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Coordination of Symmetrical and Asymmetrical Human Gait

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ABSTRACT. Most human gait forms assume symmetrical, alternating patterns of interlimb coordination (e.g., crawling, walking, running). Human galloping is a notable exception. In contrast to extensive information on galloping in animals, little is known about this gait in humans. Therefore, kinematic and topographical analyses of running and galloping were undertaken to investigate the manner in which the lower limbs are uncoupled to produce this asymmetrical gait. Seven adult females were filmed while running and galloping at their preferred speed. Analysis of the gaits revealed differences in the following: (a) preferred speed, (b) coupling between upper- and lower-limb girdles, and (c) point of foot fall (end-point trajectories). In contrast to clear differences in interlimb coordination, intralimb coordination was remarkably similar across gaits, although when galloping was adopted, the rear leg did show more variable change than the front leg.

Key words: gallop, interlimb coordination, intralimb coordination, locomotion

The scientific literature on animal interlimb coordination has distinguished the following two distinct classification patterns of movement: symmetrical and asymmetrical gaits (Howell, 1944; Wetzel & Stuart, 1976). In symmetrical gaits (e.g., walk, trot, and pace), the two forefeet strike the surface at constant successive intervals, and the same is true of the two hind feet. The step cycles of limbs from the same girdle alternate; one limb completes its cycle as the other limb is exactly halfway through its cycle (50% phasing). In asymmetrical gaits (e.g., canter, gallop, and half-bound), successive foot falls within girdles are not evenly spaced. For example, in a gallop, the right hind foot may strike the surface a short time interval after the left hind foot, but the next left hind foot strike occurs at a longer time interval after the right hind foot. Symmetrical and asymmetrical gaits of various animals have been analyzed extensively, but only symmetrical gaits have been studied in humans. In this article, the symmetrical gait of running and the asymmetrical gait of galloping in adult humans are analyzed and compared.

In human running, each leg alternately strikes the ground in an even temporal/spatial rhythm, with intervening flight phases. The human gallop occurs when the legs are oriented one in front of the other, with the lead leg executing a walking step while the rear leg executes a leaping (or running) step (Roberton & Halverson, 1984). A gallop, then, has a double-support phase when the lead leg strikes the ground while the rear leg is still planted. Subsequently, the rear and then the lead leg leave the ground, resulting in a flight phase before the rear leg strikes the ground again. Thus, not only do the lower limbs differ in their actions, they also exhibit an asymmetrical phasing relationship.

The significance of comparing the symmetrical run with the asymmetrical gallop lies primarily in terms of motor control. In the animal literature, comparisons between different gaits have been a major source of information about the behavioral organization of the neuromotor system. For example, Kelso and Scholz (1985) argued that gait patterns in animals are examples of dynamically self-organizing and synergetic patterns of behavior. Using a dynamic pattern-generation framework, they suggested that the structural and morphological form of an animal induces constraints on the dynamic stability of each particular locomotor gait. Each gait is seen as an "equilibrium state" or "periodic attractor" in which energy requirements are at a minimum for a particular velocity. The appearance of a new gait is a consequence of scaling-up a system's energetics (or some other variable) until the particular gait mode becomes dynamically unstable and, therefore, energy consuming. Further scaling-up of the variable in question causes an abrupt transition to a new stable gait (e.g., from walking to trotting).

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In humans, who have only two limbs in contact with the floor, there is a parallel example of a gait shift in that without any specific instructions to the performer, increasing the energy input for walking will result in the appearance of running. However, further increase in energy will not induce the appearance of galloping; rather, this gait form appears to be produced by willful intent. Thus the relationship between running and galloping in humans is not directly comparable with that existing between animal gaits. Instead, running and galloping appear to be alternative available coordination patterns for the lower limbs at certain energetic levels, although clearly running is the preferred coordination pattern.

In the language of dynamic pattern theory, the human walk and run are examples of an intrinsic interlimb coordination pattern (50% phasing) at different respective energetic levels. The interlimb pattern is intrinsic in the sense that it emerges spontaneously in a natural stable pattern as a function of the task (i.e., locomotion) and the bipedal symmetrical human form (Schöner & Kelso, 1988). Support for this notion comes from two sources. In designing bipedal robots, Raibert (1986) has demonstrated that the most dynamically stable gait for symmetrical bipeds is the alternating symmetrical phasing of walking and running. A second source of support comes from a study of newly walking infants, who immediately assumed an alternating phasing for their walking gait, albeit one that was a little less stable than an adult's gait (Clark, Whitall, & Phillips, 1988). In contrast, the gallop does not emerge in infancy until a year later and then only with considerable external influence (Whitall, 1990). The question of interest, then, revolves around how the neuromuscular system can adopt intentionally an asymmetrical gait rather than the intrinsic symmetrical gait.

In dynamic pattern theory, it is important, first of all, to define what changes between particular behavioral patterns. For example, the variable of temporal interlimb phasing has been identified as the (collective) variable that captures the essence of bimanual coordination and its transitions (Kelso, Schöner, Scholz, & Haken, 1987). In a previous study, both children and adults demonstrated different lower-limb temporal phasing relationships for running and galloping (Whitall, 1989). One must be cautious, however, in regarding temporal interlimb phasing as a universal collective variable. Whereas bimanual coordination has relatively few degrees of freedom, in a multiple-degree-of-freedom system such as gait, a number of relative phase relationships are possible. Relative phasing between foot falls may not be the collective variable. It is prudent, therefore, to examine a number of phasing relations as potential collective variables for coordination in gait.

The purpose of the present study, then, was to extend the previous work by providing a more comprehensive picture of the similarities and differences between the two gaits of running and galloping in adults. This first analysis describes the behavioral level of organization by focusing on kinematic variables. Two questions were asked. First, how do these kinematic variables differ between the gaits? This comparison assesses whether the intentional adoption of an asymmetrical gait results in a totally different behavioral organization or whether there are similarities among the behavioral patterns. Theoretically, similar behavioral parameters between the gaits would imply (though not prove) that the gallop is organized as a modification of the intrinsic coordination pattern rather than a completely new pattern. The second question of interest was: How consistent are the kinematic variables across subjects? This comparison assesses the degree to which individuals show similarity in the organization of either gait. The more important question here is not the degree of individual difference per se, but, given a within-subject design, the extent to which the individuals show the same degree of variability for each gait. If, for example, certain kinematic variables show greater between-subject variability for the gallop, this would imply that individual differences in anatomy or strategy have greater influence (for these variables) on asymmetric than on symmetric gait. It should be noted here that this measure of stability (i.e., consistency of gait behavior across subjects) is not the same as the within-subject variability, a measure that would assess the stability of a particular behavior across time.

To answer the questions of similarity/difference and stability across subjects, we performed a multistep kinematic and topological analysis. First, the stride parameters and relative stance time of each gait were determined to look for overall spatial–temporal parameter changes. Second, the interlimb temporal phasing patterns were quantified to determine the asymmetrical relationship of the limbs in galloping and compare these to the symmetrical run. Third, joint-angle time-histories were examined for invariant and variant characteristics of the joint displacements. Finally, angle–angle diagrams were studied to assess both intralimb and interlimb joint coupling of each gait.

Method

Subjects

Thirteen right-handed female adults were screened for possible participation in the study. The potential subjects were assessed for skillful galloping, which was defined in accordance with Sapp's (1980) mature stage of galloping. The mature stage includes a low, rhythmical flight pattern and arms not used for balance. In addition, skillful gallopers were defined here as those who could easily gallop backward and switch leading legs. Five subjects were rejected for unskillful galloping (and 1 was not used because she led with the left leg when galloping), leaving a subject pool of 7 skillful gallopers, with an age range of 19 to 32 years.

Procedures

Black circular markers with a white circular inset were affixed to the subject at the following joint center locations: metatarsal-phalangeal (toe), lateral malleolus (ankle), be-

tween the femoral condyle and the tibial plateau (knee), head of greater trochanter (hip), 3 cm below the acromium process (shoulder), lateral epicondyle of the humerus (elbow), and the medial side of the distal head of the ulna (wrist). Subjects were filmed at 64 frames per second (fps) from a sagittal view, while traversing a runway perpendicular to the optical axis of a 16mm Photosonics intermittent pin-registered camera. The camera was fitted with a 16mm focal length lens, which was located 12.2 m from the subject. This resulted in a field of view of 8 m, which allowed approximately four stride cycles of the leg nearest the camera.

Practice trials of running and galloping at the subject's preferred speed were allowed before filming. Subjects were asked to (a) travel in a straight line, (b) maintain their preferred speed along the entire length of the runway for each trial, and (c) maintain front facing when galloping (i.e., not to slide). Subjects chose their preferred leading leg for the gallop (all chose the right leg). Two trials were filmed for each gait, the first traveling right to left and the second traveling left to right, so that each side of the body was facing the camera for one trial of analysis.

