hoc* analysis with Tukey's correction was used to compare the different legs for df and t_{sw}'.

RESULTS
Morphometrics

The change in body mass and H (used for normalization) with age is shown in Fig. 2. During the first 28 h, body mass gain was limited
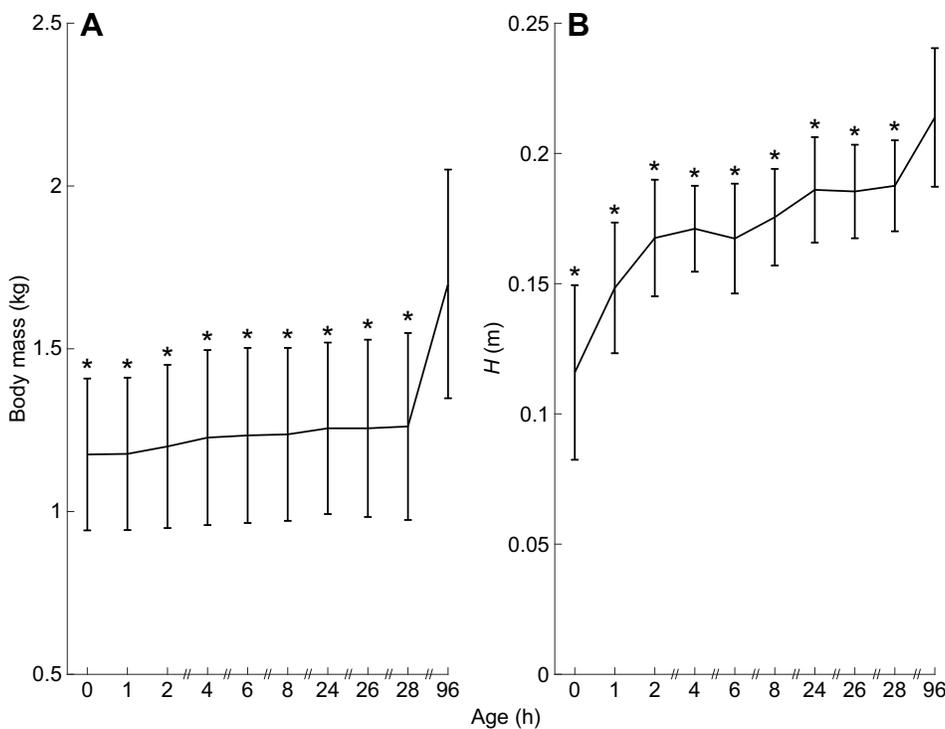

Fig. 2. Morphometrics. (A) Body mass (n=137). (B) Functional hind limb length (H, n=137). Linear mixed models, *post hoc* analysis with Dunnett's correction. All values are means±s.d. *Mean values differ significantly from the control age (CA) of 96 h ($P \leq 0.05$).

(0.46% of the body mass at birth). The rapid initial increase in H (between 0 and 2 h) can mainly be attributed to a more erect limb posture, rather than to growth.

How do absolute gait data change during early development?

Up to and including age 8 h, u was significantly lower than at CA 96 h ($P<0.0001$ for ages 0 and 1 h, $P=0.0150$, 0.0049, 0.0126 and 0.0181 for ages 2, 4, 6 and 8 h, respectively; Fig. 3A). At age 0 h, u of the piglets was only 0.09 m s^{-1}, while at CA 96 h they were walking at a pace of 0.23 m s^{-1}. l_{stride} and l_{step} showed similar results (Fig. 3B,C). Both l_{stride} and l_{step} reached a stable value between age 24 and 26 h (l_{stride}: all $P<0.0001$, except $P=0.0199$ for age 24 h; l_{step}: all $P<0.0001$, except $P=0.0210$ for age 24 h). l_{stride} increased from 0.08 m at age 0 h to 0.19 m at CA 96 h. For l_{step}, we found a similar increase from 0.06 m (age 0 h) to 0.14 m (CA 96 h). f did not significantly change with age (Fig. 3D).

Is voluntary locomotion at normalized self-selected speed dynamically similar during early gait development?

u' did not change any further 2 h after birth (Fig. 4A). This is evidenced by the fact that u', compared with CA 96 h, was only significantly different for ages 0 and 1 h ($P<0.0001$ and 0.0055, respectively). u' at these ages was significantly lower, comprising only 50.34% (age 0 h) and 63.46% (age 1 h) of the u' at CA 96 h. We saw similar results for f' and l_{stride}' (Fig. 4B,C). f' reached a stable value between ages 0 and 1 h, which is indicated by the fact that the piglets only showed a significantly lower f' at

age 0 h (85.27% of CA 96 h; $P=0.0012$). l_{stride}' took longer to reach a steady value. When compared with CA 96 h, l_{stride}' was significantly lower at ages 0 h ($P=0.0006$) and 2 h ($P=0.0125$), being 72.86% and 79.12% of the CA 96 h value, respectively.

