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Why Cats Pace on the Treadmill

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BLASZCZYK, J. AND G. E. LOEB. *Why cats pace on the treadmill.* PHYSIOL BEHAV **53**(3) 501–507, 1993.—There have been many studies suggesting that locomotion on a treadmill tends to be different than locomotion at similar velocities overground, but no satisfactory mechanical or neural mechanisms to account for the differences have been identified. The most prominent difference is the tendency to adopt a pacing gait for both walking and trotting speeds, in which the legs on one side of the body move in phase as lateral couplets rather than the typical diagonal couplet pattern seen overground. Using conventional video analysis, we quantified the gait patterns of intact, adult cats walking at various speeds overground and in a motorized treadmill. We noted that cats paced most frequently when they were at the front end of the treadmill enclosure, and that this gait was associated with an extended stride length that permitted the animals to maintain a higher duty factor of support (mean number of feet on the ground). We propose that the animal extends its stride specifically to improve the duty factor in anticipation of sudden stops of the treadmill belt and that it converts abruptly from diagonal to lateral gait because the extended stride results in collisions between ipsilateral hind and front feet.

Locomotion Treadmill Gait Cat

MOTORIZED treadmills are a great convenience for the study of cyclical locomotor behavior because long sequences at a controlled velocity can be obtained while the subject remains virtually stationary with respect to recording equipment. However, there have been long-running debates about whether the gaits so recorded are identical to those that would have been produced by locomotion at a similar speed on a stationary surface. In both humans and animals, a number of differences have been claimed using data on footfall patterns, limb segment kinematics, and EMG activity (1,4,9,13,15–18,20,21). Given the mechanical coupling among these variables, any change in the more global variables (footfall patterns or kinematics) implies changes in the lower order neuromuscular activity. Electrophysiological studies are conducted almost exclusively on the treadmill because the preparations are often surgically or pharmacologically reduced and because it is difficult to transmit multichannel, wideband data telemetrically from a small, freely moving animal. Thus, the relationship between overground and treadmill locomotion is central to the interpretation and comparability of virtually all data aimed at a reductionistic understanding of locomotion and its sensorimotor control.

One of the most frequently noted and more obvious features of treadmill locomotion in cats is a tendency to adopt a lateral-couplet rather than a diagonal-couplet gait at both walking and trotting speeds [in the terminology of (12)]. This pacing gait is characterized by in-phase motion of the ipsilateral fore- and hindlimbs, rather than the more typical overground pattern in which the hindlimb completes its swing and is set down before the ipsilateral forelimb is lifted out of stance. In this study, we quantified the gaits observed in normal cats in terms of lateral vs. diagonal tendencies in order to correlate changes in these tendencies with various aspects of treadmill locomotion. We discovered that an increased tendency to pace was correlated with the animal's momentary longitudinal position in the treadmill and with apparent attempts to maximize the mean support factor for any given forward speed.

METHOD

Six adult cats of either sex were trained to walk and run with different velocities on a motor-driven (¾ hp, Zero-max continuously variable mechanical drive), enclosed treadmill (0.3 m wide by 1.5 m long) and in a similarly narrow overground runway (0.3 m wide by 3 m long). The performance of the task was reinforced with food that was offered at the front of the runway or treadmill toward which the animal was facing. Aversive stimuli were never used.

The positions of the limbs were recorded at 60 fields/s by a video camera positioned perpendicular to the middle of the treadmill or runway so as to view the cat from the left lateral aspect through the glass enclosure. Before every experimental session the video camera was calibrated with two markers placed 0.5 m apart horizontally in the plane of locomotion. The corresponding distance between these two markers on the video images was measured and used to calibrate the limb movements.

