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CONSTRAINED AND FLEXIBLE FEATURES OF RHYTHMICAL HINDLIMB MOVEMENTS IN CHICKS: KINEMATIC PROFILES OF WALKING, SWIMMING AND AIRSTEPPING

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Summary

Although studies of walking have generated many of the principles for motor control, walking is but one of the many behaviors that an animal produces. This study investigates the relationships among the kinematic profiles of three behaviors in chicks: walking, swimming and airstepping. In addition to describing features of the hindlimb movements, such as retraction and protraction, we also examined the intra- and interjoint coordination patterns at the hip, knee and ankle. By using multiple levels of analysis, we identified some features that are common to all three behaviors, and therefore appear to be constrained, as well as some dissimilar or flexible features. Specifically, we show that resistance differentially affects the hip, knee and ankle joints. Our results also show that each joint plays a distinctive role in these behaviors. For example, we suggest that the hip stabilizes the hindlimb and regulates the rhythmicity of its movements. We also show that movement at the knee consistently precedes movement at the other joints in each behavior. Finally, differences in ankle movements are the key features that discriminate one behavior from another. Continuity among prenatal, perinatal and postnatal behaviors in chicks is discussed.

Introduction

A complete understanding of the neural basis for behavior requires an appreciation not only of the underlying neural activity but also of the form and temporal characteristics of the behavior under study. Comparative analyses can be found in evolutionary studies of locomotion (Gatesy, 1990; Gatesy and Biewener, 1991; Ashley-Ross, 1991; for a review, see Lauder, 1986) as well as in studies examining the relationships between the energetics and mechanics of terrestial locomotion (e.g. Taylor *et al.* 1982; Fedak *et al.* 1982; Heglund *et al.* 1982*a*,*b*, 1988; Heglund and Taylor, 1988). However, because a single species typically shows a diverse repertoire of behaviors, it is also of interest to examine the relationships

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among these different behaviors. Components of the behavioral profiles may be constrained by neural and/or non-neural mechanisms. Other components may be more flexible and reflect the context in which the behavior occurs. By differentiating between constrained and flexible elements, comparative analyses of the different behaviors produced by a particular species can provide significant insights into the mechanisms involved in their production.

At present, a great deal is known about the kinematics and neural control of several individual behaviors involving rhythmic leg movements in vertebrates (for reviews, see Grillner, 1981; Grillner and Wallén, 1985). For example, stepping has been examined at many levels, ranging from functional morphology (e.g. Cracraft, 1971; Goslow *et al.* 1973; Gatesy, 1989) and intersegmental dynamics (Hoy and Zernicke, 1985) to modulation of the underlying neural networks (for reviews, see Grillner and Wallén, 1985; Rossignol *et al.* 1988; Sigvardt, 1989). In contrast, there are still relatively few studies of vertebrates in which detailed comparisons of the neural activity involved in different behaviors have been made (e.g. cats: Berkinblit *et al.* 1978*a*,*b*; Smith, 1986; Abraham and Loeb, 1985; Bradley and Smith, 1988; rats: Gruner and Altman, 1980; Yakhnitsa *et al.* 1985*a*; chicks: Bekoff, 1986*a*,*b*; Bekoff *et al.* 1987*a*,*b*; Johnston and Bekoff, 1988, 1989; turtles: Lennard and Stein, 1977; Robertson *et al.* 1985; Stein *et al.* 1986; fish: Reilly and Lauder, 1989). Even fewer comparative studies have included kinematic analyses (Gruner and Altman, 1980; Mortin *et al.* 1985; Yakhnitsa *et al.* 1985*b*; Bekoff, 1988).

Chicks are ideal subjects for comparative analyses of leg motor patterns because they produce a large repertoire of behaviors that include leg movements as a significant component. For example, chicks use their legs in such diverse behaviors as hatching, walking, swimming, airstepping, foot shaking and head scratching. These behaviors can be categorized according to function such as escape from the egg, locomotion or removal of an irritant from the body. In this study we analyzed the kinematics of the right leg during three behaviors: walking, airstepping and swimming. These behaviors were chosen because they appear to be closely related in both form and function. That is, they all involve bilaterally alternating leg movements and they are all forward-directed locomotor, or locomotor-like, behaviors.

Despite these similarities, the three behaviors differ in several ways. In walking, each leg alternates between a period of weight support during which it is in contact with a solid substratum and a period during which it moves unimpeded through the air. Airstepping occurs in a continuous medium of air, without the resistance that would be provided by substratum contact. Swimming is similar to airstepping in that substratum contact is absent. However, swimming differs from both walking and airstepping in that water provides resistance throughout the leg movements.

By analyzing the kinematic profiles in these three behaviors we hope to determine the degree of heterogeneity in limb movements during different chick behaviors. Because there is considerable evidence suggesting that there are separate pattern-generating circuits controlling each limb in vertebrates (for a review, see Grillner and Wallén, 1985), focusing on a single leg is a reasonable way to simplify the analysis. We examined the different roles played by the three major joints of the hindlimb: hip, knee and ankle. Our comparative analyses reveal some kinematic features that are consistent among the three behaviors. We suggest that these represent constrained features that may be common to all locomotor behaviors. In addition, we found other features that vary among the behaviors and therefore may represent flexible features that are modified by sensory information due to resistance as a result of different media or weight support. A preliminary account of some of these results has appeared (Johnston and Bekoff, 1987).

Materials and methods

Animal preparation

Fertile White Leghorn hybrid chicken eggs were incubated under standard conditions (Bekoff, 1976). After hatching, chicks were maintained in heated chambers and provided with food and water *ad libitum*. Chicks were selected for this study based on their ability to initiate walking in response to finger tapping by the experimenter. Chicks between the ages of zero and five days post-hatching were used in this study. Each chick was anesthetized with halothane and maintained on a respirator throughout the preparation procedure. The primary feathers on the right wing were trimmed because they obscured our view of the knee; the primary feathers on the left wing were also trimmed to maintain symmetry (Cracraft, 1971). The feathers on the right hindlimb were trimmed to increase visibility of the small dots of black indelible ink that were placed on the skin. A dot was placed overlying each of the following bony landmarks of the lateral surface of the hindlimb: anterior and posterior synsacrum, the proximal and distal ends of the femur, distal end of the tibiotarsus and the midpoint of the tarsometatarsal segment. Together these points demarcate the hindlimb and its hip, knee and ankle joints (Fig. 1). Movement of the skin overlying the distal end of the femur prevents accurate determination of the knee joint from the joint markers in birds (Cracraft, 1971; Jacobson and Hollyday, 1982*a*) and cats (Goslow *et al.* 1973; Wetzel *et al.* 1975; Hoy *et al.* 1985; Halbertsma, 1983). Therefore, to ensure correspondence between the position of the joint marker and the actual location of the knee, the skin overlying the knee joint was sutured to the underlying cartilage on the lateral surface of the distal end of the femur (Grillner and Rossignol, 1978). The chicks were allowed to recover for 24 h before video recordings were made.

