Terrestrial Locomotion in the Black-Billed Magpie. I. Spatio-Temporal Gait Characteristics

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Spatio-temporal gait characteristics are determined for walking, running, and out of phase hopping magpies, at velocities ranging from 0.4 to 4 m/s. Below 1 m/s, magpies walk. At higher velocities they either run or hop, the latter being preferred. Stride length and frequency during walking and running relate to speed in an identical way. It is suggested that the control of walking and running, despite the abrupt drop in duty factor and step length at the transition from walking to either running or hopping, is represented by one single intrinsic pattern. Swing phase duration is independent of speed and similar of the three gaits, pointing to a passive, mechanical control. Stride frequencies during hopping barely change with velocity, while its stride length relates to velocity in a way highly comparable to that of walking and running. Hopping step length and duty factor are indifferent from those of running. These facts, combined with the similar spatio-temporal behavior of both legs in hopping suggest fairly comparable intra-limb coordination for running and hopping, and a simple phase-shift in inter-limb coordination to transform a run into a hop.

Key Words: gait, terrestrial locomotion, magpie

Despite the dominance of flight, terrestrial locomotion fulfils an important role in the ecology of many bird species (for instance, to forage or to collect nesting material). Like mammals, birds may show several gaits when moving on the ground: They can walk, run, and/or hop, the latter in either a symmetrical or asymmetrical way (i.e., both legs moving respectively in or out of phase; Hayes & Alexander, 1983). However, not all of these gaits are used by each bird species. Some species only hop (e.g., zebra finch [Taenopygia guttata]; cf. Hayes & Alexander, 1983); others walk and hop (e.g., crow [Corvus corone corone]; own observations); others walk and run (e.g., chicken [Gallus domesticus]; cf. Muir et al., 1996; ostrich [Struthio camelus]; cf. Gatesy & Biewener, 1991). Only a few species seem to walk, run, and hop (e.g., magpie [Pica pica]; this study; blackbird [Turdus merula]; Clark, 1975; Kunkel, 1962).

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In an effort to gain insight in the mechanics and control of terrestrial locomotion in birds (and bipedal locomotion in general), the black-billed magpie was selected as the model species because it frequently uses the three gaits mentioned above. Apart from an essential descending higher level control, locomotor patterns and behavior can be assumed to be molded to a large extent by the intrinsic (physical) properties of the entire locomotor system (electro-physiological dynamics of the neuro-muscular component; mechanical dynamics of the musculo-skeletal component) and its interactions with the environment (e.g., Diedrich & Warren, 1995, 1998; Holt et al., 1990, 1991; Latash, 1998; Schöner et al., 1990; Stewart, 1995; Stewart & Golubitsky, 1992). Therefore, many aspects of control should be reflected in the spatio-temporal characteristics of the various gaits (e.g., Latash, 1998; Mcfadyen & Bélanger, 1997; Peck & Turvey, 1997; Van Damme et al., 1998; Zernicke & Smith, 1996). Studying spatio-temporal gait characteristics in magpies (e.g., stride frequency, stride and step length, duty factor, relative phase) as a function of locomotor speed can thus provide insight in the patterns of coordination and control of non-human bipedal locomotion, without the requirement of knowing the intricate details of the dynamics and laws of all underlying processes.

Material and Methods

Four wild and 3 domesticated black-billed magpies (*Pica pica*, L.) were filmed while moving in four different experimental set-ups. For 2 of the wild birds, recordings were made while they were foraging on a freshly cut grass field. The 2 other wild magpies moved spontaneously on the ground in a 6-m long outdoor aviary. The domesticated birds ran spontaneously on an indoor running track (4 m), and on an outdoor running track (6 m). For the first three experimental set-ups, sequences were recorded at 50 Hz (Panasonic WV-F15E), while for the last set-up, animals were videotaped at 500 Hz (NAC 1000). Based on the steadiness of the locomotor pattern, 33 useful walks, 15 runs, and 40 hops (out of phase) performed by the 7 birds were selected for further analysis. (Initially, treadmill experiments were performed, but the results had to be discarded because, even after a training period of several months, locomotion bouts were very irregular, highly unrepeatable, and the specimens tended to flap their wings.)