Data Reduction

Data reduction began with the selection of strides for analysis. The objective, for each subject and each gait, was to choose from each of the two trials a stride that was approximately equal in stride time. Using the criterion of similar stride time, 8 out of 14 possible right-left pairings (i.e., run and gallop for each subject) had the same stride time, 5 were only one frame (0.0156 s) different, and 1 was two frames (0.0313 s) different.

Visual inspection of the data, frame by frame, determined the temporal/spatial landmarks of heel strikes and toe-offs. Coordinate marker data of the 14 selected stride cycles were digitized, using a Numonics digitizer with a back-lit projection system. The coordinate data were converted to real space, using standard planar calibration procedures. The displacement, velocity, and acceleration time-histories of each joint were inspected after smoothing the raw displacement data at various cut-off frequencies, using a 4th-order dual-pass Butterworth digital filter. Consequently, cut-off frequencies for each joint marker, ranging from 5 to 7 Hz, were selected, with the more distal markers having higher cut-offs. From the smoothed joint marker data, a six-link rigid-body model was constructed and used to calculate intersegmental angular position and velocity profiles. Conventions for the angular measurements are shown in Figure 1.

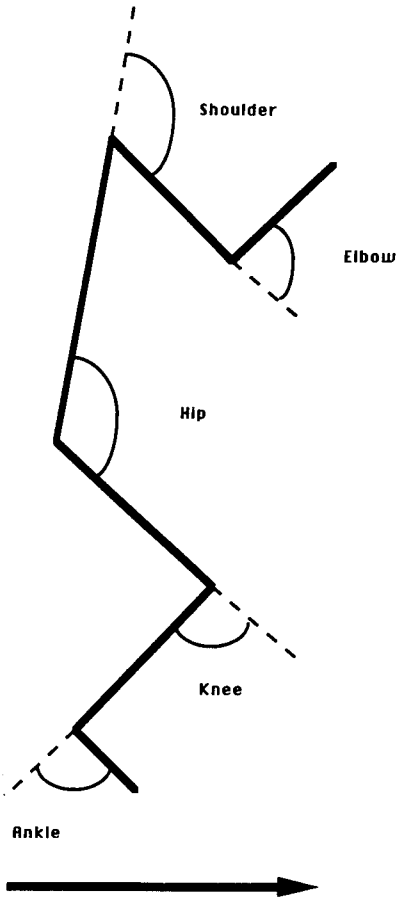

FIGURE 1. Angular measurement conventions. Anatomical position for the shoulder and hip joints is 3.14 radians; for elbow and knee, it is 0.0 radians. Due to the definition of foot angle by the ankle and metatarsal markers, anatomical position of the foot is approximately 1.1 radian.

TABLE 1
Stride Characteristics of the Right Foot Cycle for Run and Gallop

Measure	Run			Gallop		
	Time (s)	Distance (m)	Velocity (m/s)	Time (s)	Distance (m)	Velocity (m/s)
$\bar{X}$	.738	2.209	2.999	.625	1.670	2.675
SD	.035	0.172	0.256	.031	0.149	0.287
Min[a]	.688	1.956	2.665	.579	1.530	2.304
Max[a]	.781	2.513	3.315	.664	1.929	3.024

[a]The terms *min* and *max* refer to the across-individual range of the indicated measure.

Results

Stride Parameters

The initial analysis was a description of the spatial–temporal parameters of the right stride cycles for each gait, namely, stride velocity, stride distance, and stride time. These data are presented in Table 1. Two features of this table are notable. First, each of these gait parameters decreased in magnitude when the subject galloped rather than ran. On average, the reductions were 0.113 s for time (15% decrease) and 0.54 m for distance (24% decrease), resulting in a 0.33 m/s reduction for velocity (11% decrease). With the exception of 1 subject, the change in parameters was remarkably consistent across subjects. Second, the

between-subject variability for all three parameters was relatively consistent between the two gaits. Unfortunately, we found no comparable studies of female gait with which to assess the normality of either the mean or variability values (for either gait).

Relative Stance Time

Relative stance times were calculated for the right limb during the stride cycle digitized and for the left limb during the preceding left stride cycle. The formula for each subject was (stance time/stride time) × 100. These percentages are presented in Table 2. On average, the subjects showed a 39/61 stance/swing ratio for running, which is typical for this gait (Williams, 1985). This changed to a 45/55 stance/swing ratio for the gallop. An analysis of variance was conducted on relative stance, with gait and limb (2 × 2) as repeated-measure factors. Only the effect for gait was significant $F(1, 6) = 51.3$, $p < .0004$, confirming that there was a significant change from run to gallop on this parameter.

Two interesting facts emerge from Table 2. One concerns the fact that both legs exhibited the same relative stance and swing phase in galloping, even though one leg was supposedly walking and the other running (Roberton & Halverson, 1984). The second point to note is that between-subject variability was similar across gaits for the right/front leg but showed a slight increase in variability in galloping for the left/back leg.

Interlimb Phasing

Temporal phasing measures were calculated between sets of limbs, such that the position of the left-side limb was calculated as a percentage of the right-side cycle. For example, the proportion (or percentage) of a stride cycle that had elapsed when foot strike occurred on the contralateral limb would indicate the phasing between the feet (i.e., 50% [or 50/50] phasing would indicate that the left leg struck the ground exactly halfway through the right leg's stride cycle). To look at the arm phasing and to compare across limb girdles, we chose events that could be located precisely within the rhythmic cycle of all four limbs. For this purpose, the forward-to-backward reversal of the upper arms and thighs (as determined by change in the sign of the angular velocity profiles) was selected. The following phasing relationships were calculated and then analyzed statistically, using matched t tests:

1. Feet (left foot strike within right foot cycle [strike to strike]).
2. Thighs (left thigh reversal within right thigh cycle).
3. Arms (left upper arm reversal within right upper arm cycle).

In addition, the relationship among all four limbs was calculated with respect to the stride cycle, using the left and right thigh and upper-arm limb reversals.

The temporal phasing relationships of the upper arms, thighs, and feet are presented for each subject in Table 3. Data from the running trials showed a consistent symmetrical alternating phasing (50/50) for all three measures, although the arms were more variable across subjects. In contrast, the gallop data showed a relatively consistent asymmetric relationship of 66/33 for the feet, a very inconsistent relationship of 72/28 for the thighs, and a somewhat inconsistent relationship of 57/43 for the arms (similar in variability to the arms during running). In fact, inspection of the individual data revealed that 4 of the subjects showed a tendency for the symmetrical alternating arm relationships of running, whereas 3 showed an asymmetrical relationship similar to their particular feet phasing. Statistical comparisons between the gaits revealed significant differences between the foot phasing ($t = 11.66$, $p < .0001$), the thigh phasing ($t = 5.53$, $p < .002$), and the arm phasing ($t = 2.76$, $p < .03$).

In Figure 2, the relationship of all four limb reversals is shown with respect to the stride cycle. The run showed a reversal order of left thigh, right arm, right thigh, left arm, with diagonal pairs closely linked in time. The gallop showed a reversal order of left arm, right arm, left thigh, right thigh. In effect, all of the reversals moved forward in relative time with respect to the right foot strike cycle, but the left thigh actually moved ahead of the right arm, which moved only slightly forward. This corresponds to the

TABLE 2
Relative Stance and Swing Times for Run and Gallop (% Stride Cycle)

	Run (Stance/Swing)		Gallop (Stance/Swing)	
	Right	Left	Right	Left
$\bar{X}$	38.0/62.0	39.2/60.8	44.7/55.3	44.6/55.4
SD	2.5	3.0	2.3	3.9
Min[a]	42.9/57.1	44.2/55.8	47.5/52.5	48.4/51.6
Max[a]	34.4/65.6	34.5/65.5	40.3/59.8	38.9/61.1

[a]The terms *min* and *max* refer to the across-individual range of the indicated measure.

TABLE 3
Interlimb Phasing Relationships for Run and Gallop (% Stride Cycle)

	Run			Gallop		
	Feet	Thigh	Arms	Feet	Thigh	Arms
$\bar{X}$	51.2	50.3	48.7	65.7	72.3	57.1
SD	1.0	1.7	6.6	3.1	11.4	7.5
Min	50.0	48.0	38.0	62.0	58.9	48.8
Max	52.5	52.6	55.5	71.0	87.8	68.0

Note. Feet values are between foot strikes; thigh and upper-arm values are between segment reversals from forward to backward.