During the overground locomotion trials, cats were allowed to move at their own preferred speeds, which ranged from 0.6 to 1.5 m/s. The runway was long enough to accommodate about

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TABLE 1

LIMB MOVEMENT PARAMETERS IN CATS DURING OVERGROUND LOCOMOTION

Cat. No.	Velocity (m/s)	Number of Steps	Stance (ms)	Swing (ms)	Stride Length (m)	Duty Factor
g103	0.72	15	424 ± 27	243 ± 24	0.47 ± 0.07	0.64
g104	0.91	12	396 ± 34	273 ± 27	0.60 ± 0.09	0.59
jb02	1.46	8	283 ± 37	233 ± 23	0.75 ± 0.18	0.55
jb03	0.76	16	403 ± 23	271 ± 19	0.51 ± 0.11	0.60
jb04	1.05	46	312 ± 16	244 ± 11	0.59 ± 0.05	0.56
jb05	0.64	31	470 ± 21	301 ± 17	0.49 ± 0.07	0.61

six strides from a standing start, but only the central region covering 3–4 strides was recorded on videotape. Several trials of regular walking over the length of the runway were recorded for each animal. The first and last steps of these regular sequences were skipped because of differences in duty factor that are known to occur during acceleration and deceleration phases (2). Only measurements from steady-state locomotion have been used for analysis.

In the treadmill, the belt speed was brought gradually up to the preferred velocities of each cat as determined from recordings of its overground locomotion. Longer sequences of steady-state locomotion could be recorded in the treadmill, usually 20–40 s before the belt was slowed smoothly to a stop. The length of the treadmill was divided into three equal sectors: front, middle, and rear. During each trial, the number of strides performed with a particular gait was calculated for every sector, excluding those strides associated with any sudden acceleration or deceleration to change position in the treadmill.

Each sequence of cat locomotion was transferred to an instant replay videodisk (Eigen Corp., Boulder, CO) and analyzed field by field. An on-screen display of IRIG-B timecode in milliseconds (Datum Corporation, Model 2400) allowed for easy quantification of the temporal parameters of locomotion. Basic step-cycle parameters such as swing-stance duration and stride length were measured from the video stills and used to compute parameters such as hindlimb stride length, mean velocity of overground locomotion, phase difference between limb movements, and duty factor (fraction of cycle time during which the left hindlimb was in contact with the surface). We estimate that stride length should be accurate to within 10% (based on worst-case horizontal resolution of the video for overground locomotion) and temporal factors will be accurate to one video field interval (17 ms), which corresponds to less than 7% error in stance phase and 8% error in swing phase at the fastest gaits studied. The ipsilateral (left side) phase difference was calculated for each step cycle as the time interval between the onsets of stance phase in the forelimb and hindlimb divided by the duration of the step cycle—the sum of successive stance and swing epochs (12). The various kinematic parameters were analyzed using nonparametric statistics (Wilcox test).

RESULTS

Overground Locomotion

All cats studied used typical diagonal gaits on the stationary pathway for both walking and moderate trotting speeds. Their preferred locomotor speeds ranged from 0.6 to 1.46 m/s. Because of the short length of the experimental pathway, neither fast trotting nor galloping was observed. At the relatively slow speeds studied here, the gaits were always symmetrical except in the transitions described below, such that interlimb phase between fore and hindlimbs on one side was mirrored by a similar phasing contralaterally. Phase differences between the two forelimbs were 0.48 ± 0.04 and between the hindlimbs were 0.46 ± 0.06, consistent with symmetrical gait. Each cat used a similar speed in all successive trials so the parameters analyzed represented means of all collected trials. Summary parameters of these two movements are presented in Table 1. For all cats walking in the overground runway, the grand mean value of the unilateral phase difference was 0.23 ± 0.03, which is typical of a diagonal walk (12). Unilateral phase differences did not change with velocity over the range of walking speeds (0.6–1.05 m/s).