The velocity of the animals was calculated by determining the slope of the linear regression of the forward displacement of the eye against time. For the first experimental set-up, perspective corrections were carried out.) From the video recordings, the instants of first and last ground contact of individual feet were determined. These were used to calculate the following variables:

- stride frequency (SF = number of complete locomotor cycles over a period of time);
- stride length (SL = distance traveled by the center of mass during a complete cycle; velocity / stride frequency);
- step length (STL = displacement of the center of mass while a particular foot is on the ground; contact time × forward velocity);
- duty factor (DF = duration of ground contact for a foot as a fraction of the stride duration; contact time × stride frequency);
- relative phase (RP = time interval between first ground contact of the two
feet as a fraction of the stride duration; time interval between the first
ground contact of two feet × stride frequency);  
• swing phase duration (SPD duration of the period when a foot is off the
ground; stride duration − contact time);  
• swing phase length (SPL = distance traveled while a particular foot is off
the ground; swing phase duration × velocity);  
• floating distance (FD = displacement of the center of mass when no foot is
on the ground; only applicable for running and hopping);  

As all the animals used in this study were of similar size (tarsometatarsus
length of the 7 specimens ± SD: 0.46 ± 0.01 m; measured on the birds [5] and on
the video recordings [2]), scaling was not required to pool the data, and absolute
values could be used for velocity and the distances measured. (Where appropri-
ate for comparison with literature data, a hip height of 0.15 m [determined from
video-recordings at mid-stance; cf. Hayes & Alexander, 1983] must be used for
normalization.)

For this study, gaits are discerned on the basis of footfall patterns so that
they can be identified directly from the video recordings. Walking is defined as
the gait with a relative phase of 0.5 and a duty factor between 0.5 and 1.0 (i.e.,
with double support phases). For running, the relative phase equals 0.5, too, but
the duty factor is smaller than 0.5 (i.e., floating phases replace double support
phases). During hopping, the relative phase is smaller than 0.5. For this discus-
sion, it is important to mention that McMahon et al. (1987) and McMahon and
Cheng (1990) alternatively advocate the use of the pattern of energy fluctuations
of the center of mass to distinguish between walking and running gaits (i.e.,
potential vs kinetic energy out of phase: walking; in-phase: running), as this
“energy phase-shift” in some cases does not go along with the initiation of a
floating phase. This definition is retained in an important reference paper on bird
 locomotion by Gatesy and Biewener (1991; in general: Farley & Ferris, 1998;
Lee & Farley, 1998). Based on arguments from mathematical modeling (Alexan-
arbitrary set transition between walking and running at relative speeds (this is the
square root of the Froude number; see Alexander, 1977a, 1977b, 1992b; Hayes
& Alexander, 1983) between 0.6 and 0.8, assuming the presence of the just men-
tioned patterns of energy fluctuations, and irrespective the fact that in many cases
(especially for the small birds) duty factors during running are well above 0.5.
Where appropriate, we will refer to this difference in approach.

When the birds hop out of phase, the two feet are not set down simultane-
ously, nor next to each other. Thus, due to this asymmetry, a different function
might be present for both legs (see also Caldwell & Whitall, 1995; Minetti, 1998;
Peck & Turvey, 1997; Whitall & Caldwell, 1992). Therefore gait characteristics
are determined for the two legs separately. We refer further to the landing leg
(i.e., the leg first touching the ground after the floating phase, L) and the take-off
leg (i.e., the leg involved in take-off, T). Within a hopping bout, leg functions do
not change (cf. unilateral skipping according to Minetti, 1998).

To account for potential curvilinear relationships, linear regressions were
performed on log-log transformed data (SPSS for Windows) in order to express
the spatio-temporal gait characteristics as a function of the locomotor speed. The
power equations given in Table 1 are equivalent to the linear equations resulting
Figure 1 — Stride frequency as a function of velocity for walking (squares), running (triangles), and out of phase hopping (circles). Data for hopping represent the take-off leg.