Video recordings

Chicks were enticed to walk along a runway perpendicular to the video camera by tapping on the opposite end of the runway. Chicks and other birds (Kruijt, 1964) naturally locomote at a variety of speeds. To mimic the natural performance of walking in the laboratory setting, we did not restrict the speed at which the chick moved along the runway. Although the distinction between walking and running

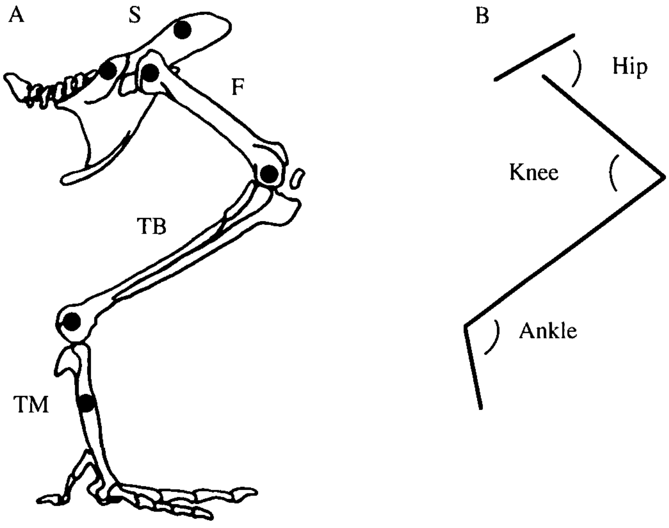

Fig. 1. (A) Diagram of the right hindlimb and pelvic skeleton of a post-hatching chick. Dots represent ink marks placed on the skin overlying bony landmarks of the lateral surface of the hindlimb: anterior and posterior synsacrum (S), the proximal and distal ends of the femur (F), distal end of the tibiotarsus (TB) and the midpoint of the tarsometatarsal (TM) segment. (B) The stick figure illustrates how the digitized x- and y-coordinates of these points demarcate the hindlimb and its hip, knee and ankle joints.

in birds can be made on the basis of energetics (Cavagna *et al.* 1977), we chose to refer to the entire range of this mode of locomotion as 'walking'. This is justified by our results, which failed to show any discontinuities as speed increased. For example, the relative onset times for extension and flexion (i.e. phase) remain constant over the entire range of cycle durations (see *Interjoint coordination* in Results). Furthermore, we did not use our results for duty factor (see Results) as an indicator of the walk–run transition, because Gatesy and Biewener (1991) state that footfall pattern alone is insufficient to define a running gait in small terrestial birds without information regarding fluctuations in the center of mass.

Swimming behavior was observed when the chick was placed in a Plexiglas tank of water (38–40°C). Chicks are buoyant and capable of propelling themselves through the water quite well. However, to keep the right hindlimb perpendicular to the camera (see *Video analysis*), a flexible, plastic-coated wire was glued to the skin overlying the synsacrum and used to hold the chick as it swam in place. The chicks showed no evidence of discomfort when restrained in this manner or when suspended as in airstepping. This method does not distort the joint markers on the back or the hip because the skin, to which the wire was glued, is firmly attached to the underlying synsacrum. Furthermore, the morphology of the synsacrum prevents dorsal, ventral or lateral flexion movements (Raikow, 1985; Young, 1981). Preliminary data analysis showed no statistical difference between stationary and unrestrained swimming.

Airstepping behavior was observed when the chick was suspended with its hindlimbs pendent. Each chick was suspended by a plastic-coated wire glued to its back as outlined above for swimming.

Following each recording, the chicks were killed with carbon dioxide as recommended by the Panel on Euthanasia of the American Veterinary Medicine Association (1978). A *post-mortem* dissection of the knee was performed to determine that the skin had remained anchored to the underlying cartilage at the head of the femur and that the suture had not disturbed the surrounding tissues.

We also made video recordings of the hindlimb movements while we manually manipulated the right leg to determine the potential range of motion for each joint. The potential ranges of the hip, knee and ankle joints were determined from digitized video recordings of manually manipulated hindlimb movements on two awake chicks and on two freshly killed chicks.

Video analysis

Periods of uninterrupted movement were selected for analysis. Neither initial movements nor stopping movements were considered in our analyses. Videotapes were replayed onto a monitor interfaced with a computer and the x- and y-coordinates of each joint marker were digitized in contiguous fields (one field=16.7 ms). Stick figure representations of the right hindlimb were generated from the coordinates digitized in each field. In addition, joint angles and segment lengths for each stick figure were measured. A major assumption of the trigonometric method used to calculate the joint angles is that the hindlimb remains planar. The accuracy of the calculated joint angles is diminished when the hindlimb deviates from the plane parallel to the camera lens. Anatomical specializations, primarily at the hip, limit abduction, adduction and rotational movements of the hindlimb and restrict movements of the hip, knee and ankle joints mainly to their parasagittal planes (Raikow, 1985; Young, 1981). Thus, the hindlimb remains roughly parallel to the plane of the camera lens throughout the performance of these three behaviors. Movements may occur out of this plane as a result of small mediolateral rotations possible at the knee (Young, 1981; Gatesy, 1989) or if the chick either deviates from its initial path in walking or sways from side to side in swimming or airstepping. To meet the assumption for accurate joint angle calculations, we analyzed only those cycles that remained reasonably planar. This was determined from the difference between segment lengths measured during rest and those calculated in each video field during hindlimb movements (Hoy *et al.* 1985). None of our data exceeded a 6 % maximum discrepancy in segment lengths.

Definition of variables

Movements of the hip, knee and ankle joints were examined and classified as either *extension*, an increase in joint angle, or *flexion*, a decrease in joint angle. A movement *cycle* was defined from the onset of ankle extension to the onset of the next ankle extension. Because swimming and airstepping lack a period of contact with the ground (i.e. stance), we could not use either Philippson's (1905) or Jacobson and Hollyday's (1982*a*) method to define movements in these behaviors. Therefore, we defined a movement cycle without referencing stance. Within each cycle we quantified the *durations* of flexion and extension at each joint. Our approach simplifies the movements, but does not compromise the details of the intra- and interjoint patterns in different behaviors. To quantify whether the onsets of flexion and extension occurred synchronously among the joints, the *latency* to flexion and extension with respect to the beginning of the cycle (onset of ankle extension) was calculated for each joint. Both duration and latency were also expressed as proportions of the cycle duration to define *normal duration* and *phase*, respectively.

In addition, we described the position of the entire hindlimb during each cycle based on retraction and protraction. In each behavior, a cycle contains one retraction period and two protraction periods: protractions 1 and 2. *Retraction* is defined from the onset of hip extension to the onset of hip flexion, which marks the beginning of the first period of protraction. *Protraction 1* lasts until the onset of knee extension which corresponds to the beginning of the second period of protraction. *Protraction 2* continues until the hindlimb begins the next retraction period.

In walking, we also quantified the durations of stance and swing. *Stance* is the portion of the walking cycle in which the foot maintains contact with the ground; *swing* is the portion of the cycle in which the foot is not in contact with the ground. Note that where we refer to swing flexion (or swing extension) for a particular joint, we mean the portion of swing during which that joint is flexing (or extending).