Treadmill Locomotion

At treadmill speeds matched to the preferred overground speed in each cat, the mean stride length and stance duration were always greater on the treadmill than overground (compare Tables 1 and 2); in some cases the differences were quite striking (jb02 and jb04). The aggregate differences were statistically significant at the 95% confidence level ($Z = 2.04$). The increased stride length on the treadmill appeared to be related to a generally lowered body posture, although not the sort of crouching gait that is commonly produced by aversive conditioning (13). The head also seemed to be carried lower on the body, although this was not quantified. There was no trend in the swing phase durations, which were more similar for all speeds and walking surfaces.

The interlimb coordination of treadmill walking was significantly different from that of overground locomotion. There was a shift from the diagonal couplet typical for overground locomotion toward a lateral couplet (pacing) on the treadmill. The mean phase difference between ipsilateral limbs was velocity dependent and changed over a relatively wide range from 0.27 to 0.11. An increase of the treadmill speed resulted in a persistence of the walking cadence (duty factor significantly greater than 0.5) accompanied by a decline of the ipsilateral phase difference. Figure 1 shows that higher mean duty factors were associated with smaller unilateral phase differences, a pattern more typical of the pacing walk (duty factor = 0.75; phase difference = 0) than with the diagonal walk (duty factor = 0.75; phase difference = 0.25) or diagonal trot (duty factor = 0.5; phase difference = 0.5).

The mean phase difference data in Fig. 1 obscure an important phenomenon. In fact, increasing speed on the treadmill usually resulted in an abrupt rather than gradual transition from diagonal to parallel coupling. Values typical of a diagonal couplet (ipsilateral phase difference = 0.25) changed to those typical of a lateral couplet (ipsilateral phase difference = 0) within one

TABLE 2

LIMB MOVEMENT PARAMETERS IN CATS STEPPING ON THE TREADMILL

Cat. No.	Velocity (m/s)	Number of Steps	Stance (ms)	Swing (ms)	Stride Length (m)	Duty Factor
g103	0.70	26	447 ± 26	237 ± 19	0.51 ± 0.09	0.65
g104	0.91	14	413 ± 29	249 ± 24	0.62 ± 0.12	0.62
jb02	1.46	22	329 ± 21	238 ± 18	0.86 ± 0.11	0.58
jb03	0.76	19	439 ± 26	265 ± 17	0.73 ± 0.08	0.62
jb04	1.05	46	449 ± 23	258 ± 12	0.76 ± 0.12	0.64
jb05	0.64	28	486 ± 31	316 ± 21	0.52 ± 0.14	0.61

stride. Figure 2 shows the footfall timing diagram and stride length changes associated with such a transition. Between step numbers 3 and 4 for the left hindlimb, the stride length increased by about 30% as the limb was kept on the treadmill surface until it was lifted nearly simultaneously with the left forelimb. Figure 3 shows another such transition in which the animal achieved a fairly abrupt increase in duty factor accompanied by an even more abrupt shift from diagonal to parallel walking.

Given that the observed gaits reflected more nearly a bimodal rather than a normal distribution, it seems more appropriate to consider the percentage of time that the animals spent in gait that was essentially diagonal (ipsilateral phase 0.13–0.5) versus essentially parallel (ipsilateral phase difference 0–0.12). This turned out to be very dependent on the longitudinal position in the treadmill at which the animal happened to be walking (Fig. 4). Lateral gaits were twice as common as diagonal gaits near the front of the treadmill, but were seen in only about one-sixth of the steps performed near the rear of the treadmill.

DISCUSSION

The Dilemma as Perceived by the Investigator

Several mechanisms have been put forward to account for differences between overground and treadmill locomotion:

1. Physics of locomotion on a moving belt. This mechanism is negligible unless the treadmill is poorly designed so that it does not maintain a steady velocity (zero acceleration) regardless of what the subject does. The treadmill can affect the cat's locomotion only if it can convey mechanical energy to the animal. This requires the application of a force via the contact points