Does interlimb coordination change during early gait development?

We found that the different time lags did not change significantly with age. Values for f-lag, h-lag, p-lag (left), p-lag (right), d-lag (left hind, right front) and d-lag (right hind, left front) were 0.53±0.16, 0.50±0.13, 0.69±0.17, 0.36±0.18, 0.25±0.19 and 0.20±0.11, respectively.

Does intralimb coordination change during early gait development?

t_{sw}' was 24.65% lower at age 2 h compared with the value at CA 96 h ($P=0.0002$; Fig. 5A). Initially, at age 0 h, t_{sw}' was similar to that at CA 96 h. t_{st}' showed a significantly higher value at age 0 h compared with the CA 96 h value (183.28% of CA 96 h; $P=0.0018$; Fig. 5B). However, between age 0 and 1 h, t_{st}' reached a steady value. l_{step}' reached a stable value between ages 2 and 4 h as shorter l_{step}' were observed at ages 0 h (78.69% of CA 96 h; $P=0.006$) and 2 h (83.46% of CA 96 h; $P=0.0495$; Fig. 5C).

Does intralimb coordination differ as a function of body build?

The front legs exhibited a higher df than the hind legs [left front (LF)–left hind (LH); LF–right hind (RH); right front (RF)–RH
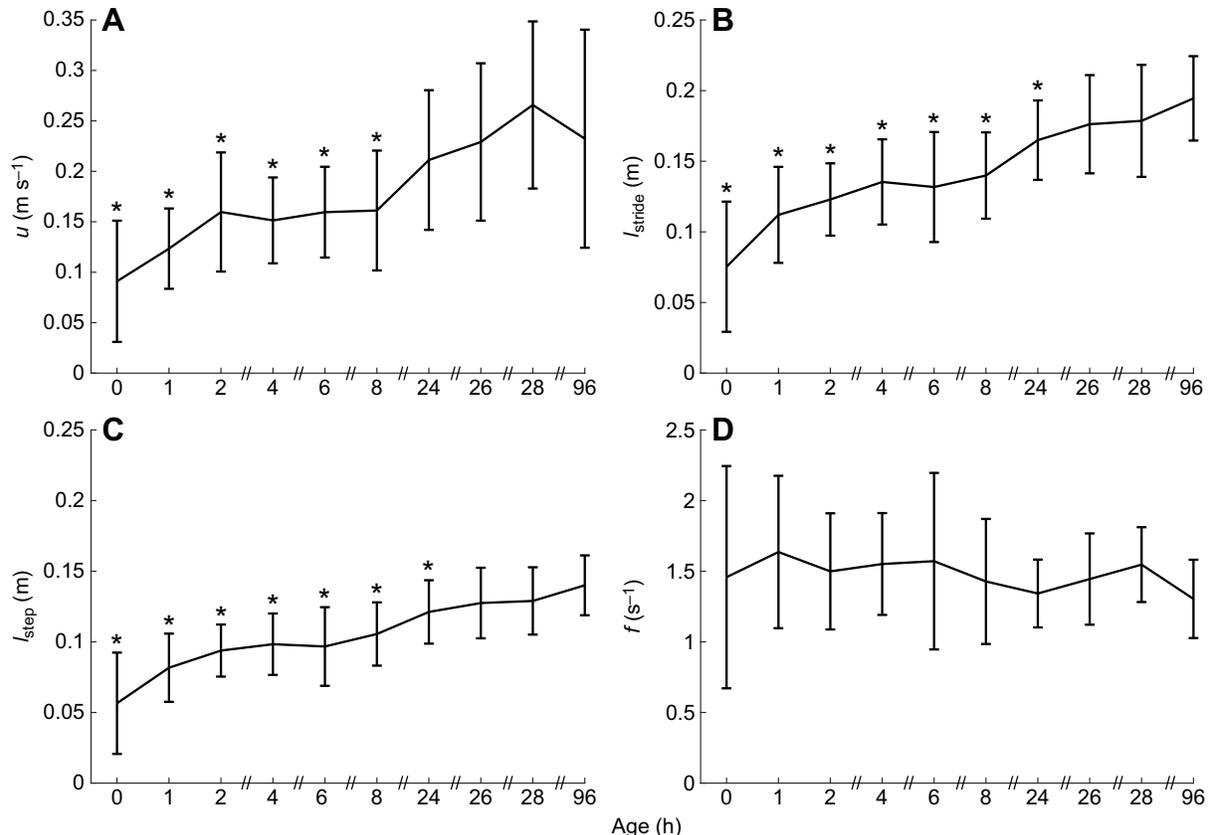