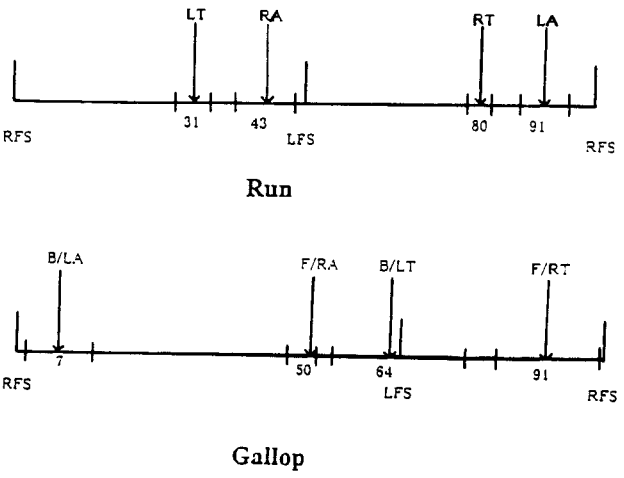

FIGURE 2. Ensemble average interlimb phasing relationships, based on thigh and upper-arm reversal across all limbs with respect to the stride cycle (right foot strike [RFS] to right foot strike). Standard deviation designated by hatch marks. LFS = left foot strike.

change from trotting to transverse galloping in quadrupeds (Wetzel & Stuart, 1976). Two subjects did not show this exact reversal order in galloping. One subject had the right arm and left (back) thigh closely linked, whereas another subject had the left thigh slightly ahead of the right arm (8% difference). Finally it is apparent that there was far greater variability in the timing of the gallop reversals, particularly for the thighs.

Joint Displacement Histories

The above analysis has given a global picture of the phase shifts that occur in the limb relationships when a human chooses to gallop instead of run. To assess the movements of each joint throughout the entire stride cycle, we compared ensemble average displacement-time histories both qualitatively (Figures 3 and 4) and quantitatively (Table 4) for their consistency across subjects and across gaits. For the quantitative assessment, a coefficient of variation (CV) was calculated (Equation 1). This formula differs from that of Winter (1983) because the range of motion, not the mean angle, appears in the denominator. This is preferred because the differences between joints or gaits are concerned with the range of motion rather than the mean value, which is arbitrary and therefore meaningless in this context.

$$CV = \left(\frac{1}{N}\sum_{i=1}^{N}\sigma_i^2\right)^{1/2} / |\theta_{max} - \theta_{min}|, \quad (1)$$

in which N is the number of intervals over the stride period; θ_{max} and θ_{min} are the maximum and minimum joint angles, respectively; and σ_i is the standard deviation of the mean angle at time i.

In Table 4, mean coefficients of variation are presented. It is clear that the elbow joint showed a wide range of variability. This was true regardless of gait or arm, and indicates that elbow action was highly individual in terms of the timing and amount of displacement. Part of this variability may have been due to measurement errors caused by out-of-plane motion, but, in any case, it is not possible to talk meaningfully of a mean elbow joint pattern or to interpret the elbow displacement-time graphs.

All of the other joints had coefficients of variation that were within a range of interpretation. The variability of the shoulder joint patterns for the arms in running was much smaller than in galloping (approximately 10 vs. 28% CV). This was due, presumably, to the individual phasing variability of the arms when galloping, which was noted in the previous section. For the leg joints, the run showed similar variability across joints and legs (between 9 and 14% CV), indicating consistent joint patterns for all subjects (see Figures 3 and 4, and Table 4). Curiously the right/front galloping leg also showed a stable across-subject pattern (between 11 and 12% CV), with the exception of the knee joint (17% CV). The left/back leg, however, was consistently twice as variable, when galloping is compared with running (between 20 and 24% CV).

When comparing the ensemble joint-angle histories across gaits, the run and gallop showed similar movement patterns for all joints, when comparing the front/right side, but considerably less similarity for the back/left side ankle, knee, and hip. The differences in the front/right side appeared to be limited to magnitude (range of motion), whereas differences in the back/left side were also found in the timing of joint reversals. However, quantification of joint magnitude and timing reversals for the deepest joint flexion during the stride cycle proved that there were statistical differences between gaits for almost all of these parameters. Following Beuter, Duda, and Widule (1989), the means and standard deviations of the magnitude and timing reversals are presented in Table 5. An analysis of variance was conducted on the magnitude scores, with gait and limb (2 × 2) as repeated-measures factors. For the hip magnitudes, a significant Gait × Limb interaction, $F(1, 6) = 78.8$, $p < .0001$, showed that the back hip when galloping was less flexed than the back hip when running or than the front hip when either running or galloping. The knee magnitudes showed only an effect for gait, $F(1, 6) = 92.6$, $p < .0001$, indicating reduced range of motion for either leg, when comparing galloping with running. The ankle magnitude show an effect for limb, $F(1, 6) = 15.7$, $p < .008$, although the Gait × Limb interaction approached significance, $F(1, 6) = 5.4$ $p < .059$. In this case, it was the front limb that displayed smaller ankle dorsiflexion in galloping.

For the timing reversals of these deepest joint flexions, a one-way analysis of variance was conducted, with gait as a repeated-measures factor. All analyses indicated significantly different timing reversals for each joint in either leg when changing gait: front hip, $F(1, 6) = 13.9$ $p < .01$; back hip, $F(1, 6) = 276.8$, $p < .0001$; front knee, $F(1, 6) = 22.8$, $p < .003$; back knee, $F(1, 6) = 50.4$, $p < .0004$;

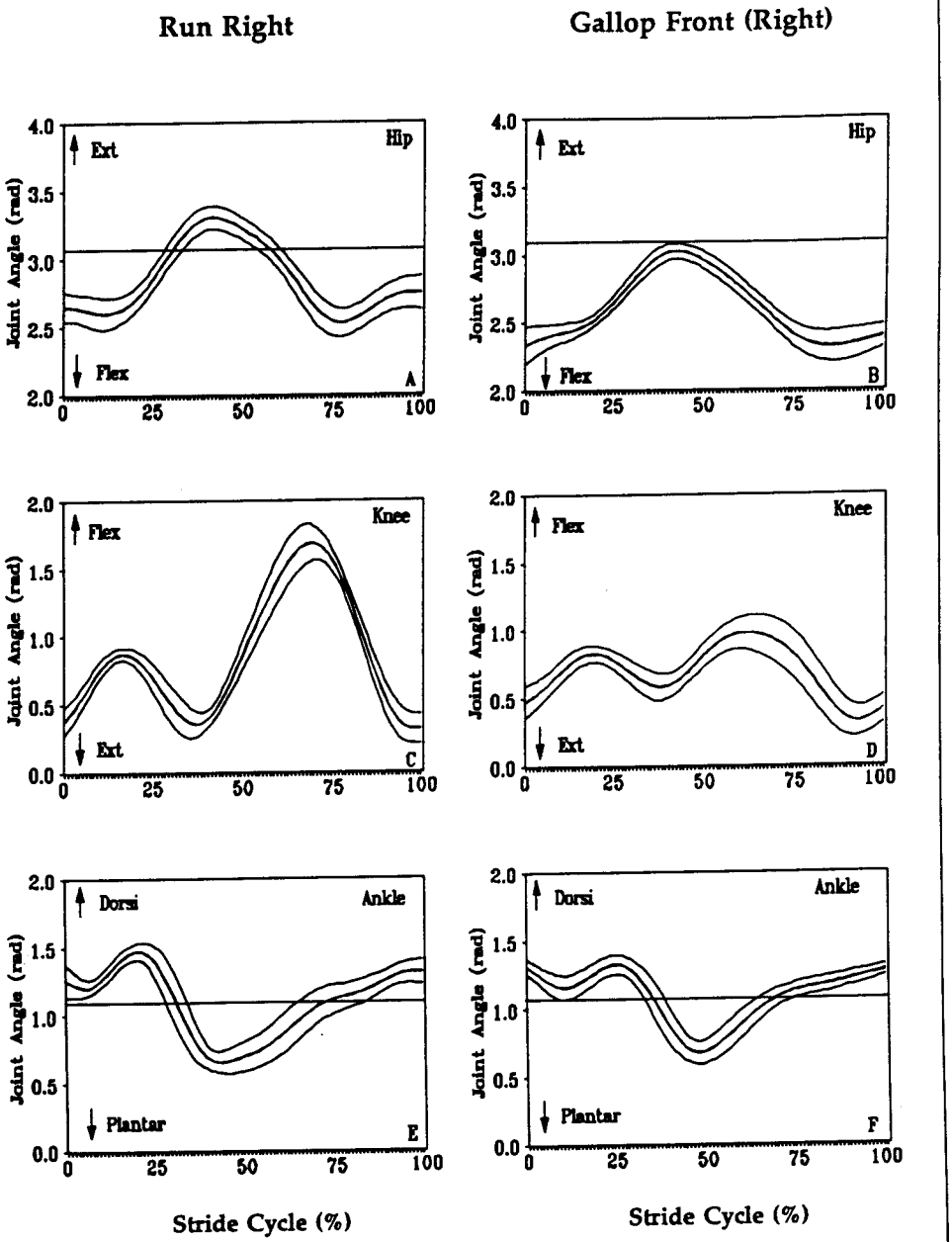

FIGURE 3. Ensemble average of right (front) leg joint displacements over stride period, with run on the left and gallop on the right. Standard deviation is plotted on either side of the mean. Straight lines demarcate anatomical position for hip and ankle (0.0 radians for knee).