Figure 2 — Stride length as a function of velocity for walking (squares), running (triangles), and out of phase hopping (circles). Data for hopping represent the take-off leg.
Figure 3 — Duty factor as a function of velocity for walking (squares), running (triangles), and out of phase hopping (circles). Data for hopping represent the take-off leg.

Figure 4 — Relative phase as a function of velocity for walking (squares), running (triangles), and out of phase hopping (circles). Data for hopping represent the take-off leg.
Figure 5 — Step length as a function of velocity for walking (squares), running (triangles), and out of phase hopping (circles). Data for hopping represent the take-off leg.

Figure 6 — Floating distance as a function of velocity for walking (squares), running (triangles), and out of phase hopping (circles).
from the regressions on the log-log transformed data. Slopes and intercepts of these linear regressions are compared between gaits or between the landing and take-off leg during hopping by means of an ANCOVA (SPSS for Windows). As we expressed the relationships in the form of the equivalent power equations, we refer to similarities in exponents and factors, respectively.

Results

Walking

At velocities below 1.0 m/s, the birds walk (measured range: 0.4–1.0 m/s). Figures 1–6 and Table 1 present the graphs and the equations for stride frequency, stride length, duty factor, relative phase, step length, and floating distance versus velocity. The constant relative phase of 0.5 (Figure 4) is caused by the coinciding decrease of the time interval between the touch down of the two feet, and the stride duration. The latter decrease (from 0.62 to 0.40 s) results from the shorter contact time (0.41 to 0.23 s), as the duration of the swing phase remains constant (±0.19 s). The distance traveled by the center of mass during the swing phase increases (from 0.08 to 0.17 m) with increasing velocity.

Running

At a velocity of 1.0 m/s, a gait transition occurs. The birds start either to run or to hop. Running velocities between 1.0 and 2.2 m/s could be measured. In Figures 1–6 and in Table 1, stride frequency, stride length, duty factor, relative phase, step length, and floating distance are expressed as a function of velocity. As with increasing velocity, the contact time and the stride duration decrease at almost the same rate, the duty factor is constant (0.39, Figure 3). The time needed to swing the leg forward remains constant (about 0.2 s), while the distance traveled by the center of mass during this phase increases (from 0.23 to 0.37 m).

Out of Phase Hopping

Out of phase hopping was observed at velocities ranging from 1.0 to 3.77 m/s. In their relationship with speed, only the factors of the power equations (equivalent to the intercepts of the log-log regressions) representing duty factor \( F_{1,77} = 7.32, p = .008 \), swing phase duration \( F_{1,77} = 7.80, p = .007 \), and swing phase length \( F_{1,77} = 7.80, p = .007 \) against speed, show small differences between the landing and the take-off leg. However, despite the statistical difference, the magnitudes of these factors are very similar in these three cases (see Table 1).

Figures 1–6 and Table 1 present the graphs and the equations for stride frequency, stride length, duty factor, relative phase, step length, and floating distance versus velocity. With increasing velocity, the contact time and the time interval between the touch down of the feet decrease faster than the stride duration, thus the duty factor (Figure 3) and the relative phase (Figure 4) both decrease. The swing phase duration remains constant when magpies hop faster, but the distance traveled by the center of mass during this phase increases.
Table 1  Power Equations Relating Gait Characteristics to Velocity