Fig. 3. Absolute gait data. (A) Self-selected speed (u, n=137). (B) Stride length (l_{stride}, n=548). (C) Step length (l_{step}, n=548). (D) Stride frequency (f, n=548). Linear mixed models, *post hoc* analysis with Dunnett's correction. All values are means±s.d. *Mean values differ significantly from CA 96 h ($P\leq0.05$).
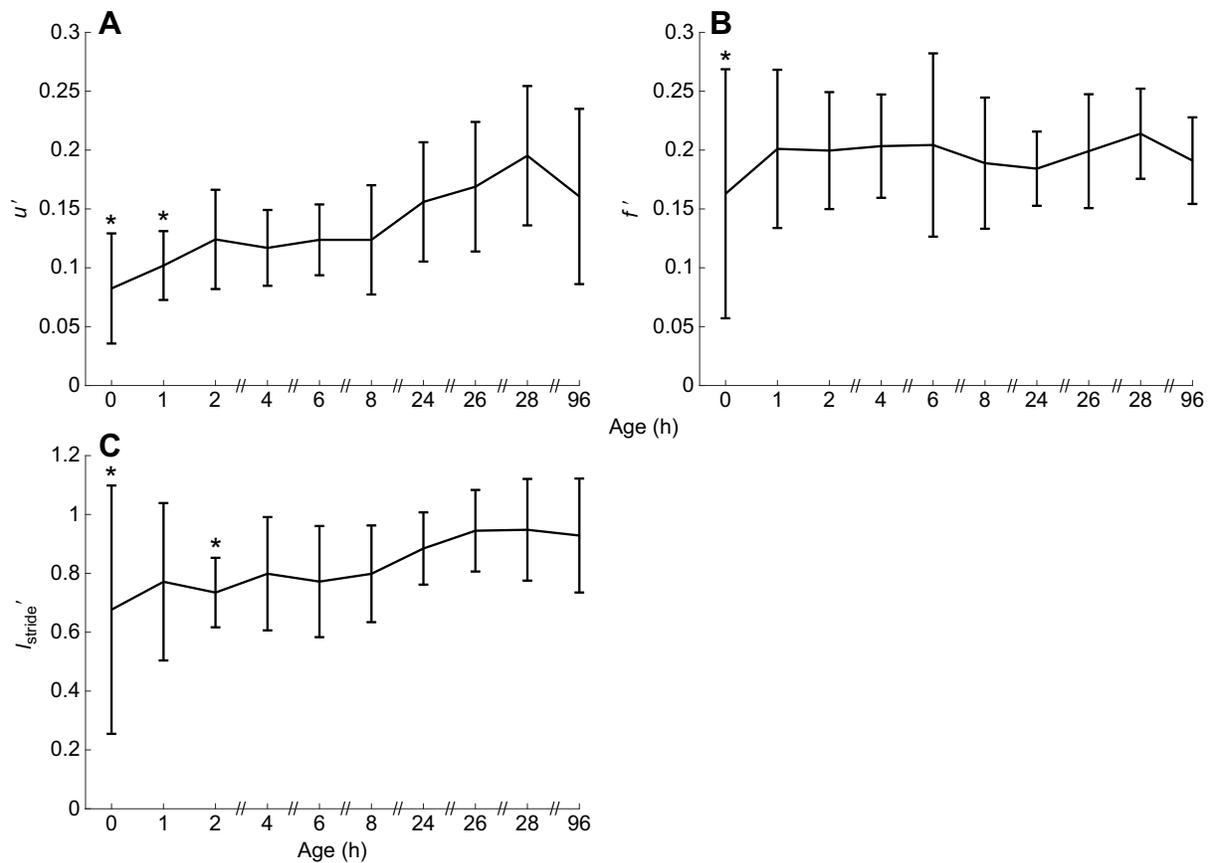
Fig. 4. Dimensionless gait data. (A) Normalized self-selected speed (u', $n=137$). (B) Normalized stride frequency (f', $n=548$). (C) Normalized stride length (l_{stride}', $n=548$). Linear mixed models, *post hoc* analysis with Dunnett's correction. All values are means±s.d. *Mean values differ significantly from CA 96 h ($P \leq 0.05$).

differ significantly with a $P<0.0001$; RF–LH differ with a $P=0.0004$], with differences within both leg pairs being negligible (LF 0.76±0.07, RF 0.75±0.08; versus LH 0.72±0.08, RH 0.71± 0.09; Fig. 6A). The hind legs showed an overall t_{sw}' that was 15.33% longer than that of the front legs (LF and RF versus RH: $P<0.0001$, LF versus LH: $P=0.0002$; RF vs LH: $P=0.0003$; Fig. 6B).

Does gait (a)symmetry change during early gait development?