TABLE 4
Mean Coefficients of Variation (%) Over Stride for the Joint-Angle Displacements

	Run		Gallop	
Joint	Right	Left	Front (Right)	Back (Left)
Elbow	86.6	106.6	274.7	180.4
Shoulder	9.4	10.3	29.5	26.6
Hip	12.6	9.7	11.3	20.7
Knee	7.8	9.7	17.6	23.4
Ankle	13.1	14.3	12.6	24.3

front ankle, $F(1, 6) = 175$, $p < .0001$; back ankle, $F(1, 6) = 390.6$, $p < .0001$. Comparison of the F values indicated a much bigger change for the back leg in all joints.

Angle–Angle Diagrams

The interaction of two joints was assessed by plotting one joint angle against the simultaneous value of another joint angle. The corresponding plots, known as angle–angle diagrams, give insight into the coordination or covariation between the joints (Grieve & Gear, 1966; Winstein & Garfinkel, 1989). If the joints are on the same limb, for example, left hip and knee, then the resulting plot can be interpreted as the intralimb joint coordination, incorporating

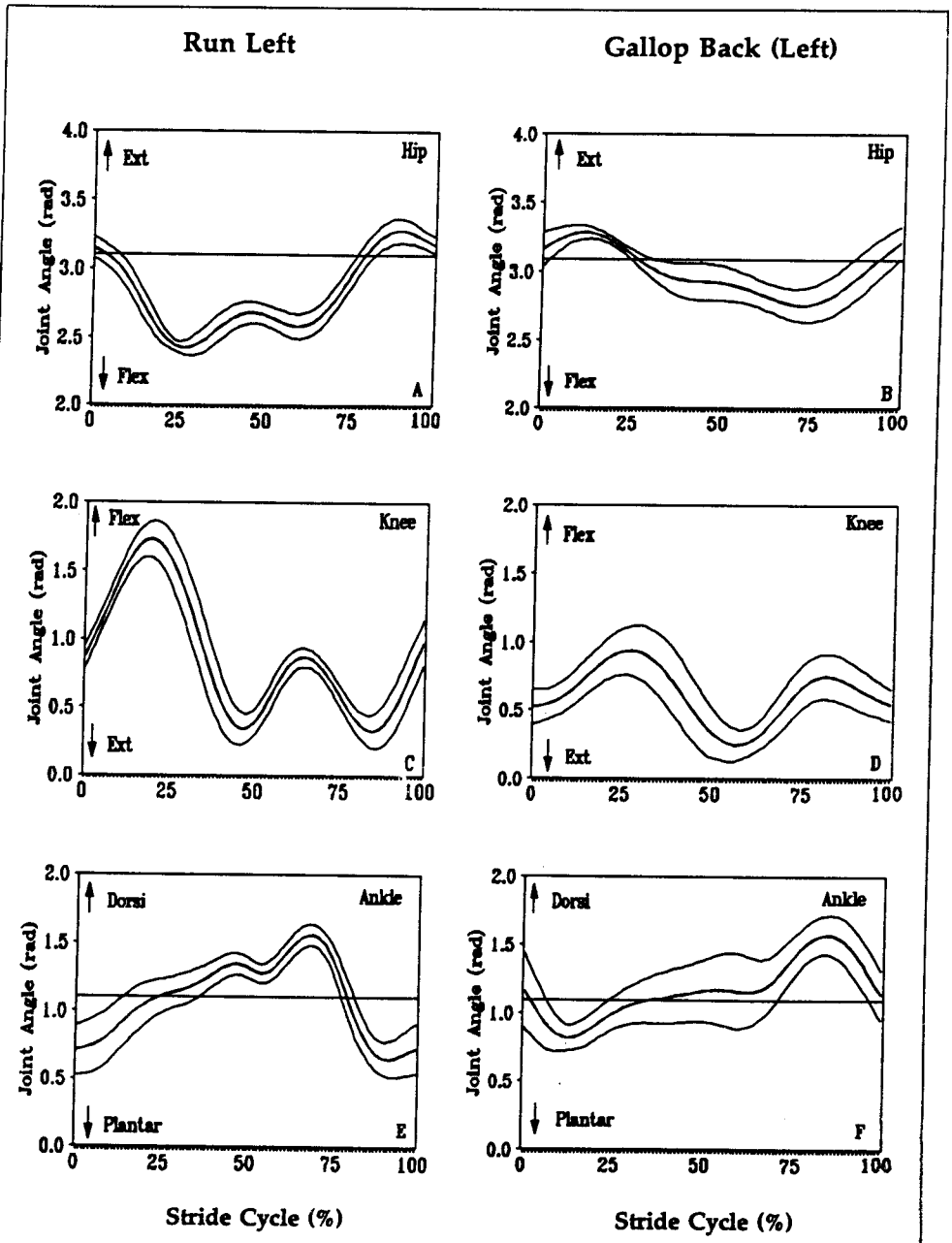

FIGURE 4. Ensemble average of left (back) leg joint displacements over stride period, with run on the left and gallop on the right. See Figure 3 caption for details.

the action of three linked segments. If the joints are on different limbs, for example, left and right ankles, then the resulting plots can be interpreted as the interlimb joint coordination between the limbs of the lower girdle. Given the variability of the arms in many of the variables already described, the present investigation was limited only to the intralimb joint and contralateral interlimb joint coordination of the legs.

Intralimb Joint Coordination

Ensemble averages of the intralimb joint pairings for hip–knee, knee–ankle, and hip–ankle are presented in Figures 5, 6, and 7, respectively, with run on the left and gallop on the right. Please note the conventions for flexion and extension used for different joints. The guidelines proposed by Winstein and Garfinkel (1989) were used to interpret the plots.

For example, consider the plot of the right hip–knee joints when running (Figure 5a). Beginning at right heel strike (see arrow marked 1), the knee flexed while the hip remained stationary. This was followed by in-phase extension of both joints, which was carried out at a constant (1:1) ratio. Both joints reached their maximum just before toe-off, with the knee switching to flexion just before the hip joint. During the first half of the swing, both joints flexed in a constant ratio, but the knee flexed more quickly. In the

TABLE 5
Means and Standard Deviations of Intralimb Joint-Angle Maximum Flexion (Radians) and Normalized Time to Maximum Flexion (% Stride Cycle)

	Run		Gallop	
Variable	Right	Left	Front (right)	Back (left)
Max hip flexion				
X	2.519	2.403	2.304	2.736
SD	0.117	0.062	0.120	0.109
Max knee flexion				
X	1.691	1.740	0.995	0.957
SD	0.149	0.128	0.136	0.186
Max ankle flexion				
X	1.480	1.559	1.333	1.596
SD	0.066	0.087	0.073	0.172
Time to max hip flexion				
X	77.4	27.6	86.6	72.3
SD	2.0	2.9	6.5	5.8
Time to max knee flexion				
X	69.8	19.9	62.5	28.5
SD	1.3	1.7	4.5	3.8
Time to max ankle flexion				
X	21.2	68.7	26.3	85.3
SD	1.9	1.0	1.6	2.2

latter half of the swing, the joints extended again to prepare for landing; again the knee switched first. As would be expected, the hip extended more slowly than the knee.

Comparing Figure 5a with 5c, one can see immediately the similarity in the left running hip–knee plot. Comparing across gait (Figures 5a and 5b), it appears at first glance that there are major differences between the two plots. Closer inspection reveals this is not the case, however. Obviously, the limited range of motion found in the joint-displacement curves is represented by differences in the relative size of the plots. Of more importance, though, is whether the joints acted together in the same fashion in both gaits. If one follows the direction and orientation of the arrows from foot strike (1) in Figure 5a and 5b, the same directional order will be seen (i.e., right, left, right, left). Small differences in the arrow orientations can be observe in the plots of early stance, when the hip extended as the knee flexed (giving the gallop arrow a slight upward orientation), and of late swing, when the hip flexed as the knee extended (a slight downward orientation for the gallop). The same is found in the left/back leg comparison (Figure 5c and 5d).

Because it is the difference between gaits that is of primary concern, the ankle–knee (Figure 6) and ankle–hip (Figure 7) plots are not examined in similar detail to Figure 5, but rather are summarized in general in terms of overall shape.