Experimental design and statistical analyses

Our sample size consisted of 10 chicks per behavior with 10 separate measurements per chick. Based on preliminary data, we calculated that this sample size would detect true differences, if they existed, in a two-level nested design (Sokal and Rohlf, 1981; Machlis *et al.* 1985). A critical level of $P<0.05$ and two-tailed probabilities were used to determine statistical significance throughout this study. We used correlation analysis to measure the interdependence between specific pairs of variables. Because we wished to describe functional relationships between specific pairs of dependent variables we calculated Model II regressions (Sokal and Rohlf, 1981). Also, we compared sample means within and among behaviors using analysis of variance (ANOVA). The assumptions for these statistical procedures were satisfied. Because we tested multiple hypotheses, two conservative precautions were taken to guarantee that the family comparison error rate would not exceed the critical value of 0.05 (Wilkinson, 1989). First, the significance of Pearson's correlation coefficients (r) was determined from Bonferroni probabilities. Second, Tukey's HSD tests were used for *post hoc* multiple comparisons in ANOVA. Comparisons among correlations were calculated according to procedures presented in Sokal and Rohlf (1981).

In addition to these tests, we also used discriminant function analysis, which views each behavior as a composite of several interrelated variables. Discriminant function was the appropriate statistical tool to determine which variables contribute most to differentiating among these behaviors. A cross-validation approach was used to avoid overestimating the behavioral classifications (Wilkinson, 1989). Complementary variables (e.g. normal durations of flexion and extension) were not included in the same discriminant function. Instead, groups of non-complementary variables were used to discriminate among these three behaviors.

Results

Hindlimb movements

Walking

During a step cycle in walking (Fig. 2A) each hindlimb flexes and extends in three sequential periods: swing flexion, swing extension and stance. These movements refer to the hindlimb as a whole and have been described previously in birds by Jacobson and Hollyday (1982*a*). In general, our description of the hindlimb movements is similar to theirs as well as to descriptions of walking in other birds including pigeons (Cracraft, 1971; Clark and Alexander, 1975) and guinea fowl (Gatesy, 1989). Swing begins when the chick's foot is removed from contact with the ground and the hip, knee and ankle flex as the hindlimb is pulled up towards the body. Next, each joint extends, moving the hindlimb rostrally. As ground contact is made, swing is terminated and stance begins. The joint movements are more complex in stance than in swing (Fig. 2C). The hip shows a gradual extension ($\leqslant 15°$) throughout stance while the knee gradually flexes. The ankle shows a brief flexion ($\leqslant 10°$) at the onset of stance, and then remains extended at a constant angle until just prior to the onset of swing; then the ankle shows a brief extension ($\leqslant 10°$) at the termination of stance. We observed both of these brief ankle movements in all cycles. Gatesy (1989), using cineradiographic methods, reported similar brief excursions for running in the guinea fowl. Therefore, we believe these small movements are not artifacts.

In walking, the mean cycle duration is 353±97 ms. Duty factors describe the proportion of a cycle during which the foot maintains contact with the ground. Because the right and left hindlimbs alternate, the duty factor for one hindlimb also describes the other hindlimb. Thus, duty factors less than 0.50 indicate that there is an aerial phase within the cycle when neither foot contacts the ground; duty factors greater than 0.50 describe cycles with periods of double support during which both feet are in contact with the ground. Our data show a duty factor of 0.52 for the average cycle, indicating a period of double support in walking (McMahon, 1985). For cycle durations less than 330 ms, we observed an aerial phase. Throughout the remainder of the cycle duration range (330–735 ms) we observed periods of double support. Duty factors calculated from Jacobson and Hollyday's (1982*a*) data do not indicate an aerial phase; however, their range of

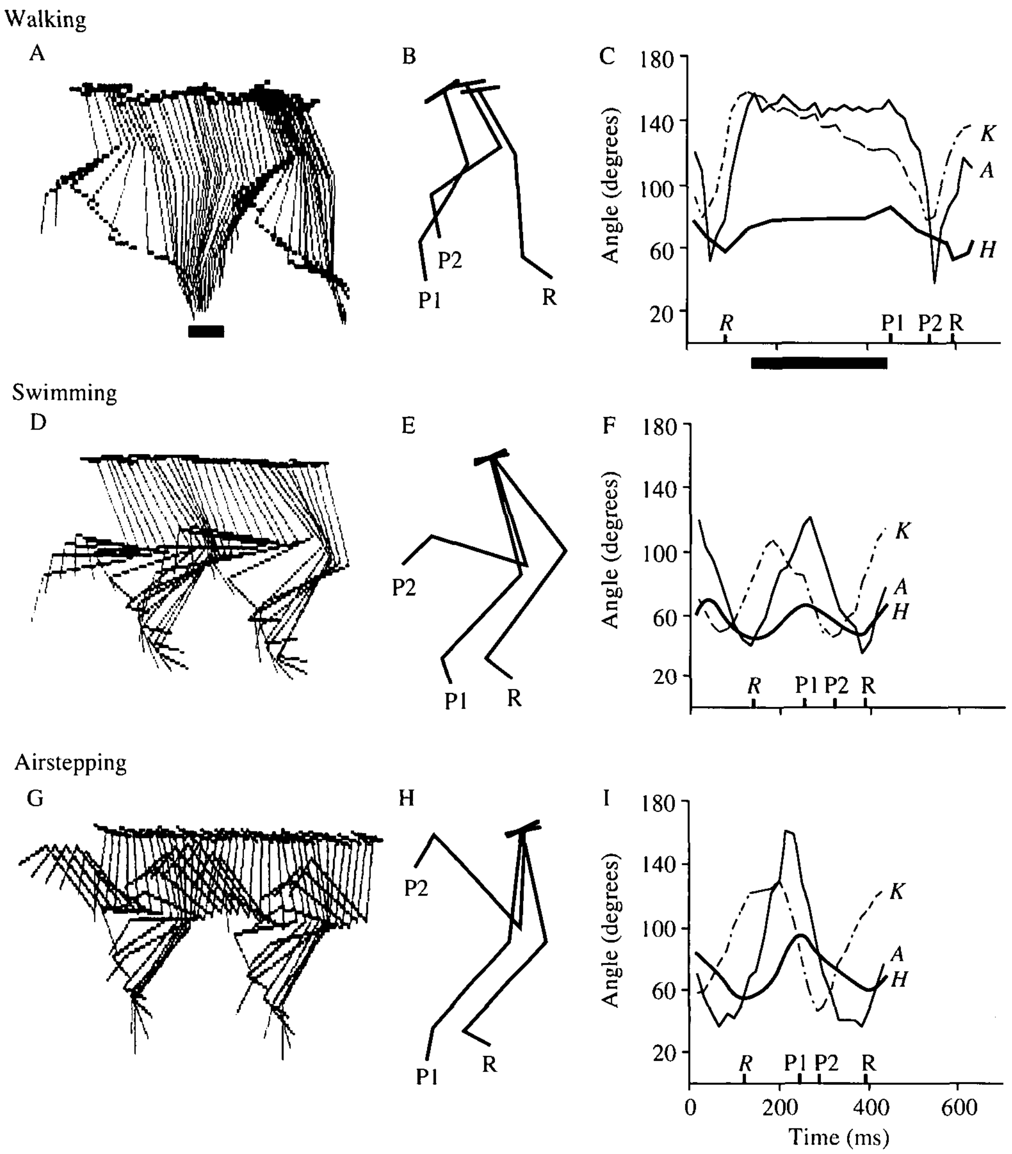

Fig. 2. Stick figure representations of right hindlimb movements in contiguous video fields during walking (A), swimming (D) and airstepping (G). Movement occurs from left to right in each behavior. The middle panel shows only the sticks that correspond to the onset of protraction 1 (P1), protraction 2 (P2) and retraction (R) of the hindlimb. The joint angles corresponding to the stick figures are shown in the panels on the right (C, F and I). Plotted against time, the hip (*H*), knee (*K*) and ankle (*A*) joints show increases (extension) and decreases (flexion) in angle. The onsets of P1, P2 and R are also shown. To illustrate the interval between R and P1, the retraction period prior to the one shown in the middle panel is also identified on the angle diagrams (*R*). In walking (A,C), the solid bar denotes the stance period. The data for each behavior are from different chicks and were chosen as typical examples.