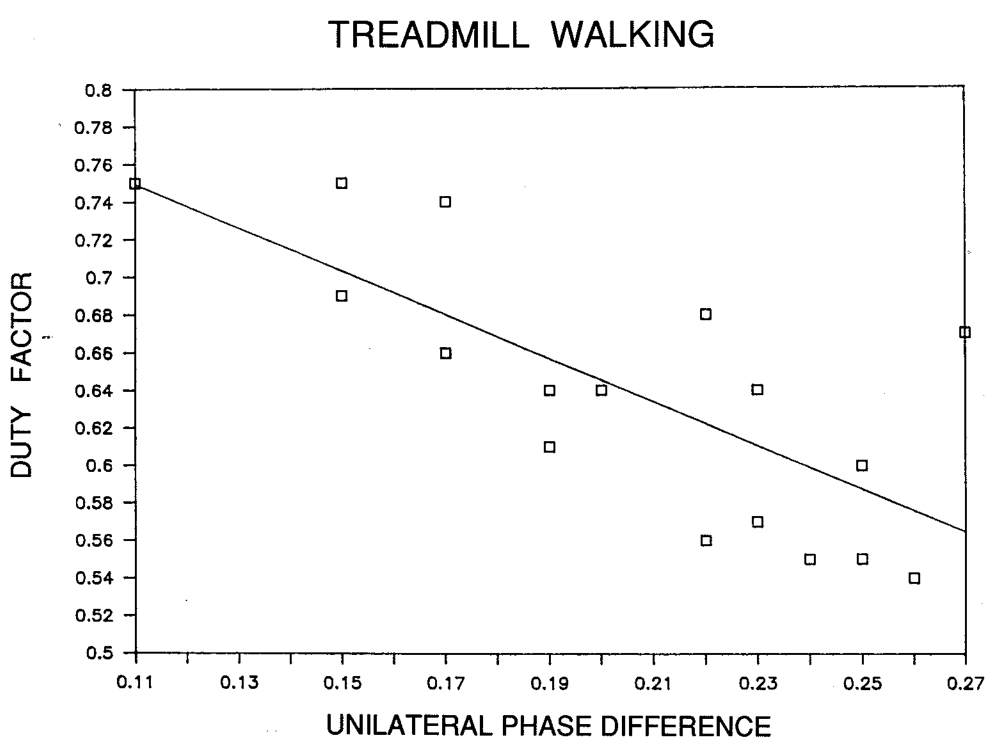

FIG. 1. Mean duty factor (proportion of step cycle during which the left hindlimb was in contact with the treadmill surface) plotted against mean unilateral phase difference (difference between onset of stance in left hind- and left forelimbs as proportion of step cycle duration) for sequences of locomotion at various speeds in all six animals (slope = −1.15, r = 0.75).