For the ankle–knee coordination presented in Figure 6, the plots are characterized by in-phase flexion, extension, and flexion during stance and early swing, and out-of-phase knee extension and ankle dorsiflexion during late swing. During stance, the ankle moved at a faster rate, whereas during swing, the knee moved faster. Other than the restricted magnitude of the knee action during swing, there are no major differences between the run and gallop plots of either leg. One minor difference occurred immediately after right foot strike in the right/front leg. In the gallop, there was an initial plantarflexion of the ankle (Figure 6b), which did not occur in the run (Figure 6a).

In Figure 7, the ankle–hip coordination was characterized mostly by in-phase flexion in late swing and early stance and by in-phase extension in late stance and early swing. Again, for the right/front leg, the only difference for the gallop was immediately after foot strike, when there was a brief period of ankle plantarflexion before dorsiflexion. For the left/back leg, the only difference between gaits occurred just before left foot strike where the ankle dorsiflexion and hip extension of the run was replaced with continuing hip flexion and a constant ankle angle.

For each intralimb joint coupling, the differences that did occur were around the time of foot strike. In the right/front leg, the coordination was changed by the action of the hip and ankle. Instead of extending before and flexing after foot strike, the hip remained flexed before and extended briefly after foot strike. This action was caused by the orientation of the leg with respect to the body. Because the leg was farther in front of the body in galloping, hip extension was not needed to place the foot down but occurred after foot strike as the body caught up with the leg. This forward orientation of the leg also explains the initial ankle plantarflexion at foot strike because it is the heel that struck the ground first, followed by the rest of the foot. This produced an initial plantarflexion before the shank "rode" over the foot, causing dorsiflexion. In contrast, when running at a preferred speed, the foot tended to strike the ground in a parallel (flat foot) fashion, from which the ankle went straight into dorsiflexion.

Similarly, the different coupling in the left/back leg occurred with changes at the hip and ankle and again is attributed to the orientation of the leg with respect to the body. In galloping, this leg was behind the body for the entire stride cycle. In late swing, the hip continued to flex before foot strike because it was being brought to a position closer to the body. Unlike in running, it did not extend before foot strike, implying that the foot was not actively placed on the ground but was allowed to "fall" to the ground at a fixed angle. This inactive placing of the foot was also reflected in the lack of dorsiflexion prior to foot strike. In the run, the ankle dorsiflexed prior to landing to bring the foot into the parallel position for landing. In the gallop, the foot remained in a plantarflexed position, and the sole of the foot struck the ground first.

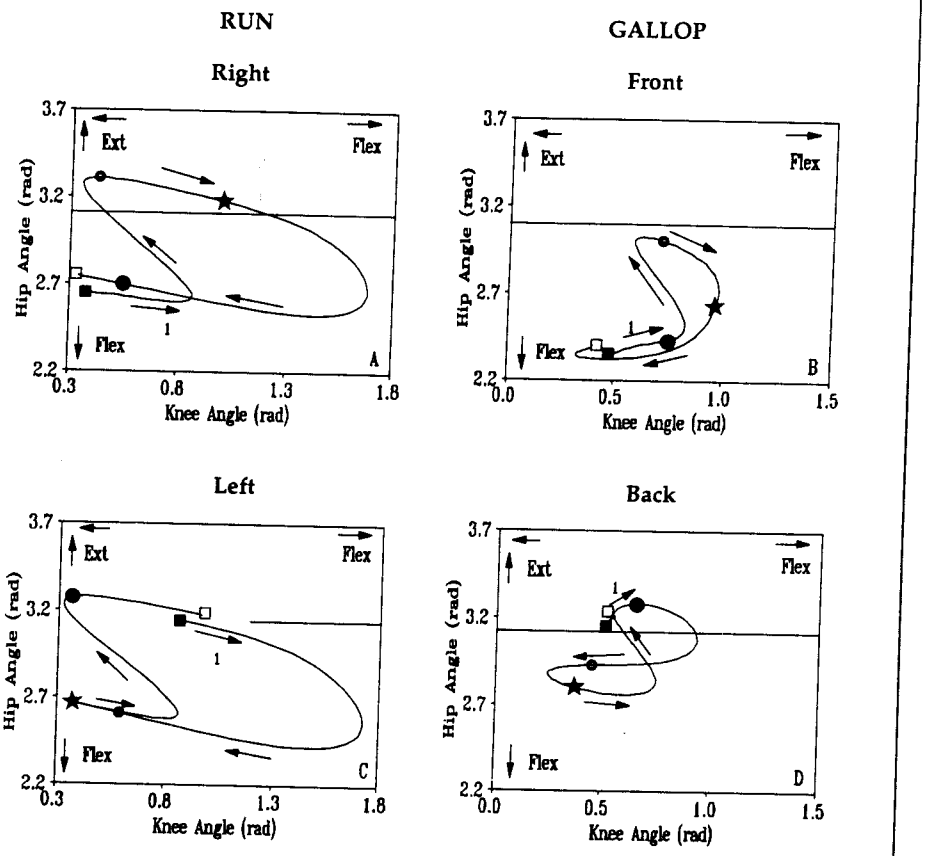

FIGURE 5. Intralimb angle–angle diagram of ensemble average hip–knee joint displacements over stride period. (a) Right leg running, (b) front (right) leg galloping, (c) left leg running, and (d) left (back) leg galloping. Events during the stride are indicated by symbols: Initial right (front) foot contact = ■; right toe-off = O; left (back) foot contact = ★; left toe-off = ●; subsequent right foot contact = □. Arrows indicate temporal order, beginning with arrow designated as 1. Straight lines indicate anatomical position for hip (0.0 radians for knee).

Interlimb Joint Coordination

This analysis is a more comprehensive (continuous) assessment of interlimb coordination, as opposed to the interlimb phasing data that examined specific points within the stride. The ensemble average contralateral interlimb joint coupling of the leg joints are presented in Figure 8. Looking first at the hips when running (Figure 8a) the plot is characterized by symmetrical rounded trajectories. The symmetry indicates that the hips were coupled the same for both halves of the stride cycle, whereas the rounded trajectories indicate smooth decoupled coordination (Winstein & Garfinkel, 1989). After right foot strike, the left hip began to flex and then the right hip extended, so that for a short period of time the hips were completely out of phase. Consequently, the left hip stopped flexing while the right hip continued to extend. Just before toe-off, the hips extended in phase and then flexed in phase as left foot strike occurred. The plot of the second half of the cycle repeats the first half, but with the leg actions reversed.

In contrast, the interhip coupling for galloping appears to be represented by a differently shaped plot (Figure 8b) with less smoothly rounded shapes. One difference occurs after right/front foot strike when the hips briefly extended together before the left toe-off. From here until right toe-off, there was an out-of-phase constant relationship, with the left/back hip flexing to bring the leg under the body and the right/front hip extending to keep this leg in front of the body. After right/front toe-off, the hips flexed in phase and continued until about a third of the way through left/back foot stance, when the left/back hip extended rapidly and the right/front hip was extending only slightly. In general, then, the major change in interhip coupling occurred after right/front foot strike until left/back toe-off, that is, the time of double support in the galloping stride cycle. The single-support sections show similar coupling, although the slopes are different, with a more linear relationship during right/front limb stance and a more curvilinear relationship during left/back limb stance. Last, the flight phase is completely linear in the gallop but shows a curvilinear relationship in the run.