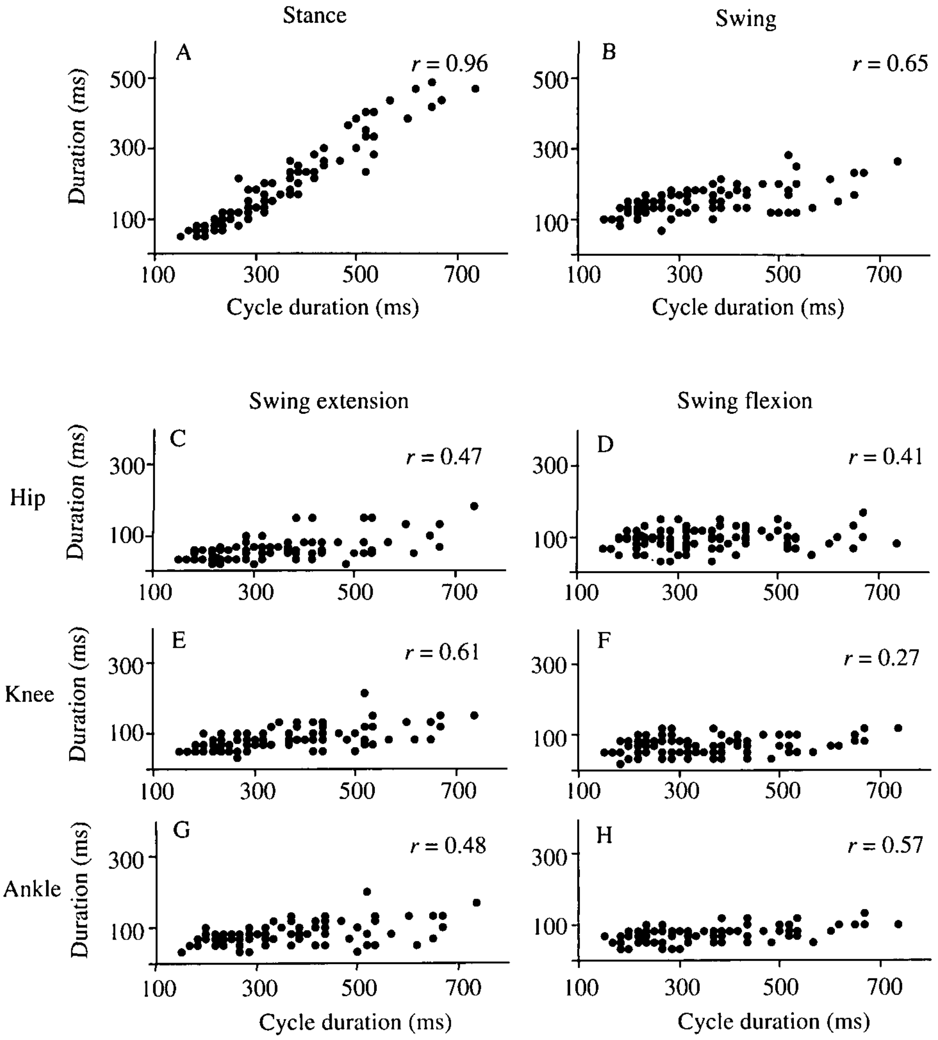

Fig. 3. Scatterplots showing the extent to which movement durations at the hip, knee and ankle covary with cycle duration in walking. In addition to the durations of stance and swing movements, the durations of the extension and flexion components of swing are plotted against cycle duration. Pearson's correlation coefficients (r) are shown for each plot. $N=100$ for each scatterplot.

cycle durations does not include the faster cycles examined in our study. All of our results that describe walking are the same for cycles with and without an aerial phase.

As anticipated from other walking studies in a variety of animals (for reviews see Grillner, 1981; Halbertsma, 1983), our results also show that stance and swing respond differently to changes in cycle duration. Fig. 3A,B shows that slowing of the step cycle is accompanied by longer periods of stance with no appreciable changes in the swing duration (also see Jacobson and Hollyday, 1982*a*). Although the duration of swing shows little variation during walking, we also examined the two components of swing at each joint to determine whether swing extension and flexion durations are differentially affected by changes in cycle duration. Our results show that, for the knee, swing extension covaries significantly more with cycle duration than does swing flexion (Fig. 3E,F). Swing extension and flexion movements at the hip (Fig. 3C,D) and the ankle (Fig. 3G,H) show similar covariation with cycle duration. Thus, variation in the duration of swing associated with cycle duration is the same between extension and flexion at the hip and ankle; in contrast, at the knee, swing extension and flexion durations are differentially affected by changes in speed.

Stance and swing occur only in behaviors that involve ground contact. Because we were also interested in behaviors that do not involve ground contact, we described the hindlimb movements in terms of more general parameters: retraction and protraction. In all three behaviors we found one period of retraction and two periods of protraction. In walking (Fig. 2B,C), retraction begins during the swing phase when the hip starts to extend prior to foot contact with the ground and continues throughout the stance phase. Protraction 1 and 2 both occur during the swing phase of a walk cycle. Retraction of the hindlimb occupies the majority of the walking cycle (69 %). Protraction 1 makes up 21 % of the cycle and the remaining 10 % occurs during protraction 2.

Swimming

The mean cycle duration for swimming is 347±43 ms. As in walking, a swimming cycle contains one retraction and two protraction periods (Fig. 2D,E). During retraction, the hindlimb moves posteriorly as the joints extend. Flexion at the three joints occurs as the hindlimb is drawn towards the body (protraction 1); extension is seen as the hindlimb is moved anteriorly (protraction 2). Like the other behaviors, retraction of the hindlimb in swimming occupies the largest portion of the movement cycle (48 %). Also, in swimming, protraction 1 occupies more of the cycle (32 %) than protraction 2 (20 %).

Airstepping

In contrast to walking and swimming, the mean cycle duration for airstepping is considerably shorter: 255±37 ms. As we hypothesized, the differences in cycle durations appear to reflect the relative amount of resistance the leg movements encounter during these three behaviors. The mean cycle duration of airstepping is faster than either swimming or walking, whose means do not differ significantly from one another.

As seen in both walking and swimming, the hindlimb movements in airstepping (Fig. 2G–I) contain one retraction and two protraction periods. Once again, retraction occurs as the hindlimb moves posteriorly while the joints extend. Then the hindlimb is pulled up towards the caudal region of the body accompanied by flexion at the hip, knee and ankle joints (protraction 1). The cycle is completed as the joints extend to move the hindlimb anteriorly (protraction 2). As noted above

Table 1. *Mean angular joint excursions and mean minimum and maximum angles (degrees) in walking, swimming and airstepping*

	Excursions			Minimum and maximum angles		
	Hip	Knee	Ankle	Hip	Knee	Ankle
Walking	31	86	92	49–80	62–148	60–152
Swimming	38	71	96	48–86	55–126	37–133
Airstepping	28	76	114	57–85	59–135	48–162
Motion limit	51	130	153	35–86	35–165	25–178

N=10 for each behavior.

for walking and swimming, in airstepping retraction of the hindlimb occupies the largest portion of the movement cycle (47 %). Furthermore, the percentage of the cycle devoted to retraction of the hindlimbs does not differ between airstepping and swimming. Unlike the other behaviors, protraction 2 occupies more of the cycle (35 %) than protraction 1 (18 %) in airstepping.