<table>
<thead>
<tr>
<th></th>
<th>Walking</th>
<th></th>
<th>Running</th>
<th></th>
<th>Hopping</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>SF</td>
<td>2.51 $v^{0.48}$</td>
<td>0.47</td>
<td>2.63 $v^{0.41}$</td>
<td>0.34</td>
<td>L</td>
<td>2.91 $v^{0.08}$</td>
</tr>
<tr>
<td></td>
<td>T</td>
<td>2.96 $v^{0.08}$</td>
<td>0.14</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>SL</td>
<td>0.40 $v^{0.52}$</td>
<td>0.51</td>
<td>0.38 $v^{0.59}$</td>
<td>0.52</td>
<td>L</td>
<td>0.34 $v^{0.92}$</td>
</tr>
<tr>
<td></td>
<td>T</td>
<td>0.34 $v^{0.92}$</td>
<td>0.95</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DF</td>
<td>0.57 $v^{-0.16}$</td>
<td>0.22</td>
<td>0.39 $v^{-0.03}$</td>
<td>0.00</td>
<td>L</td>
<td>0.40 $v^{-0.27}$</td>
</tr>
<tr>
<td></td>
<td>T</td>
<td>0.44 $v^{-0.28}$</td>
<td>0.46</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>STL</td>
<td>0.23 $v^{0.36}$</td>
<td>0.32</td>
<td>0.15 $v^{0.56}$</td>
<td>0.39</td>
<td>L</td>
<td>0.14 $v^{0.65}$</td>
</tr>
<tr>
<td></td>
<td>T</td>
<td>0.15 $v^{0.64}$</td>
<td>0.72</td>
<td></td>
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</tr>
<tr>
<td>SPD</td>
<td>0.17 $v^{-0.23}$</td>
<td>0.08</td>
<td>0.23 $v^{-0.39}$</td>
<td>0.15</td>
<td>L</td>
<td>0.20 $v^{0.86}$</td>
</tr>
<tr>
<td></td>
<td>T</td>
<td>0.19 $v^{0.87}$</td>
<td>0.09</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SPL</td>
<td>0.17 $v^{0.77}$</td>
<td>0.49</td>
<td>0.23 $v^{0.61}$</td>
<td>0.31</td>
<td>L</td>
<td>0.20 $v^{1.05}$</td>
</tr>
<tr>
<td></td>
<td>T</td>
<td>0.19 $v^{1.07}$</td>
<td>0.95</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FD</td>
<td>na</td>
<td>0.00</td>
<td>0.03 $v^{0.76}$</td>
<td>0.02</td>
<td>na</td>
<td>0.08 $v^{1.52}$</td>
</tr>
<tr>
<td>RP</td>
<td>0.50 $v^{-0.01}$</td>
<td>0.00</td>
<td>0.45 $v^{0.11}$</td>
<td>0.05</td>
<td>na</td>
<td>0.31 $v^{-0.47}$</td>
</tr>
</tbody>
</table>

Note: DF, duty factor; FD, floating distance; L, landing leg; RP, relative phase; SF, stride frequency; SL, stride length; SPD, swing phase duration; SPL, swing phase length; STL, step length; T, take-off leg; v, velocity.

Exponents of bolded equations not signif. diff. from zero ($p > .05$, i.e., no signif. correlation with velocity). Equations in italics represent cases where the exponent does not differ significantly from 1 ($p > .05$, i.e., linear relationship with velocity present).

Discussion

In 1983, Hayes and Alexander already presented gait variables for hopping corvids, including the magpie. However, only a limited number of walking cycles (4) and hops (8) of presumably one single specimen of the latter species was incorporated in their study. The present paper provides an extended sample of spatio-temporal gait characteristics, covering a larger velocity range and including the three observed gaits. Thus, the description is completed (i.e., running added) and more definite relations with speed during unrestrained voluntary locomotion are established. In the context of the “hybrid” dynamic pattern approach to locomotion (cf. Latash, 1998, p. 178), this intentional speed can probably be considered as the basic control variable (in the form of a simple, graded, higher level feed forward command; e.g., Grillner, 1985; Jacobson & Hollyday, 1982; Latash, 1998; McMahon, 1984), being essential in the initiation and maintenance of locomotor activity. According to this (“hybrid”) dynamic approach however, the actual pattern of the limb cycles will arise a great deal from the intrinsic (physical) properties of the entire locomotor system (electro-physiological dynamics of the neuro-muscular component; mechanical dynamics of the musculoskeletal system) and its interaction with the environment (Kugler & Turvey, 1987; Latash, 1998; see the introduction). This leads automatically to a stable behavior of the
locomotor apparatus. From this point of view, a substantial component of locomotor control might be embedded in the design of the organism itself (cf. Full & Kubow, 1998). Spatio-temporal gait characteristics are robust and easily accessible exponents of the locomotor behavior, reflecting the interaction between the independent descending signal and the self-organizing system.