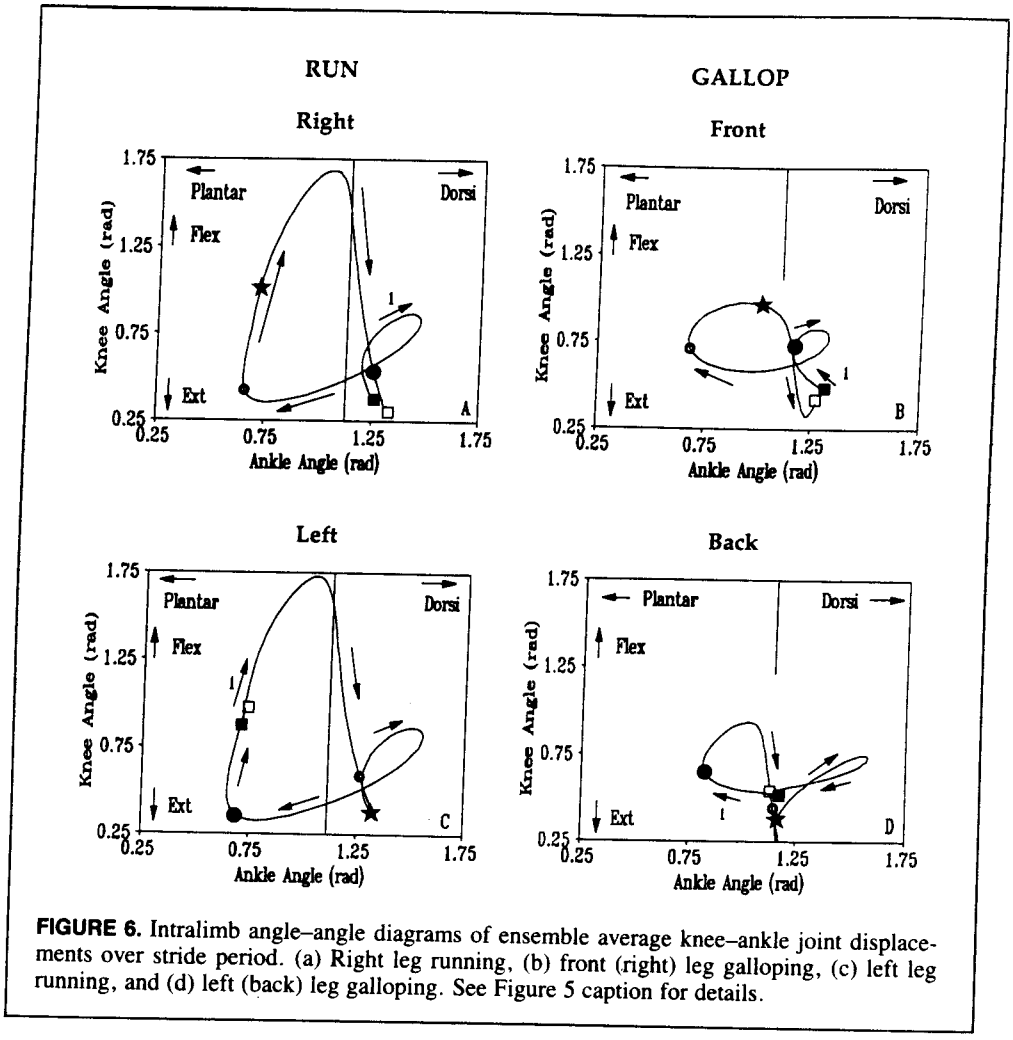

FIGURE 6. Intralimb angle–angle diagrams of ensemble average knee–ankle joint displacements over stride period. (a) Right leg running, (b) front (right) leg galloping, (c) left leg running, and (d) left (back) leg galloping. See Figure 5 caption for details.

The interknee coupling of the run and gallop is shown in Figures 8c and d, respectively. Again, the qualitative shapes are different, although this time both gaits have smooth rounded trajectories. The run is characterized by in-phase relationships during the stance phase of each leg as the knees flexed and then extended together. The plot of the gallop shows a similar, though less tightly coupled, in-phase relationship during right/front leg stance, but during left/back leg stance there is an out-of-phase relationship where the right/front knee extended and then flexed instead of the reverse action. Finally, the interankle coupling plots in Figure 8e (run) and 8f (gallop) are also quite different. In running, the plot is characterized by a symmetrical negatively oriented figure-eight, with long diagonal straight segments. Thus, during right leg stance there was a period of in-phase dorsiflexion, followed by a period of out-of-phase coupling where the right ankle switched to plantarflexion for take-off and the left continued to slowly dorsiflex. The flight phase from right toe-off to left foot strike shows a turning point synchronization as the ankles reversed their actions. In galloping, both ankles initially plantarflexed after right/front foot strike until left/back toe-off, then the ankle resumed the same coupling relationships as the run for the rest of right/front leg stance. During flight, when the right/front foot left the ground, it immediately dorsiflexed, whereas the left/back ankle remained constant. After left/back foot strike, the ankles again behaved as they did in running during left leg stance. Thus, like the hips, the major coupling differences occurred during double support and flight, that is, just after right/front foot strike and just before left/back foot strike.

Discussion

The purpose of this study was to describe the kinematic similarities and differences between the symmetrical coordination pattern of running and the asymmetric coordination pattern of galloping. From this description, several inferences can be made concerning the organizational strategies for adopting an asymmetrical gait instead of the preferred symmetrical gait. To interpret the data from a dynamic-pattern theoretical viewpoint, it is necessary, first, to make a distinction between the hypothetically separable coordination (essential or collective) and control (nonessential) variables (Kugler, Kelso, & Turvey, 1980). Coordination variables describe the relationship between components of behavior and tend to be invariant, that is, to

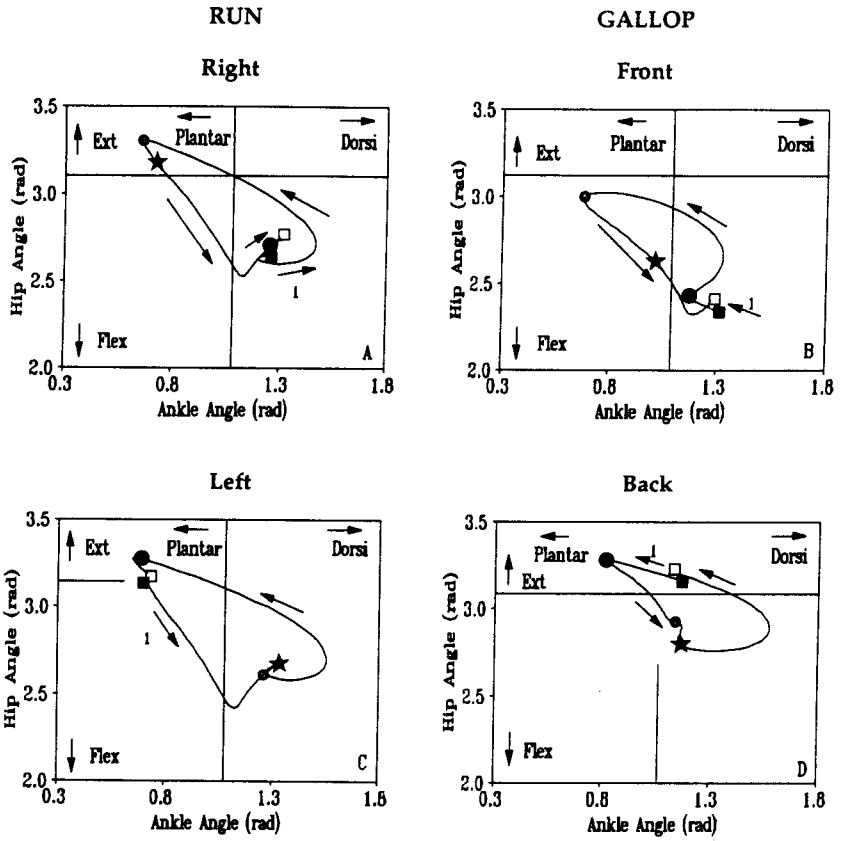

FIGURE 7. Intralimb angle–angle diagrams of ensemble average ankle–hip joint displacements over stride period. (a) Right leg running, (b) front (right) leg galloping, (c) left leg running, and (d) left (back) leg galloping. See Figure 5 caption for details.

maintain their form over other changes in behavior. As noted earlier, temporal interlimb phasing has been proposed as an appropriate variable to describe bimanual coordination (Kelso, Schöner, Scholz, & Haken, 1987), but a suitable collective variable for running and galloping patterns has yet to be identified. Control variables are absolute scalar values that may change certain characteristics of the behavior without altering its essential form unless scaled beyond a critical value. For example, the speed of walking would be a control variable that does not alter the interlimb phasing of a walking cat until it is scaled above a certain value, after which a new form of interlimb phasing (trotting) will emerge. A similar principle of invariant coordination and variant speed has been found at the intralimb level of analysis. For example, a change in walking speed can occur without changing the relative timing of the muscle activation patterns (Grillner, 1975; Yang & Winter, 1985) or the joint displacement reversals (Winter, 1983).

Looking first at the potential control variables, the adoption of alternative interlimb patterns resulted in different values for stride time, distance, and velocity between the two gaits. Specifically, there was a consistent drop in speed from the run to the gallop because of a shorter stride length accompanied by a shorter stride time. The consistency of these changes across subjects indicates that each coordination pattern has a distinct preferred rate of locomotion. Because preferred rates of locomotion for quadrupedal and human locomotion have been demonstrated to be associated with minimal energy consumption (e.g., Alexander, 1984; Hoyt & Taylor, 1981), the drop in preferred speed from running to galloping suggests that the two gaits may have different overall energy requirements at any particular velocity of progression.