Movements at individual joints

Joint excursions

We quantified the angular excursions at each joint to determine whether they were constrained similarly in these different behaviors. In all three behaviors, the ankle shows the greatest excursions followed by the knee; the smallest excursions are displayed by the hip (Table 1). In each behavior, the excursions at the hip, knee or ankle utilize between 55 and 75 % of their potential ranges (Fig. 4).

Although we hypothesized that changes in cycle frequencies would affect the angular excursions at each joint, our results show only nonsignificant slopes for the

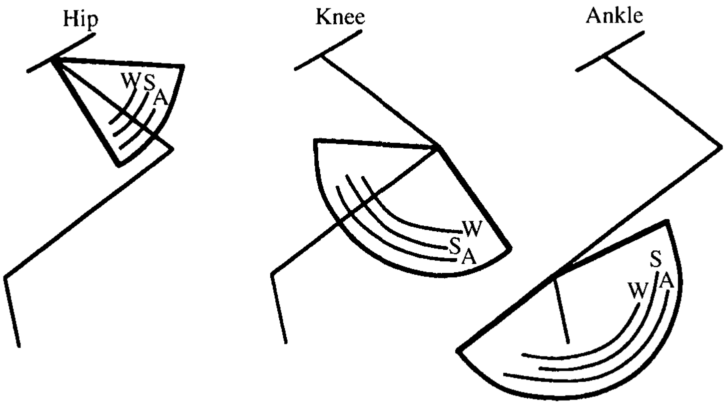

Fig. 4. Diagram showing the angular boundaries for motions at the hip, knee and ankle joints. The angular excursions for walking (W), swimming (S) and airstepping (A) are also shown.

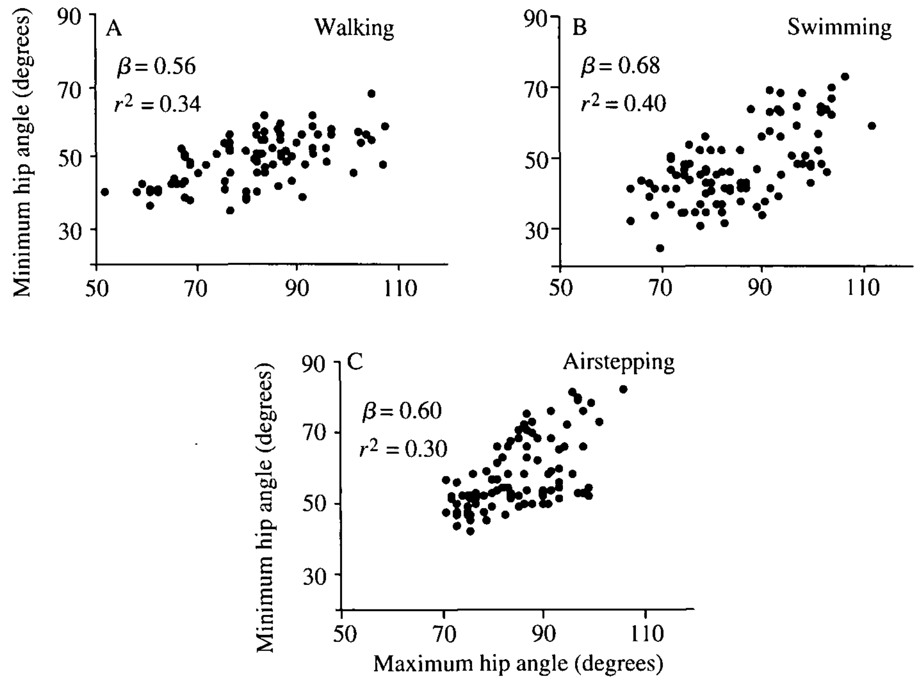

Fig. 5. Scatterplots showing the functional relationships between the maximum and minimum hip angles in walking, swimming and airstepping. The slopes (β) describe the extent of these relationships. $N=100$ for each behavior.

relationships between individual joint excursions and cycle durations. However, further analyses reveal significant relationships between minimum hip angles and maximum hip angles (Fig. 5A–C). Moreover, the slopes describing these relationships at the hip are similar among walking, swimming and airstepping. Only nonsignificant slopes were found for relationships between minimum and maximum angles at the knee and ankle, with the exception of the knee in swimming.

Intrajoint coordination

By further partitioning the hindlimb movements into extension and flexion durations we could approach the question of whether the extension and flexion components at each joint are differentially affected by changes in cycle duration. In walking, the movement durations that fall predominantly within the stance phase (hip and ankle extension, knee flexion) show a significantly stronger relationship with cycle duration than with their respective counterparts that occur mainly during the swing phase (Fig. 6A–F). To simplify these descriptions of covariation with cycle duration, we interpret the correlations as either asymmetrical or symmetrical. *Asymmetry* refers to significant differences between corre-

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Fig. 6. Scatterplots showing the extent of correlation at each joint between extension or flexion durations and cycle duration. Pearson's correlation coefficients (r) are shown for each plot. $N=100$ for each scatterplot.