The manner in which stride frequency and length relate to speed is fairly identical in case of walking and running. The curves representing these relationships for running in Figures 1 and 2 neatly extend those established for walking, as also evidenced by the exponents and factors of the power equations presented in Table 1, which do not statistically differ from each other (stride frequency exponent: $F_{1,44} = 0.15, p = .698$ and factor: $F_{1,45} = 0.14, p = .708$; stride length exponent: $F_{1,44} = 0.16, p = .694$ and factor: $F_{1,45} = 0.13, p = .715$). Contrary to other small birds (Gatesy & Biewener, 1991), magpies increase stride length more than stride frequency when walking or running faster (cf. higher exponents for stride length than for frequency in Table 1). Perhaps this discrepancy originates from differences in leg morphology between magpies and the galliforms making up the group of “small birds” in the study by Gatesy and Biewener (1991).

The relationship between frequency and speed changes drastically however when hopping is considered. Hopping faster is almost entirely due to an increase in stride length (Figures 1 and 2; see also the small velocity exponents for hopping in Table 1), whereby the graphical representation (Figure 2) suggests that hopping stride lengths are not very different from running strides (compare triangles and circles). This confirms the results by Hayes and Alexander (1983), who reported a frequency for hopping magpies “more or less independent” of speed (3.3 Hz).

A similar constancy of frequency is observed in human bilateral and unilateral skipping (Minetti, 1998). The latter gait (described as bipedal galloping by Caldwell & Whitall, 1995; Peck & Turvey, 1997; Whitall & Caldwell, 1992) is entirely analogous to corvid hopping. In-phase hopping by humans also shows a frequency that is constant over a range of speeds (Farley et al., 1991; Taylor, 1985). The same holds true for trotting and hopping mammals (Dawson & Taylor, 1973; Farley et al., 1993). It has been suggested that the (nearly) constant hopping frequency reflects the forward bouncing of a simple spring-mass system (e.g., Farley et al., 1991, 1993; McMahon, 1984; Taylor, 1985). However, since the frequency set by the mass and the spring constant refer to the time of ground contact only, the rationale of this analogy is not directly evident to date. (Recall that the time of ground contact [duty factor/frequency] in hopping magpies decrease significantly with speed.) Moreover, the importance of elastic recoil in terrestrial locomotion of magpies is questionable because of the many tendon oscifications (Verstappen et al., 1998) and the small size of the birds (cf. the high stiffnesses of the leg tendons of small bipedal mammals; Biewener et al., 1981; Heglund et al., 1982; Van Leeuwen, 1992).

When magpies hop faster, the relative phase of the footfalls becomes smaller (cf. the negative exponents of the power equations defining the relation between the relative phase and velocity in Table 1). This is also observed in galloping humans [reference to oral paper by Whitall & Clark, 1986, in Peck & Turvey, 1997]. From the present power equations for hopping (relative phase/ frequency; see Table 1) it is calculated that, even at the highest recorded hopping speeds, the difference in footfall is practically no longer detectable with the
naked eye (<50 ms). This explains why field observations suggest in-phase hopping at very high velocities. The observed decrease of the relative phase contrasts with the theoretical deductions and simulations carried out in the framework of the dynamic approach to locomotion by Peck and Turvey (1997), where the relative phase of bipedal galloping (hopping) appears as an attractor (next to jumping and running) in the behavioral phase-space of two coupled oscillators.

Apart from the phase difference (temporal separation), hopping magpies also place one foot ahead of the other at ground contact (spatial separation: stagger; cf. Hayes & Alexander, 1983). Measured directly on the video recordings, stagger is found constant (0.14 m; see also Hayes & Alexander, 1983). This suggests that during hopping the precise initial placement of the feet relative to each other (and most likely relative to the center of mass of the body too; cf. Verstappen et al., 1998) is rather critical for proper performance. Based on angular leg excursions of running birds, Gatesy and Biewener (1991) came to the same conclusion.