Related to the change in speed from running to galloping is the observed shift in relative stance/swing ratios from 39/61 in running to 45/55 in galloping. Previous studies have shown that relative stance time is a function of the speed of locomotion (e.g., Rosenrot, Wall, & Charteris, 1980). Thus, a normal walk has a 60/40 stance/swing, but this approaches 50/50 as the walk gets faster. Conversely, a run has a normal percentage of 40/60 and approaches 50/50 as the run gets slower. Using conventional kinematic definitions, a walk must be more than 50% stance and a run must be less than 50% stance. Consequently, for the gallop, both limbs are actually engaged in a slow running step, although the front leg of the gallop is typically described as walking

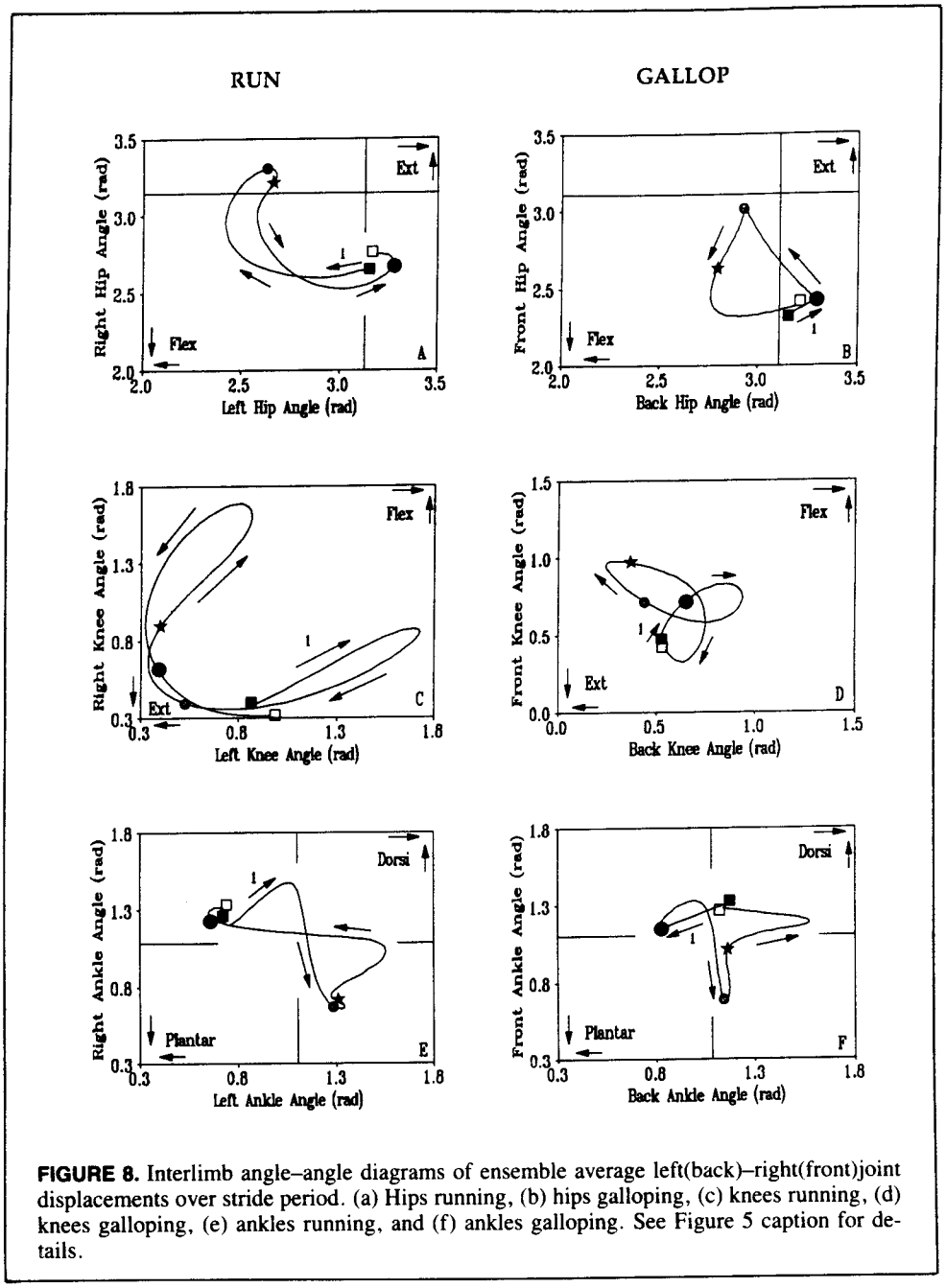

FIGURE 8. Interlimb angle–angle diagrams of ensemble average left(back)–right(front)joint displacements over stride period. (a) Hips running, (b) hips galloping, (c) knees running, (d) knees galloping, (e) ankles running, and (f) ankles galloping. See Figure 5 caption for details.

because its action involves a double-support phase. This apparent contradiction is the result of one leg's catching up with the other, to the extent that there is an overlap in support phase. It may, in fact, be more appropriate to categorize galloping as a "limping run" rather than a combination walk/run.

The fact that both legs exhibited the same relative stance phase is evidence that there is an organizational consistency in the way both legs are controlled despite the clear phase shift in their interlimb relationship and some differences in the intralimb timing of the walking and running legs, as discussed later. This temporal correspondence of the legs despite varying spatial patterns is an illustration of the tendency of the neuromuscular system to coordinate limbs for a functional purpose, in this case, balance. A similar kind of temporal coordination despite spatial variance has been described previously for upper-limb movement (e.g. Kelso, Southard, & Goodman, 1979).

Turning next to the coordination variables, the phasing relationships within and between the upper and lower limbs were observed first. These data revealed four basic differences between running and galloping. First, as noted in a previous paper (Whitall, 1989), there were significant differences in the lower-limb phasing relationships, regardless of whether one measures thigh reversals or foot falls. Secondly, although there was a significant difference across gait between the arm phasing relationships, it appeared that 4 subjects were using the alternating (1:1) pattern of running

while galloping, whereas the other 3 used a 2:1 phase relationship. Thirdly, the temporal order of limb reversals changed from an LT, RA, RT, LA order to an LA, RA, LT, RT order, with minor exceptions. Finally, interlimb phasing appeared to be more variable across subjects for the gallop. The size of the difference depended on the particular comparison being made, however; for example, phasing of the thigh reversals in the gallop was far more variable than in the run, but the foot fall phasing data was not.

Taken as a whole, these data suggest that there is not one obligatory (attractive) asymmetric interlimb phasing relationship for humans. Different linkages between upper- and lower-limb girdles were found also in a study by Muzzi, Warburg, and Gentile (1984), who asked subjects to clap and walk simultaneously at preferred speeds. Out of 18 subjects, they found 12 who tightly synchronized the clap with heel strike, 2 who used a harmonic 2:1 ratio (i.e., frequency uncoupling), and 4 who were classified as demonstrating loose phase linkage because they had no specific phase relationship (i.e., phasing uncoupling). One possible reason for flexibility of intergirdle coupling is the different constraints imposed on the two sets of limbs. Unlike quadrupedal locomotion, only the lower limbs are constrained to interact with the ground, whereas the upper limbs are free from external constraints. Consequently, mechanical interaction with the environment occurs during foot fall of either lower limb. The results of this external constraint can be seen in the relative lack of between-subject variability when the lower limbs were compared with the upper limbs in both running and galloping (see Table 3). Similarly, displacement curves of all the lower-limb joints are more stable than those of the elbow joint, which was free to vary in a number of ways, for example, by being held at a fixed angle or allowed to react mechanically to upper-arm movement (see Table 4).

Lack of mechanical constraints on the arms also allowed subjects to "choose" between the familiar symmetrical and the less familiar asymmetrical coordination. Conceivably, the asymmetrical arm pattern was the more reactive or passive pattern, which was driven by the leg phasing, whereas the symmetrical arm phasing was a more active pattern selected for its familiarity. Whether subjects who showed the 50% phasing arm pattern would eventually by attracted to the 66/33 ratio (or vice-versa) is not addressable in this study. In support of the reactive/passive action of the arms, however, Muzzi et al. (1984) documented that the foot fall patterns tend to drive the arm coordination and not vice-versa. They found that changing step-cycle walking rate affected the temporal patterning of the clapping but not the reverse. The authors concluded that heel strike was the potent reference point about which the clap cycle was modulated. Different phase linkages were still observed, however, which precluded a deterministic view of lower-limb to upper-limb influence, a finding that the present data support.

Support for this idea that the organization of interlimb coordination is centered around the foot falls is the fact that the foot strike phasing in galloping was so stable across subjects (66/33 ± 3%) compared with the phasing measured at the thigh (72/28 ± 11%). This suggests that the lower limb is free to use a wide range of thigh actions to accomplish the task of asymmetric coordination. The fact that this discrepancy of thigh versus foot fall phasing does not occur in running may be due to the differing segmental properties of the subjects. These segmental properties are influential in determining the nonmuscular forces that occur in the leg segments in running (Chapman & Caldwell, 1983; Chapman, Lonergan, & Caldwell, 1984). If nonmuscular forces in galloping vary for each leg, as is suggested by the magnitude of kinematic patterns, the patterns of muscular moments at the hip necessary to achieve similar foot fall positions may be different in each leg. Furthermore, differences in subject anthropomorphics may cause the hip muscle moment adaptation for galloping to vary from subject to subject. In any case, these data support an "end-point hypothesis" for motor control in which the final position of the limb in space is specified. Recently, Winter (1989) has suggested similar arguments for the foot trajectory in walking. From this viewpoint then, the selection of galloping requires a different end-point foot trajectory (for each foot) than the one in place for running.