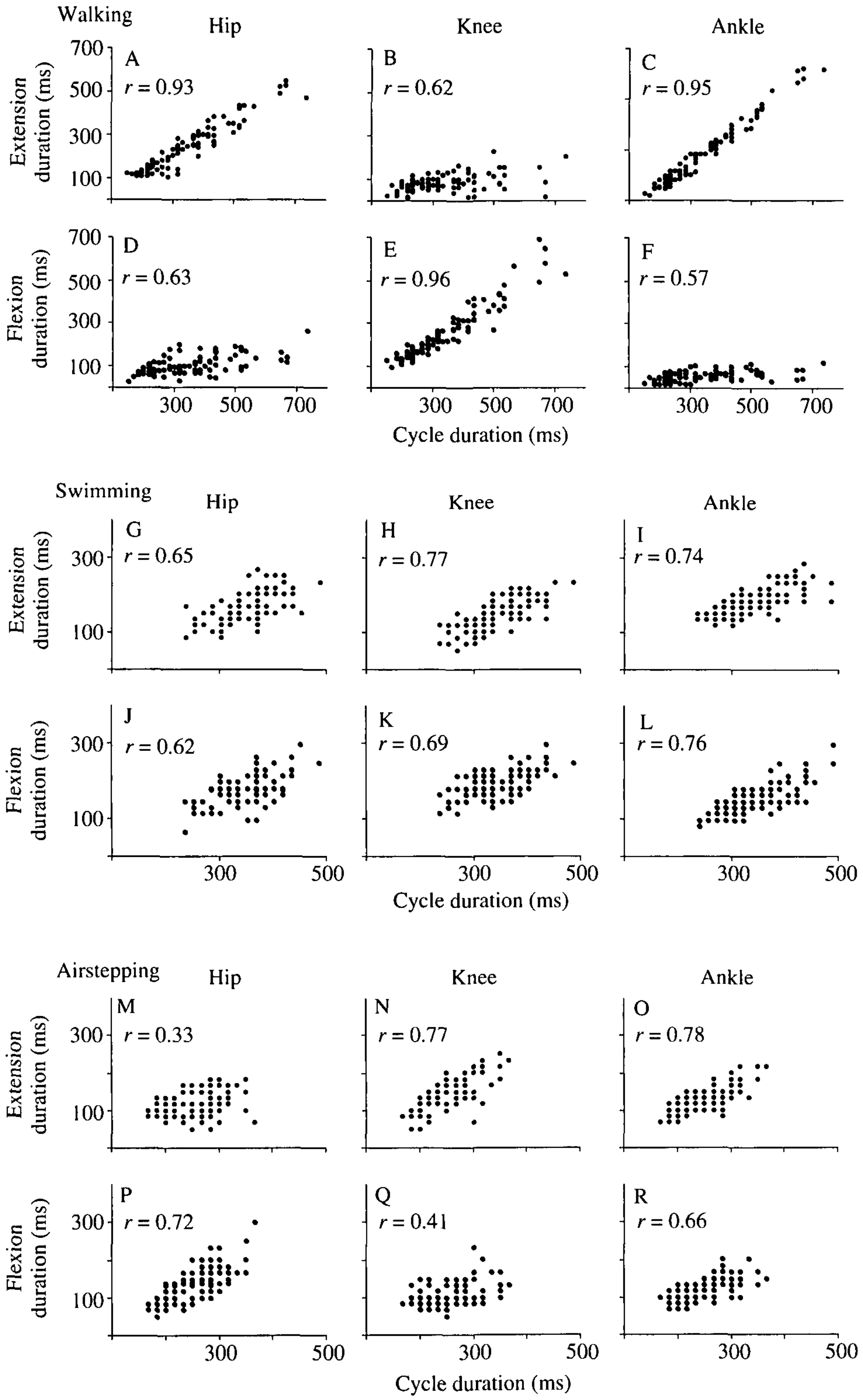
Walking
Hip
Knee
Ankle
Extension duration (ms)
Flexion duration (ms)
700
500
300
100
A
r = 0.93
B
r = 0.62
C
r = 0.95
D
r = 0.63
E
r = 0.96
F
r = 0.57
300 500 700
Cycle duration (ms)
Swimming
G
r = 0.65
H
r = 0.77
I
r = 0.74
J
r = 0.62
K
r = 0.69
L
r = 0.76
300 500
Cycle duration (ms)
Airstepping
M
r = 0.33
N
r = 0.77
O
r = 0.78
P
r = 0.72
Q
r = 0.41
R
r = 0.66
300 500
Cycle duration (ms)

Fig. 6

lation coefficients for extension and flexion durations at a joint; *symmetry* refers to correlation coefficients that do not differ statistically. Thus, walking shows asymmetries at all three joints (Fig. 6A–F).

Swimming shows symmetry between extension and flexion durations at all three joints (Fig. 6G–L). Airstepping also shows symmetry, but only at the ankle. The hip and knee show asymmetries between extension and flexion pairs (Fig. 6M–R); these asymmetries are the opposite of those described for walking.

Movement durations vary widely among behaviors, in part because cycle durations differ for each behavior. To adjust for this, movement durations were expressed as a proportion of their cycle durations, converting these values from real to relative time. The proportion of the cycle occupied by flexion and extension at each joint is graphically represented in Fig. 7. In walking, extension at the hip (0.69) and ankle (0.81) and flexion at the knee (0.75) (the movements that occur during stance) represent a significantly greater proportion of the walking cycle than their respective movement counterparts (Fig. 7A). In swimming, the proportions of the cycle devoted to flexion at both the hip (0.52) and at the knee

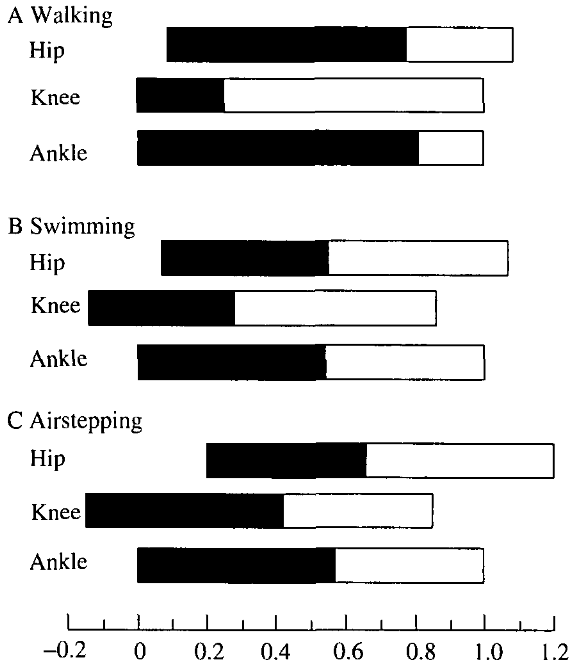

Fig. 7. Bar, diagrams showing the proportion of each cycle occupied by extension (filled bars) and flexion (open bars) durations at each joint in walking, airstepping and swimming. The latency to extension or flexion with respect to the beginning of each cycle is shown for each joint and describes the interjoint patterns for the initiation of extension and flexion in each behavior. The beginning of an open bar corresponds to the onset of extension; the beginning of a filled bar corresponds to the onset of flexion. The values represent the means for each joint based on a sample size of 10 chicks for each behavior. Onset of ankle extension is taken as the start of the cycle.

(0.58) are significantly greater than their respective extension movements (Fig. 7B). In contrast, in swimming, significantly more of the cycle is devoted to ankle extension (0.54) than to ankle flexion. In airstepping (Fig. 7C), hip flexion (0.54) and extension at the knee (0.57) and ankle (0.57) each occupy a significantly greater proportion of the cycle than their complementary motions.

Interjoint coordination

In each behavior, the joints show periods of concurrent extension or flexion. However, these movements are not initiated simultaneously at the hip, knee and ankle. The degree of asynchrony, based on latency and expressed as phase, among the joints for the initiation of extension or flexion is shown in Fig. 7. In general, the patterns in these three behaviors show either complete or partial asynchrony among all three joints; for patterns of complete asynchrony, movement at the knee precedes that at the ankle, which is followed by motion at the hip (*K–A–H*; as in airstepping flexion and extension and swimming extension); for patterns of partial asynchrony, either the knee precedes the ankle and hip movements (*K–AH*; as in walking and swimming flexion) or the knee and ankle precede movement at the hip (*KA–H*; as in walking extension). For either complete or partial patterns of asynchrony, we observed that the ankle never precedes the knee and that the hip never precedes the ankle. In each behavior, the phase for extension and flexion remains constant over the entire range of cycle durations.

Discriminating among behaviors

We used discriminant function analysis to quantify the extent of similarity or dissimilarity among these behaviors as well as to determine which variables contribute the most to differentiating among these behaviors (see *Statistical analyses* in Materials and methods). Discriminant functions for flexion variables are better than extension variables at discriminating among the behaviors; on average, flexion variables correctly classify the behaviors (87 %) better than extension variables (75 %). Fig. 8 shows the results from discriminant function analysis for a typical flexion variable group, phase. We conclude that swimming and airstepping are closely related to each other, whereas walking is quite distinct from the other behaviors, because the difference in discriminant scores is small between swimming and airstepping (0.82), but larger between swimming and walking (2.53), and between airstepping and walking (3.35).