Values for AI_f and $AI_{l_{stride}}$ at 0, 1, 2 and 6 h differed significantly from those at CA 96 h ($P<0.0001$, 0.0037, 0.0388 and 0.0333, respectively, for AI_f; and $P<0.0001$, 0.0004, 0.0315 and 0.0231, respectively, for $AI_{l_{stride}}$; Fig. 7A,B). Both AI_f and $AI_{l_{stride}}$ were higher at early ages (for ages 0, 1, 2 and 6 h, AI_f was 54.69±35.32%, 30.13±26.63%, 23.99±18.58% and 27.20± 31.14%, respectively, and $AI_{l_{stride}}$ was 107.08±232.13%, 30.28± 20.47%, 21.33±12.49% and 28.67±25.80%, respectively). At CA 96 h, AI_f and $AI_{l_{stride}}$ were reduced to 9.75±6.72% and 12.4± 8.12%. We also observed a reduction in $AI_{t_{sw}}$ (Fig. 7C). While at age 0 h we noted an $AI_{t_{sw}}$ of 53.86±41.49%, this was reduced to 25.94±13.71% at CA 96 h ($P=0.0065$). $AI_{t_{st}}$ reached a stable value between the ages of 6 and 8 h (Fig. 7D). $AI_{t_{st}}$ at ages 0, 1, 2 and 6 h was significantly higher (70.59±32.82%, 36.67±30.79%, 28.54± 21.76% and 35.53±37.04%) than $AI_{t_{st}}$ at CA 96 h (12.49±9.12%; $P<0.0001$, =0.0019, =0.0291 and =0.0071, respectively). $AI_{l_{step}}$ at

ages 0, 1, 2 and 6 h was 120.34±227.76%, 37.11±23.65%, 23.27± 14.18% and 34.50±34.30% (Fig. 7E), and thus significantly higher when compared with the value at CA 96 h ($P<0.0001$, <0.0001, =0.0091 and =0.0012, respectively). At CA 96 h, we observed an $AI_{l_{step}}$ of 11.06±7.95%. Comparing leg pairs, we saw that the front leg pair showed a lower AI_{df} (10.56±9.70%) than the hind leg pair (13.08±9.41%; $P=0.0010$; Fig. 7F). For $AI_{l_{sw}}$, we did not observe a difference between the front and the hind leg pair.

DISCUSSION
Morphometrics
The present results show that early neonatal development in piglets is characterized by growth in terms of body mass, contributing to a longer H. Along with growth, we also saw postural changes during the first few hours. This more upright position of the piglets and extension of the legs resulted in a better positioning of the limbs for walking and a longer H. Both growth and the postural changes go along with an increase in u, l_{stride} and l_{step}. These changes in body mass and limb length during early development were also observed in other studies (on different species, including pigs; e.g. Sutherland, 1997; Clarke and Still, 2001; Stavrakakis et al., 2014; Back et al., 1994). However, the observed shifts in the absolute spatio-temporal gait may equally well represent additional effects to those of growth and postural changes such as neuromotor maturation. We argue (see Introduction) that, if only growth and posture contribute in this early phase, spatio-temporal gait
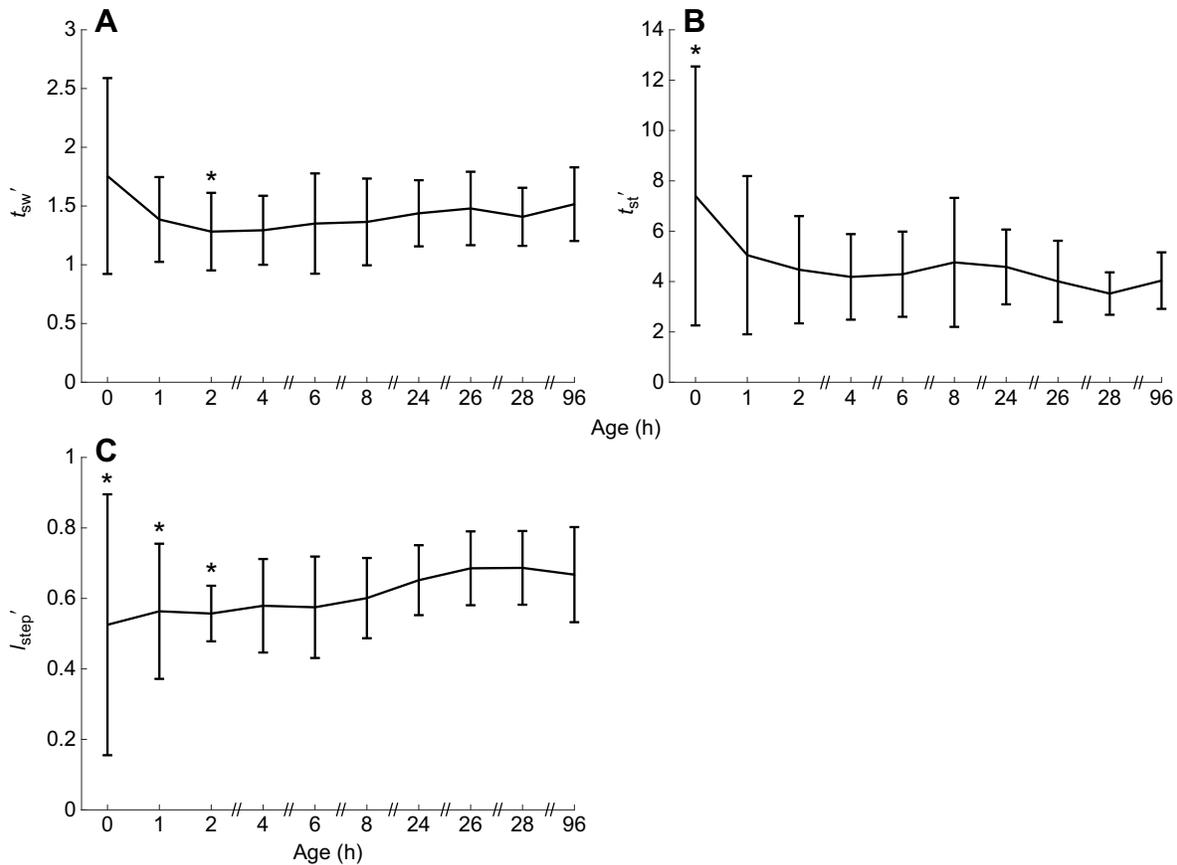
Fig. 5. Intralimb coordination – age differences. (A) Normalized swing duration (t_{sw}', n=548). (B) Normalized stance duration (t_{st}', n=548). (C) Normalized step length (l_{step}', n=548). Linear mixed models, *post hoc* analysis with Dunnett's correction. All values are means±s.d. *Mean values differ significantly from CA 96 h ($P \leq 0.05$).