During a locomotion cycle, a single leg alternates between stance and swing (recovery). It is remarkable that the absolute duration of the swing phase (in seconds) is independent of locomotor speed over the different gaits (see Table 1: SPD about 0.20 s), despite the decrease of the cycle duration (at least in walking and running). This points at a passive pendulum-like and/or spring-driven leg protraction mechanism. Roberts et al. (1997) were able to show that, in the turkey, leg protraction relies almost entirely on the passive spring-like behavior of the muscles indeed. Also walking and trotting cats and dogs show nearly constant swing times (Arshavsky et al., 1965; McMahon, 1984), but in walking humans swing times slightly decrease with higher speeds (e.g., Gatesy & Biewener, 1991; Nilsson & Thorstensson, 1987; Rosenrot et al., 1980), but are definitely below the half-period of the leg acting as a passive pendulum (i.e., additional muscle action is needed to protract the leg fast enough; McMahon, 1984). Maybe, only animals with less massive legs (like birds and cats) can rely on a passive recoil of muscle-tendon systems for recovery, as the period (i.e., swing duration) of such systems is proportional to the mass of the leg.

A consequence of the constant swing time is the reduction of stance time when the cycling frequency (hence the speed) increases (Arshavsky et al., 1965; McMahon, 1984). This is not necessarily linked to a comparable decrease in duty factor (stance time × frequency) because frequency will be affected by the duration of the double stance period in walking and the duration of the floating phase in running and hopping, too (Figure 6). At a speed of about 1 m/s the duty factor abruptly falls to about 0.39 (walk-run/hop transition) and remains fairly constant at the higher speeds (especially in running; see Table 1: DF independent of speed). Neither the stepwise change, nor the constancy at running speeds are observed in the walking and running birds studied by Gatesy and Biewener (1991) or Muir et al. (1996). The walk-run transition in humans however does show the sudden drop in duty factor as it is presently found for the magpies (Alexander, 1989, 1992a, 1992b; Bennett, 1992; Farley & Ferris, 1998; Gatesy & Biewener, 1991; Lee & Farley, 1998).

Magpies increase step length when walking faster. Coincident with the sudden drop in duty factor at transition, the step length abruptly falls to about 0.15 m (see Figure 5) to increase again when hopping or running faster. It is remarkable that none of the birds studied by Gatesy and Biewener (1991) show
this sudden drop in step length (nor in duty factor; see above), whereas for the walk-run transition in humans such a drop is definitely present (Gatesy & Biewener, 1991). Based on this, it was concluded that birds change the kinematics of locomotion less dramatically at the walk-run transition than humans do (Lee & Farley, 1998). The present data suggest that this cannot be generalized to all birds.

The above mentioned facts can be combined in the next interpretation of the walk-run transition. Whenever during the usual course of a step, the body is launched into a floating phase, a coincident step-wise change of both step length and duty factor must occur, since the normal displacement of the center of mass during stance (step length) and the contact time are interrupted. Such a floating phase can be initiated when gravity can no longer counter the centrifugal forces of the body vaulting over the stance leg (i.e., "stiff leg" walking of the inverted pendulum paradigm; e.g., Alexander, 1992a, 1992c; Farley & Ferris, 1998), and/or if the velocity of leg extension (in a compliant walk) during the second half of the stance suddenly drops so that early lift off can occur. Recall that, in reality, legs in walking birds (e.g., Cracraft, 1971; Dagg, 1977a, 1977b; Gatesy & Biewener, 1991) and humans (Lee & Farley, 1998) do not behave like rigid struts but do show a flexion-extension cycle (which in humans is velocity dependent) during the walking stance. From this point of view, transition to running is inevitable when a threshold walking speed is reached.