Discriminant function analysis also revealed differences among the joints. Canonical loadings reflect the extent to which each variable contributes to the discrimination. The canonical loading for the ankle (−0.90) is much greater than that for either the knee (+0.31) or the hip (−0.35). This indicates that the ankle is more influential in discriminating among the behaviors than is the hip or the knee. Although we only show loadings based on flexion variables, we also see large loadings at the ankle with results based on extension variables. Thus, in general, movement parameters for the ankle discriminate best among these three behaviors.

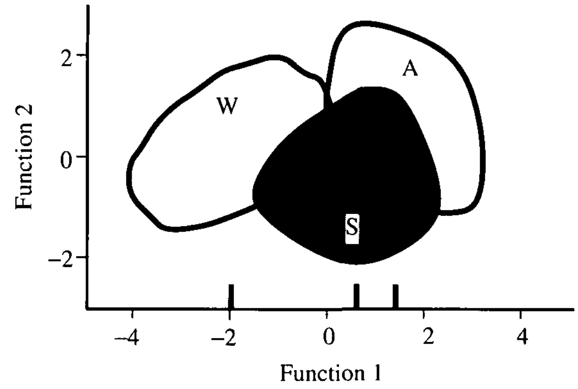

Fig. 8. Plot showing the results from discriminant function analysis for the flexion variable group, phase. The lines circumscribe the distribution of points in walking (W), swimming (S) and airstepping (A) (N=100 for each behavior). The shading is meant to help distinguish the boundaries for each behavior. The axes are in discriminant scores, a unit of measurement that reflects the extent of similarity and dissimilarity between behaviors. Only the first function, shown on the x-axis, significantly discriminates the three behaviors. The discriminant scores for walking (−1.96), swimming (+0.57) and airstepping (+1.39) indicate that swimming and airstepping are more related to each other, whereas walking is quite distinct from the other behaviors. The correct classifications for walking (90 %), swimming (83 %) and airstepping (86 %) are all considered high. Furthermore, 86 % of the small number of total misclassifications are explained by either swimming or airstepping being wrongly classified as the other. These results are representative of the other variable groups for flexion (duration or normalized duration).

Discussion

Role of the knee in walking: chicks compared to cats

Our results for walking show that stance duration in chicks is prolonged as cycle duration increases, whereas swing duration remains basically unchanged (Fig. 3A,B). This in agreement with Jacobson and Hollyday (1982*a*) and is a basic feature of terrestrial locomotion in all animals that have been examined, including mammals and birds (Grillner, 1981; Halbertsma, 1983; Cracraft, 1971; Jacobson and Hollyday, 1982*a*; Gatesy, 1989). Furthermore, in cats both flexion (F) and extension (E_1) portions of the hindlimb movement during swing show the same weak response to changes in cycle duration (Goslow *et al.* 1973). In chicks, where we have examined swing extension and swing flexion at each joint individually, we find that the hip and ankle fit the pattern seen for the whole hindlimb. However, at the knee, swing flexion is more strongly correlated with cycle duration than is swing extension. Therefore, our walking data suggest that extension and flexion durations at the knee are differentially affected by conditions during swing. Furthermore, during the swing phase, the knee is controlled differently from either the hip or the ankle. Our preliminary analyses of the electromyograms recorded during walking suggest that there is also differential modulation of knee muscle activity (Johnston and Bekoff, 1989). On the basis of these results, we propose that complex differential modulation at the knee is an important feature of walking in chicks. It is interesting that, despite the obvious differences in kinematic profiles of the knee in cats and chicks (for cat, see Goslow *et al.* 1973), differential control of knee movements (Hoy and Zernicke, 1985, 1986) and knee muscles (Smith, 1986) has also been proposed for walking in cats. We suggest that this is a general feature of walking in vertebrates.

Although birds and mammals share this general feature of walking, many of the specific details differ. The differences between chicks and cats are important when generalizing about the control of rhythmic hindlimb movements among different species. The most dramatic difference in the kinematic profiles occurs at the knee during the stance phase. In cats, the knee flexes or yields in early stance, but extends throughout the rest of stance (Goslow *et al.* 1973). In chicks, the knee flexes throughout the entire stance phase. The patterns of concurrent movements also differ substantially. During much of stance and swing flexion, the cat's hip moves in the opposite direction from the knee or ankle. In chicks, the knee moves in the opposite direction to the hip or ankle only during stance; however, during swing all three joints move in the same direction (Figs 2B, 7A). Another difference is seen in the relative angular excursions. In cats, the angular excursions of the hip, knee and ankle fall within the same range (Goslow *et al.* 1973). However, in chicks, the knee and ankle excursions are substantially larger than the hip excursions and are twice as large as those in cats.

Differences in hindlimb morphology, compliance and location of the center of mass are likely to account for at least some of the differences between the kinematic profiles of walking in chicks and cats. In cats, the majority of weight (60 %) is supported by the forelimbs (Manter, 1938; Alexander, 1985). In addition, the nearly horizontal orientation of the cat's femur places the foot under the center of mass during stance. This probably affects the forces produced during contact with the ground. In contrast to cats, anatomical features of the bird's hindlimb restrict rotational, abduction and adduction movements (Young, 1981; Gatesy, 1990). The hindlimbs of birds support all of the body mass because they are bipedal and the center of mass is located anterior to the acetabulum, well in front of the hip joint (Young, 1981). Gatesy (1990) suggests that these constraints result in birds using knee flexion to move the foot beneath the center of mass during walking. Furthermore, terrestrial birds do not use a spring-like mechanism, typical of mammalian locomotion, to accelerate and decelerate the body; the bird's hindlimb is highly compliant and acts to dampen vertical oscillations during the movement (Gatesy, 1989). This is seen as the knee flexes throughout the stance phase, apparently absorbing the forces generated by foot contact with the ground.

Kinematic profiles: comparisons among chick behaviors

As shown in the preceding section, the conventional method of describing locomotion based on stance and swing is useful. However, it applies only to behaviors that include contact with the ground. Several of the chick's behaviors do not involve a contact phase (e.g. swimming and airstepping). Our approach for quantifying hindlimb movement, in which a cycle is defined from the onset of ankle extension to the onset of the subsequent ankle extension, can be used to compare among these and other diverse behaviors in the chick's repertoire (Johnston *et al.* 1991).

Hindlimb stabilization and rhythmicity: role of the hip

Despite the differences in resistance encountered during walking, swimming or airstepping, in all three behaviors the hip shows the smallest excursions followed by larger excursions at the knee; the largest excursions are consistently seen at the ankle ($H<K<A$) (Table 1; Fig. 4) (see also Jacobson and Hollyday, 1982*a*, for data on chick walking and Cracraft, 1971, and Gatesy, 1989, 1990, for data on walking in other bird species). This pattern is also present in several other postnatal behaviors in chicks as well as in hatching, a perinatal behavior (A. Bekoff, R. M. Johnston and M. Dussault, unpublished results), and even in embryonic motility, a prenatal behavior (Watson and Bekoff, 1990) in which the angular joint excursions are considerably smaller than in other behaviors. Together, these results suggest that during prenatal development the range of motion at each joint is constrained relative to the others and that the underlying mechanisms, whether neural or non-neural, are retained and re-used in the production of hindlimb movements in later behaviors.