characteristics, normalized according to the dynamic similarity principle (see, for instance, Alexander, 2003, for details), would remain constant over the considered developmental period. If the dynamics of the motor task (implicitly taking size into account) do not change during development, then the neuromotor patterns are also assumed to remain constant. This implies no further maturation at this level. Otherwise, changes of the normalized data (according to dynamic similarity) would indicate neuromotor maturation on top of pure 'size' effects. In case of altricial species, both absolute and normalized gait characteristics will presumably change during early development. In precocial species, in contrast, normalized gait characteristics are assumed to be constant or to stabilize very rapidly after birth. Below, we discuss the locomotor developmental data of the piglets from this point of view.

Is voluntary locomotion at self-selected speed dynamically similar during early gait development?

Apart from the 2 h after birth, u' seemed to be invariable during the first 4 days, suggesting a very rapid stabilization of the motor task. During the first hour after birth, u' was lower compared with the CA value. Between the ages of 1 and 2 h, a steady value for u' was reached, which was due to an adjustment of both l_{stride}' and f' (the product equalling u'). The first component of u, i.e. l_{stride}, increased up to and including the age of 24 h, as a result of the growth of the piglets. This has been reported for wildebeest, where a comparison of juveniles and adults showed an increase of l_{stride} with age (Pennycuick, 1975). However, as l_{stride}' reached a stable value

between the ages of 2 and 4 h, we deduce that during these first 4 h, neuromotor maturation takes place.

f, the other component of u, remained constant during early development, while f' rapidly increased after birth, reaching a consistent value between ages 0 and 1 h. This difference between f and f' is explained by the rapid increase in H in this early developmental period. One of the few longitudinal studies available on precocial species is on the horse, detailing f (not f') (Back et al., 1994). Contrary to our (non-normalized) results, Back et al. (1994) reported a decrease in f with age (until 26 months), as a result of increased height at the withers. The result for wildebeest also shows a decrease in f from juvenile into adulthood (Pennycuick, 1975). This might imply a great difference in gait maturation among precocial animals, as we saw no change in f with age for pigs. Clearly, the developmental period considered in these previous studies differs considerably from ours. Studying pigs up to and including the age of 84 days, Liu et al. (1999) concluded that the absolute growth rate of the legs increases with age. This implies that, for older piglets (beyond the age of 96 h), absolute gait variables, such as l_{stride} and f, might change in a fashion similar to the horse and the wildebeest. Furthermore, the apparent contrast with our results stresses the importance for the need for normalized data in order to tell whether the decrease in f in horses and/or wildebeest is exclusively an effect of growth, or whether this represents a neuromotor maturation pattern.