It is conceivable that just after this transition, upon touch down for the next running step, the dynamic constraints of the system are changed (e.g. altered landing configuration; higher touch down speed), which automatically leads to an altered kinematic behavior of the system without a necessary adjustment of the basic control (cf. dynamic equilibrium approach to locomotion; Diedrich & Warren, 1995; Latash, 1998; Peck & Turvey, 1997). In humans, the transition (and thus the sudden drop in step length and duty factor) is further characterized by a stepwise change of stride frequency and stride length (Diedrich & Warren, 1995; Minetti et al., 1994). This does not occur in the magpie (see above; Figures 1 & 2). Together with the fact that the floating distances during running remain very small, this suggests that, at transition, no drastic dynamic changes occur. From the control point of view, running in magpies might well be an overpowered style of walking (i.e., "walking" above the threshold speed where floating phases are inevitable), thus emerging as an alternative for hopping at the higher speeds. (Peck and Turvey, 1997, also consider the walk-run as one identical intrinsic pattern.)

As mentioned, running and hopping are alternatives for fast terrestrial locomotion in magpies, with a clear preference for hopping. It is remarkable that, in humans, a similar hopping gait (i.e., skipping according to Minetti, 1998; bipedal galloping according to Caldwell & Whitall, 1995; Peck & Turvey, 1997; Whitall & Caldwell, 1992) may show up as an alternative for the preferred running gait (see also Farley & Ferris, 1998), especially in younger children. In adults, the automatic expression of this gait seems dismissed (too costly; see Minetti, 1998), but it can readily be reproduced in a stable and highly reproducible way (Caldwell & Whitall, 1995; Minetti, 1998; Whitall & Caldwell, 1992). It is concluded that the neuro-muscular organization of human bipedal hopping is rather similar to that of running (Caldwell & Whitall, 1995; Whitall & Caldwell, 1992), and Peck and Turvey (1997) argue that bipedal galloping is
characterized by a relatively stable coordination, derived directly from the walk-run pattern by a shift in the communication between the oscillating limbs. Based on other arguments, Minetti (1998) suggests that galloping (skipping) might originate when the pattern of walking persists beyond a certain threshold speed (induction of a floating phase). Judging (a) the similar duty factors (exponent: $F_{1,51} = 1.43$, $p = .237$ and factor: $F_{1,52} = 2.44$, $p = .124$) and step lengths (exponent: $F_{1,51} = 0.15$, $p = .701$ and factor: $F_{1,52} = 0.27$, $p = .607$) for running and hopping in magpies (Figures 3 and 5, Table I), and (b) the very similar gait characteristics of the landing and take-off leg in hopping (only intercept for duty factor and swing phase differ, but differences are minimal; see the Results section and Table 1), the intra-limb coordination must be fairly comparable between both gaits as well. Thus, a simple phase-shift in the inter-limb coordination could transform a run into a hop.

If the above deductions are correct, it seems that no intricate shifts in control and coordination are required for gait transitions in magpies. Running emerges from “overpowered” walking (see above), and hopping is like running with a reduced phase difference between the limb oscillators. This suits the hypothesis by Minetti (1998) that human skipping arises from a too fast walk and that galloping in quadrupeds might have evolved directly from walking. Two questions remain, however. What triggers whether a bird will either run or hop? Why is running preferred by man, while magpies favor hopping for fast locomotion? In humans, bipedal galloping is a playful behavior of children and can intentionally be reproduced by adults. However, under some circumstances, like fast descending or turning corners, it still arises spontaneously (cf. Minetti, 1998). In the context of the dynamic approach to locomotion (Kugler & Turvey, 1987; Latash, 1998), it is likely that the typical running pattern becomes temporarily unstable under such circumstances, prompting the control automatically to the skipping attractor in the behavioral space of the coupled oscillators of the legs (cf. Kugler & Turvey, 1987; Peck & Turvey, 1997). But, in the magpie, hopping and running appear under identical conditions (level, straightforward locomotion), with a preference for hopping. In the light of the same theory, it can be postulated that the intrinsic features of the bird’s build (e.g., body proportions) normally evoke the hopping gait at speeds above walking but that subtle changes in the initial state of the neuro-muscular construct (e.g., posture) are sufficient to shift the point at which the walk-run coordination becomes unstable towards higher speeds. For a better understanding, more information on the detailed kinematics and kinetics of magpie locomotion is needed.

References


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