Movement at the hip is characterized by two basic features. First, extension and flexion movements at the hip initiate retraction and protraction of the entire hindlimb. Therefore, it is possible that hindlimb rhythmicity, i.e. the rhythmical alternation between retraction and protraction movements, is controlled at the hip. This is also suggested by studies of the role of hip position in cats (Andersson *et al.* 1978; Berkinblit *et al.* 1978*b*; Grillner and Rossignol, 1978). Second, the excursions at the hip are constrained in these three behaviors as shown in Fig. 5A–C. This form of constraint on hip excursions is also seen in hatching (A. Bekoff, R. M. Johnston and M. Dussault, unpublished results) and suggests some form of active control of hip position common to perinatal and postnatal behaviors. Thus, the limitations for hip excursions in chicks and other birds (Clark, 1988; Cracraft, 1971; Jacobson and Hollyday, 1982*a*; Gatesy, 1989) may reflect the hip's role in stabilizing the hindlimb during movement. In summary, our data suggest the presence of neural and non-neural strategies for controlling hip movements that are shared by the three rhythmical motor behaviors we have studied.

Interjoint coordination patterns: precedence of the knee

The interjoint patterns in walking, swimming and airstepping show either complete asynchrony among all three joints (K–A–H) or partial asynchrony, in which either the knee precedes the ankle and hip (K–AH) or the knee and ankle precede the hip (KA–H) (Fig. 7). For these as well as many other chick behaviors that have been examined (e.g. embryonic motility, Watson and Bekoff, 1990), the hip never precedes the ankle and the ankle never precedes the knee. The morphology of the hindlimb does not prevent other patterns from occurring because by manually manipulating the hindlimb we produced movements in which the hip and/or the ankle preceded the knee. However, other biomechanical limits or the neural networks underlying the muscle activation patterns may prevent the hip or ankle from preceding the knee during rhythmic movements. Why movement initiation begins at the knee is not known; this consistent feature of interjoint coordination may be required to produce smooth and coordinated movements and to maintain stability (Alexander, 1977; Wetzel and Stuart, 1977) for interjoint dynamics, given the unique hindlimb morphology of birds (as discussed in Materials and methods: *Video recordings* and *Video analysis*).

The effects of resistance on movement durations

Despite different degrees of resistance during these three behaviors, they each show three phases of hindlimb movements: retraction, protraction 1 and protraction 2. Although the relative durations of each phase can vary, each of these behaviors is characterized by a triphasic movement pattern. This is again consistent with the idea that the leg movements share some common features, i.e. constraints, regardless of sensory context. Nevertheless, some of the differences among the three behaviors appear to be due to differences in resistance. For example, previous electromyogram (EMG) studies of swimming in intact chicks (Bekoff, 1986*b*) and walking in chicks with deafferented hindlimbs (Bekoff *et al.* 1987*b*) concluded that sensory input due to weight support plays an important role in producing certain asymmetrical features of the motor patterns typical of walking: in contrast to flexors, extensors are active for a greater proportion of the cycle as well as showing a stronger relationship with changes in cycle duration. Our kinematic data as well as EMG data (Johnston and Bekoff, 1989) also indicate that the asymmetrical relationships seen in walking are not found in behaviors that lack weight support, such as airstepping and swimming (Figs 6, 7).

Sources of resistance other than weight support may also help shape the hindlimb movements in these behaviors. For example, resistance encountered during protraction of the hindlimb may explain the differences in the relative durations of protraction 1 and protraction 2. By examining the two components of protraction, our data suggest that protraction 1 and protraction 2 are differentially controlled. Jacobson and Hollyday (1982*b*) proposed that horizontal movements may be controlled differently from vertical hindlimb movements during walking in chicks. Protraction 1 consists of vertical movement of the hindlimb. Therefore, we suggest that the differential control of vertical and horizontal movements is not restricted to walking and may be a common feature of these three rhythmical behaviors. We are addressing whether this hypothesis is a general feature of hindlimb movements in chicks by analyzing kinematic data synchronized with EMG data during walking, swimming and airstepping.

Our kinematic data also suggest that the presence or absence of resistance differentially affects the hip, knee and ankle. The relationships at the hip differ according to the resistance encountered in each behavior. During swimming, where the water provides uniform resistance to the hindlimb, hip movements show symmetrical correlations. In walking, asymmetrical correlations exist at the hip, where resistance due to weight support results in a stronger extension relationship. Somewhat unexpectedly, we found that during airstepping, where the hindlimb movements would appear to encounter negligible resistance from the air, the hip also shows asymmetrical correlations. However, the stronger flexion correlation may result from resistance that occurs during early protraction of the hindlimb as flexion movements counteract inertia from the previous rapid retraction phase.

In contrast, the extension and flexion movements at the knee show asymmetrical correlations in all three behaviors and the asymmetries differ from those seen at the hip or ankle. The knee movements that occur during retraction of the hindlimb in all three behaviors, whether extension as in swimming and airstepping or flexion as in walking, show strong correlations with cycle durations (Fig. 6). This may result from purely neural mechanisms or may reflect the common effects of gravity or other kinetic factors acting on the knee during retraction. Only the asymmetry in swimming shows strong correlations for both extension and flexion at the knee. This suggests that the durations of knee movements are influenced by resistance from the water present during both extension and flexion motions. We are examining synchronized EMG and kinematic recordings to validate these suggestions for the hip and knee and to explain the relationships shown in Figs 6 and 7.

When resistance due to weight support is absent, as in swimming and airstepping, the ankle reverts to symmetrical correlations (Fig. 6). These results suggest that, at the ankle, a uniform source of resistance, such as that provided by water, is functionally similar to the absence of resistance encountered in air.

Our data show significant differences among behaviors that can be related to differences in sensory input due to resistance. We therefore suggest that the relationship between movement duration and cycle duration is a feature of the locomotor pattern that is modulated by sensory information. In addition, the three joints respond differently, emphasizing the problems associated with extrapolating general rules of locomotor control from analyses of a single joint.

Discriminating features among behaviors: role of the ankle

Based on our discriminant function results, we conclude that the major features that distinguish the three behaviors are the effects of weight support at the ankle: walking is at one end of the discriminant scale, and swimming and airstepping are at the other end (Fig. 8). Only the ankle, and not the hip or the knee, influences this separation. Although airstepping and swimming each show similar correlations at the ankle (Fig. 6), differences in their interjoint patterns for flexion initiation (Fig. 7) may account for the clean discrimination between these two closely related behaviors (Fig. 8). Results discussed above show that constrained features of hip and knee movements shape the kinematic profiles for hindlimb movements in all three behaviors. However, the subtle differences associated with phasing of ankle movements are the key features that discriminate among the three behaviors.

In conclusion, these results show the utility in reducing the hindlimb movements to the details of the individual joints. By quantifying the hindlimb movements, we have provided a description of the behavioral output that is useful in suggesting some of the underlying neural and non-neural mechanisms responsible for continuity among many chick behaviors; we have also identified elements that discriminate among these behaviors. These data lay the foundation for interpreting even subtle differences in the kinematic and motor patterns associated with specific chick behaviors.

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