The increase of both l_{stride}' and f' (with a higher u' as a consequence) we saw in piglets has also been reported for humans
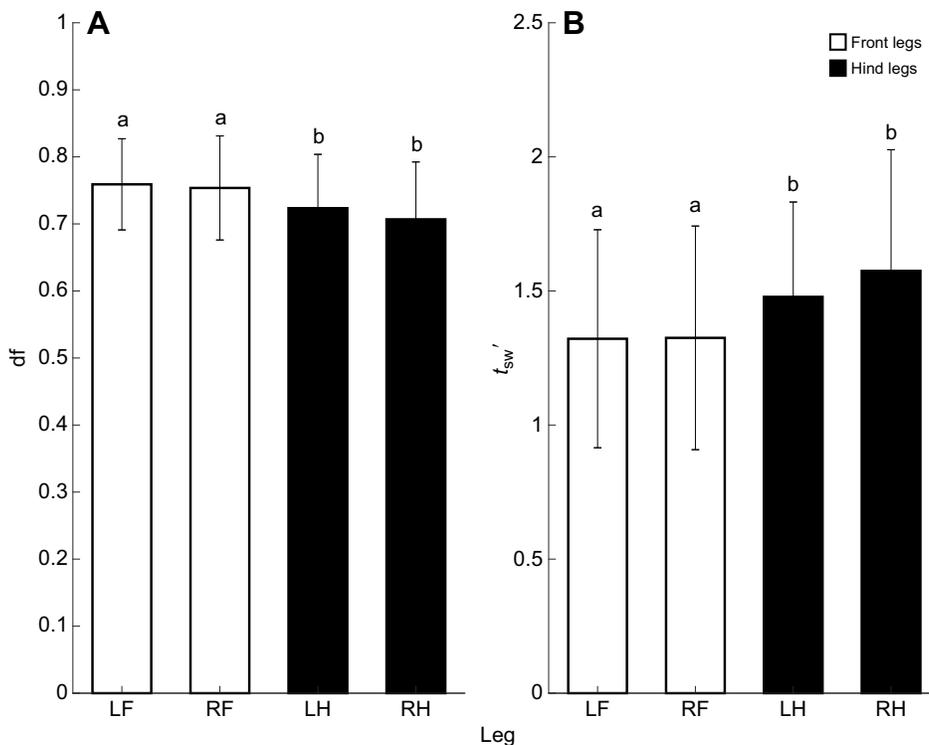
Fig. 6. Intralimb coordination – leg differences. (A) Duty factor (df, $n=548$). (B) Normalized swing duration (t_{sw}', $n=548$). Linear mixed models, *post hoc* analysis with Tukey's correction. All values are means±s.d. Significant differences ($P \leq 0.05$) are indicated by different letters.

by Sutherland (1997). By looking at these normalized parameters, it was concluded that both growth and a maturation process influence spatio-temporal gait parameters for children aged 1–4 years. This is similar to our results, although the time frame is considerably longer in humans, which illustrates the difference between altricial and precocial species.

Overall, once u' stabilizes, its components also stabilize, which supports our hypothesis of a very quick neuromotor maturation. The very slight discrepancies in maturation intervals for u', f' and l_{stride}' are likely to be due to the large amount of variation in the data.

Does interlimb coordination change during early gait development?

The footfall pattern of the gait of piglets did not change during early development, which implies that interlimb coordination (relative phasing of the limbs) is completely innate in pigs. Our results indicate that piglet gait can be classified as the 'lateral walk' type, with f-lags and h-lags of around 50% and one p-lag (in this case, left) of more than 50% of the total cycle duration (Abourachid, 2003; Abourachid et al., 2007). This is in accordance with findings for adult pigs (von Wachenfelt et al., 2008).

Does intralimb coordination change during early gait development?

Unlike interlimb coordination, intralimb coordination does not seem to be fully innate, which is indicated by t_{sw}' and t_{st}', as well as l_{stride}', showing a fast maturation process. From our results, it seems the duration of t_{sw}' is rather unstable and short during the first 2 h after birth. Piglets are born with very limited energy reserves (consisting mainly of glycogen). After 20–30 min, they have to start taking in new energy by means of colostrum, to sustain not only their physical activity but also thermoregulation (Theil et al., 2011, 2014; Noblet et al., 1997; Le Dividich et al., 2005). Because of this limited amount of available energy, we propose that during the first hours after birth, the piglet would adopt a means of locomotion that is as energy

efficient as possible. One way of accomplishing this is by limiting t_{sw}'. During the swing phase, the front or rear end of the animal is only supported by one leg. However, maintenance of stance requires not only the support of the body against gravity but also that the COM remains within the limits of support in the horizontal plane (Fung and Macpherson, 1995). By means of a shorter t_{sw}', the piglet can return more quickly to a phase where the front or rear end of the body is supported by two legs. In addition, it has been argued that the leg swing may consume a substantial part of the stride energy (e.g. Marsh et al., 2004; Arellano and Kram, 2014). Shortly after the age of 2 h, we noted a slight increase in t_{sw}' that led to a stable value between the age of 2 and 4 h. Generally, little is known about the link between t_{sw} and age, let alone t_{sw}' and age. The longitudinal pattern of t_{sw} has been studied in one precocial species so far: the horse (Back et al., 1994). Back et al. (1994) revealed that t_{sw} divided by height decreased up to 26 months in the horse. This decrease (although on a smaller time scale) of t_{sw} is also visible in altricial species, i.e. mouse and rat (Clarke and Still, 2001; Bolles and Woods, 1964). However, as mentioned earlier, the former studies lack normalized data, which makes it impossible to distinguish maturation from growth and hence make a correct comparison to our piglets.