Additional evidence that foot falls are the significant distinguishing feature between the gaits comes from the continuous measures of inter- and intralimb coordination as defined by angle–angle covariation (see Figures 5, 6, 7, and 8, and accompanying text). These plots show that coupling of the joints follows similar patterns across gait, with differences occurring primarily around the foot falls. This suggests that the same leg synergies used for running are used again for galloping, with minor modifications at the point of external interaction with the ground. This strategy carries obvious benefits because it is not necessary to completely redefine the timing relationships of the lower-limb joints, except for just before and after foot strike. In general, the changes in interlimb joint coordination are greater than those seen for intralimb joint coordination. Although this claim is based on qualitative analysis, it indicates that adopting an asymmetric interlimb coordination pattern with the legs does not require similar changes in intralimb coordination. In a similar vein, it has been noted already that the coordination pattern of all four limbs is not dependent on the new coordination pattern of the legs. In other words, each level of coordination has some flexibility in its operation.

The level of coordination with the fewest degrees of freedom is the relationship between segments of a single limb, that is, the joint displacement profiles. According to Winter (1983, 1989), the joint-angle patterns of the leg, when walking, are quite invariant in terms of the timing of reversals and the shape of the displacement curves. When subjects are asked to change the speed of walking, small differences occur only in the magnitude of the flexion/extension peaks and not in the timing of the peaks. In this study, a similar change in peak magnitudes was found for

either leg, particularly at the knee, when galloping was adopted. However, relatively small but significant time-to-peak shifts were detectable for the right/front leg, compared with quite large changes in the left/back leg. Thus, the neuromuscular organization for the gallop requires a change in the magnitude of joint action for both limbs and in the timing of joint reversals, particularly in the trailing leg. Because these changes tend to occur at each joint, however, the intralimb synergies between the joints do not change very much, as noted above.

A final aspect of these data is the increased between-subject variability of the back/left compared with the corresponding front/right joint displacement curves. Given the remarkably similar lack of variability across subjects for the run or even the front leg when galloping, the high back-leg variability indicates a less deterministic source of organization for the new leg orientation. This variability may be due to whether the subject stiffens the leg or allows it more flexibility, as is seen in running.

One might argue that the increased between-subject variability seen in some of these variables in galloping could be the result of a lack of practice in this seldom used form of locomotion. This argument is rejected for several reasons. First of all, the subjects were adults who were screened for skillful galloping. Secondly, these subjects showed small within-subject variability for the interlimb phasing of their galloping (Whitall, 1989), indicating that they had already learned the skill to an acceptable level of performance. In fact, when they were asked to simultaneously perform a cognitive task, there was no effect on their mean or variability of interlimb phasing (Whitall, 1991). This indicates that the organization of this asymmetric pattern, once set, requires little attention, and appears to self-organize. It is unlikely, therefore, that further practice would reduce the across-subject variability unless subjects were asked specifically to change their style. Rather, the only learning that would take place would be a small further reduction in within-subject variability. Finally, the lack of practice argument cannot account for those variables that change little in variability from run to gallop, for example, stride parameters, stance/swing ratios, foot fall interlimb phasing. The fact that the subjects behaved more similarly for some variable adaptations than they did for others provides insight into the generality or individuality of coordination changes.

In conclusion, the data from this study provide evidence that the run and gallop share similar, but not identical, intralimb coordination patterns. Differences appear to be due to the orientation of the two legs in galloping, in particular around the ankle at foot strike. In contrast, there is a clear distinction across gait in the interlimb coordination of the lower limbs. In other words, the lower limbs appear to change their phase relationship or coupling linkage without changing the manner in which each individual limb operates, except when dictated by the leg orientation and foot/ground interaction.

Although a dynamic pattern theory viewpoint has been used throughout this article, another way of interpreting these results from a neurophysiological perspective is to use the central pattern generator concept, first derived from animal work (Grillner, 1975, 1977) and later extended to humans (e.g., Forssberg, 1985). In this view, spinal pattern generators are presumed to exist for each individual limb (and each joint). Our data suggests that it was the coupling (coordinating neurons) between each limb pattern generator that altered the interlimb phasing and produced the gallop, whereas peripheral feedback regarding segmental orientation allowed minimal adjustment of each limb's pattern generator. Further investigation of these ideas in humans is rather difficult, however. In contrast, the dynamic pattern theoretical framework offers a rich source of potential avenues of investigation. For example, based on the observation that foot fall temporal phasing is the coordination variable that shows the most distinct differences between the gaits, this seems a possible candidate for the status of a collective (low-dimensional) variable. Further evidence of this possibility would be found from a thorough investigation of the relationship between potential control variables (e.g., velocity) and this potential collective variable, that is, systematic scaling of each control variable with these gait patterns. This strategy would provide additional information on the stability of these coordination patterns (the intrinsic dynamics in dynamic pattern theory language) and enable one to proceed with investigating intentional real-time transitions between the gaits as well as developmental-time transitions. One further research avenue derives from the observations that subjects adopt consistent but different preferred velocity levels for the two gait modes and that the gallop has kinematic features of both walking and running (i.e., both double-support and flight phases). These kinematic signatures have been associated with distinct and different energy-saving mechanisms (Cavagna, Heglund, & Taylor, 1977). These observations lead one to speculate on the form of the underlying energetics and kinetics during galloping and will be the focus of future work.

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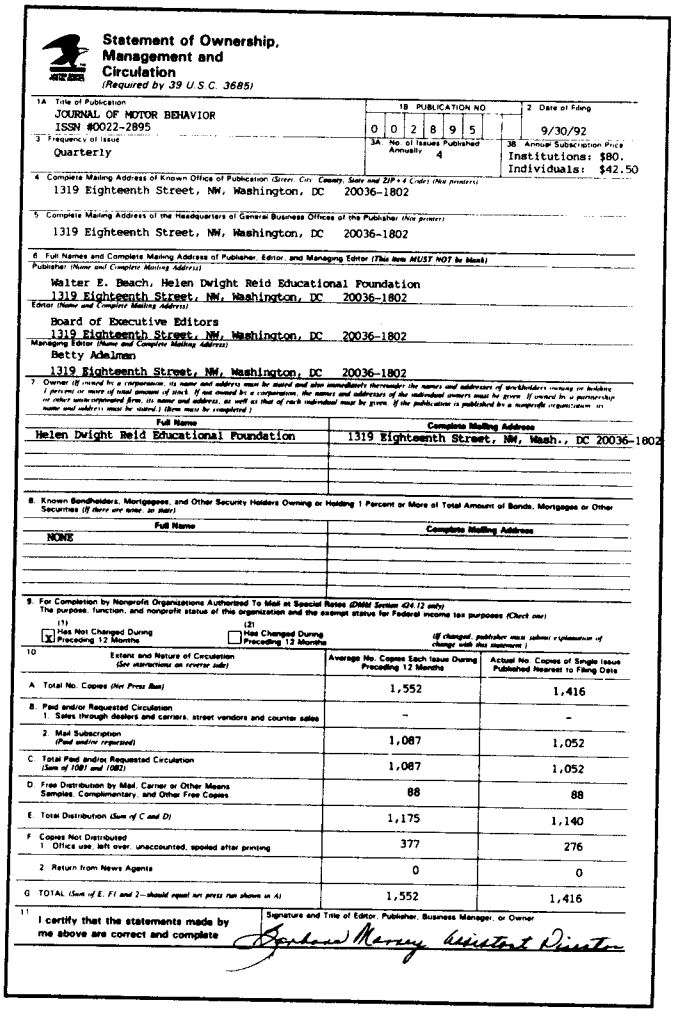

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10 Extent and Nature of Circulation (See instructions on reverse side)	Average No. Copies Each Issue During Preceding 12 Months	Actual No. Copies of Single Issue Published Nearest to Filing Date
A. Total No. Copies (Net Press Run)	1,552	1,416
B. Paid and/or Requested Circulation 1. Sales through dealers and carriers, street vendors and counter sales	-	-
2. Mail Subscription (Paid and/or requested)	1,087	1,052
C. Total Paid and/or Requested Circulation (Sum of 10B1 and 10B2)	1,087	1,052
D. Free Distribution by Mail, Carrier or Other Means Samples, Complimentary, and Other Free Copies	88	88
E. Total Distribution (Sum of C and D)	1,175	1,140
F. Copies Not Distributed 1. Office use, left over, unaccounted, spoiled after printing	377	276
2. Return from News Agents	0	0
G. TOTAL (Sum of E, F1 and 2—should equal net press run shown in A)	1,552	1,416

11 I certify that the statements made by me above are correct and complete. Signature and Title of Editor, Publisher, Business Manager, or Owner: Assistant Director

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