t_{st}' was initially longer, but reached a lower, stable value during the first hour after birth. We believe there are three possible explanations for this decrease in t_{st}'. Firstly, the initially prolonged t_{st}' might be important to increase support immediately after birth. Secondly, we might consider the link between t_{st}' and u'. It is a well-known phenomenon that decreasing t_{st} or t_{st}' leads to an increase in u or u' (Pearson, 1976; Verdugo et al., 2013). Thirdly, the decrease in t_{st}' we saw for piglets might in large part be a consequence of the normalization procedure (see Table 1). This way, the initial increase in H due to a more erect positioning of the limbs might greatly influence the values of t_{st}', possibly without influencing t_{st}.

l_{step}' only reached a steady value between 2 and 4 h, which still indicates a very fast maturation process, albeit a little slower than that of t_{sw}' and t_{st}'. We argued in the Introduction that single limb
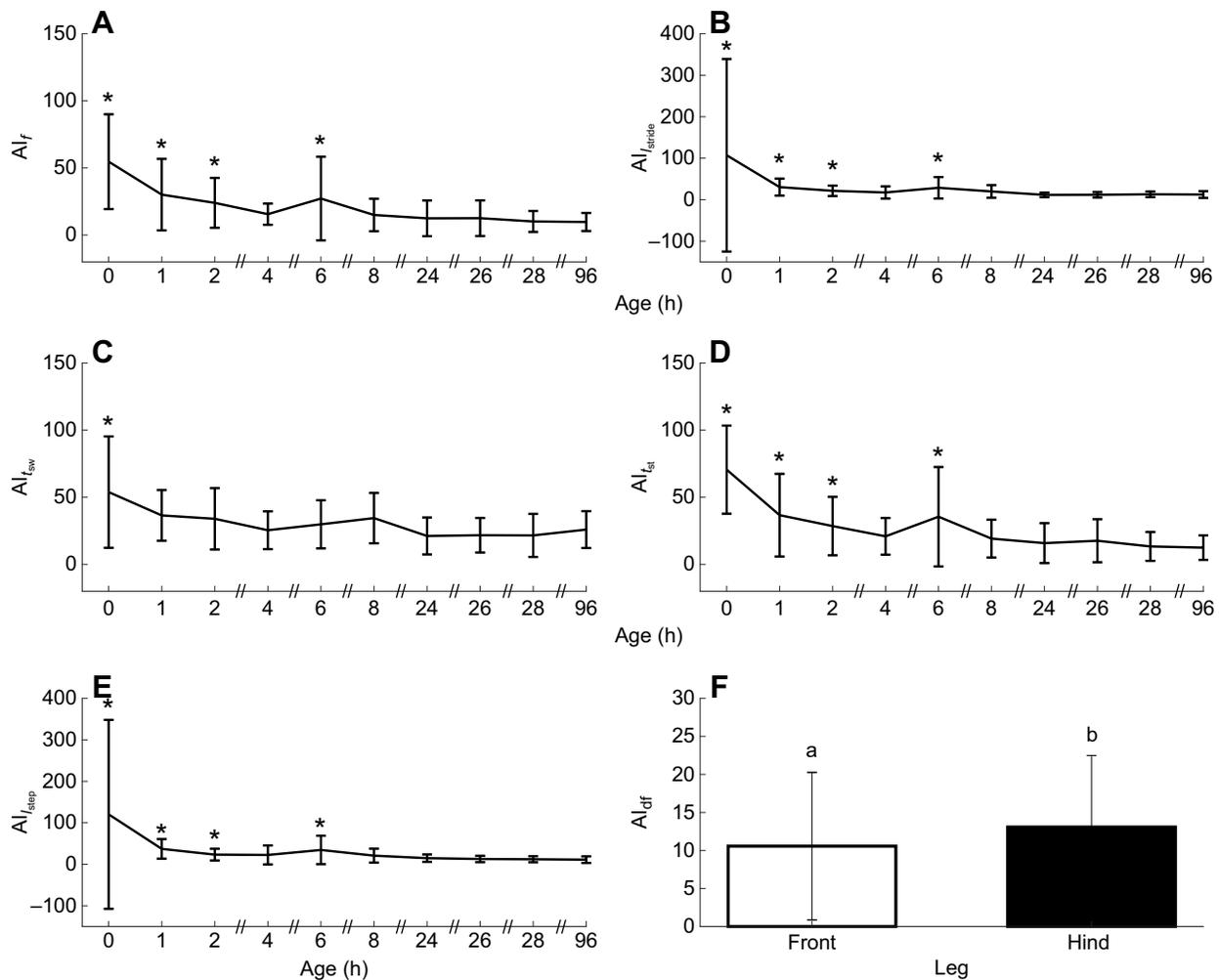
Fig. 7. Asymmetry indices. (A) Asymmetry index of stride frequency (AI_f, n=274). (B) Asymmetry index of stride length ($AI_{l_{stride}}$, n=274). (C) Asymmetry index of swing duration ($AI_{t_{sw}}$, n=274). (D) Asymmetry index of stance duration ($AI_{t_{st}}$, n=274). (E) Asymmetry index of step length ($AI_{l_{step}}$, n=274). (F) Asymmetry index of duty factor (AI_{df}, n=274). Linear mixed models, *post hoc* analysis with Dunnett's correction for A–E. Linear mixed model, *post hoc* analysis with Tukey's correction for F. All values are means±s.d. *Mean values in A–E differ significantly from CA 96 h ($P \leq 0.05$). Significant differences ($P \leq 0.05$) in F are indicated by different letters.

spatio-temporal behaviour can be considered as a collective measure for intralimb coordination. In humans, l_{step}' keeps on increasing until the age of 4 years (Sutherland, 1997) and intralimb coordination rapidly evolves towards mature behaviour, reflecting the inverted pendulum within a few months of independent walking experience (Ivanenko et al., 2004a). This shows once more the difference between precocial and altricial animals.

Does intralimb coordination differ as a function of body build?

Body mass distribution in pigs (Meijer et al., 2014) and other animals is approximately 30% on each front limb and 20% on each hind limb (Besancon et al., 2004; Budsberg et al., 1987; Kim and Breur, 2008; Kano et al., 2016). In line with this, Thorup et al. (2007) showed 54% of body mass is carried by the pig's forelimbs, which demonstrates that the centre of gravity is relatively close to the forelimbs. In accordance with this unequal distribution of body mass, front limbs and hind limbs generally differ biomechanically, with front limbs receiving higher peak vertical forces than hind limbs. This has been observed for pigs (Thorup et al., 2007), sheep (Kim and Breur, 2008), dogs (Besancon et al., 2004), cats (Verdugo et al., 2013) and

mice (Clarke and Still, 1999). As hypothesized, this difference in body mass distribution leads to a difference in df between the front legs and hind legs. The front legs spend a longer time on the ground (see Thorup et al., 2007), as a result of a shorter t_{sw}'.

Does the (a)symmetry change during early gait development?

Symmetry is generally assumed to be a characteristic feature of normal and stable locomotion (Oosterlinck et al., 2010; Herzog et al., 1989; Jeleń et al., 2008; Budsberg et al., 1987; Besancon et al., 2004; Duberstein et al., 2014). Results obtained by Meijer et al. (2014) indicate a very high degree of symmetry in healthy adult pigs. This is in accordance with our findings. We note higher AIs at an early age (ages 0–6 h), and AIs that decrease with time, reaching a value of around 10% at the control age (similar to AIs in adult pigs; Meijer et al., 2014). This confirms our hypothesis that the variability of the gait pattern (described by means of the AIs) decreases with age, leading to a stable gait pattern a few hours after birth. Keeping in mind that the maximal value of the AI can be 200%, piglets show a high degree of symmetry. The remaining amount of asymmetry (±10%) may exist because a gait can never be

absolutely symmetric, as the body itself does not show perfect left–right symmetry (either anatomical or physiological). Furthermore, to maintain speed, direction and balance, adjustments need to be continuously made by the locomotory system. Even successive walking cycles will not be completely identical and a single trial will have two types of asymmetry: the inherent left–right asymmetry and asymmetry caused by the control system making adjustments (Crowe et al., 1996).

A difference between the front and hind legs was visible in the AI_{df}. The front legs showed a lower AI_{df} than hind legs, indicating that the time the front legs spend on the ground shows less overall variability than the time hind legs spend on the ground. As mentioned above, pigs show an unequal distribution of body mass, with the front limbs receiving higher peak vertical forces (Meijer et al., 2014). As such, the greater left–right symmetry of the front legs could play an important role in maintaining the overall balance of the animal while walking.

Conclusion

Normalization of the gait data is suggested as a method to distinguish neuromotor maturation from size effects and postural changes. Aside from the first hour, voluntary locomotion is dynamically similar during early gait development in piglets. As for interlimb coordination, this does not change at all during early gait development, implying this aspect of gait is innate for piglets. Intralimb coordination shows a very fast maturation process, as indicated by rapidly achieved steady values for swing and stance duration, as well as step length. The variability of the gait pattern, indicated by left–right asymmetry, decreases with age and leads to a stable gait pattern within 8 h of birth. This shows that coordinated movement patterns in pigs are not entirely innate, but that a rapid neuromotor maturation, potentially also the result of the rearrangement or recombination of existing motor modules, takes place in these precocial animals.

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