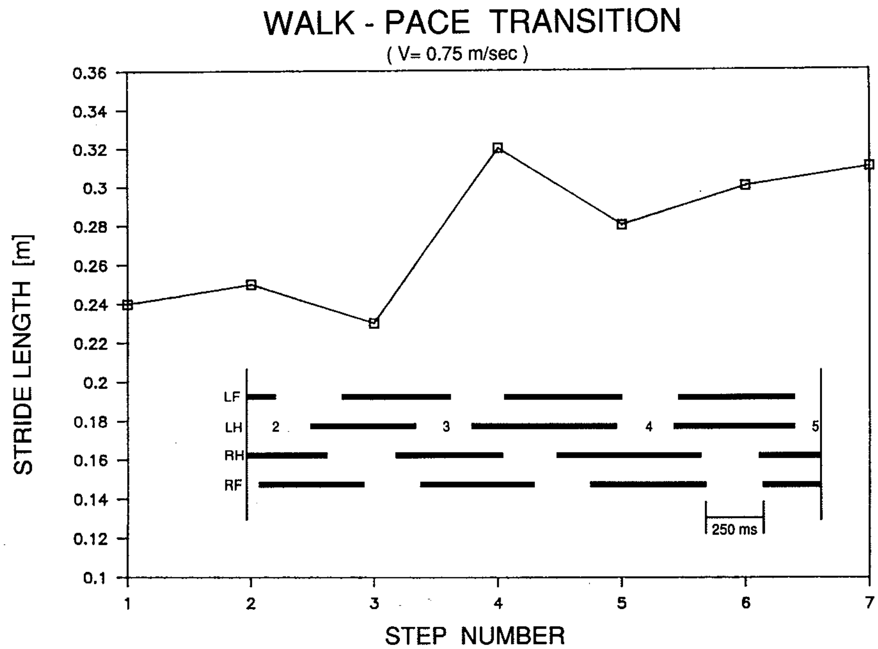

FIG. 2. Step-by-step changes in left hindlimb stride length for transition from diagonal to pacing walk between steps 3 and 4 at 0.75 m/s on the treadmill. Inset shows periods of stance versus time (black bars) for left forelimb (LF), left hindlimb (LH; step numbers keyed to main plot), right hindlimb (RH), and right forelimb (RF).

with the animal, that is, the feet. The vertical component of the ground reaction force should be the same as overground if the belt is flat and moving purely horizontally. The horizontal component is likewise the same except that there is a constant velocity with respect to the external inertial reference frame. From Newton's Law (F = mA), it is apparent that a zero acceleration (i.e., constant velocity) cannot create a force on the mass of the cat. Physically, walking in the treadmill should differ from walking overground only by the resistance of air flow, which is negligible at these speeds of around 1 m/s. However, poor design of the treadmill can produce artefactual differences such as inclines, fluctuations in forward speed of the belt, or inconsistencies in the vertical support. These may affect both the mechanics and the perceived stability in ways that could cause the subject to change motor program.

2. *Exteroceptive cues when walking in a stationary enclosure.* Normal walking on a stationary surface results in visual flow fields and acoustic doppler shifts as a result of relative velocity between the subject and stationary features in the environment. Walking on a moving belt results in a cognitive dissonance between these expectations and the experience that most visual and auditory features of the environment are not moving relative to the subject. Why or how this should affect gait has never been stated explicitly.

3. *Learning effects.* Walking on a powered treadmill starts out as a novel experience for subjects who have not tried it before. In order to avoid striking either end of the finite enclosure, the subject must adjust locomotor speed to match that of the belt rather than adopting a purely voluntary and perhaps fluctuating gait speed. Essentially this means reinterpreting the exteroceptive cues noted above to control directly the gait that the subject selects. Gait changes have been noted over successive trials of treadmill walking (20) but, again, no specific reasons or mechanisms have been put forward.

The adoption of a lateral, rather than a diagonal, gait has been viewed as counterintuitive in a novel or demanding situation such as a treadmill because lateral gait is less stable (21), requiring a shift of the entire body support from one side to the other. At walking speeds, diagonal gait permits an almost constant, statically stable support system in which three legs are always on the ground, whereas lateral gait fluctuates between periods of two-legged and four-legged support although obtaining the same mean duty factor [see Fig. 2 and (12)]. Coss et al. (4) could only conclude that "the abnormal use of the pace by cats on a treadmill must relate to the mechanics of support and the dynamics of the situation more than the sensory cues of vision and hearing."

The Task as Perceived by the Animal

We would argue that the main demand of treadmill locomotion is matching gait speed to a belt speed that is being changed unpredictably by the operator. A mechanical consideration of this problem suggests strategies that agree remarkably well with those apparently adopted by the cat:

1. The most drastic change in speed likely to be encountered is sudden stopping of the motor.
2. Coping gracefully with such a stop becomes more difficult the closer one gets to the front wall of the treadmill.
3. Sudden changes in forward velocity require horizontal ground reaction forces.
4. Ground reaction forces are most easily produced when there are more feet in contact with the ground.
5. Increasing the mean duty cycle of support points requires increasing the duration of the stance phases relative to the step cycle period.
6. Forward speed of locomotion, with respect to the ground, is the product of stride length (horizontal motion of the foot in the swing phase) divided by step cycle period.

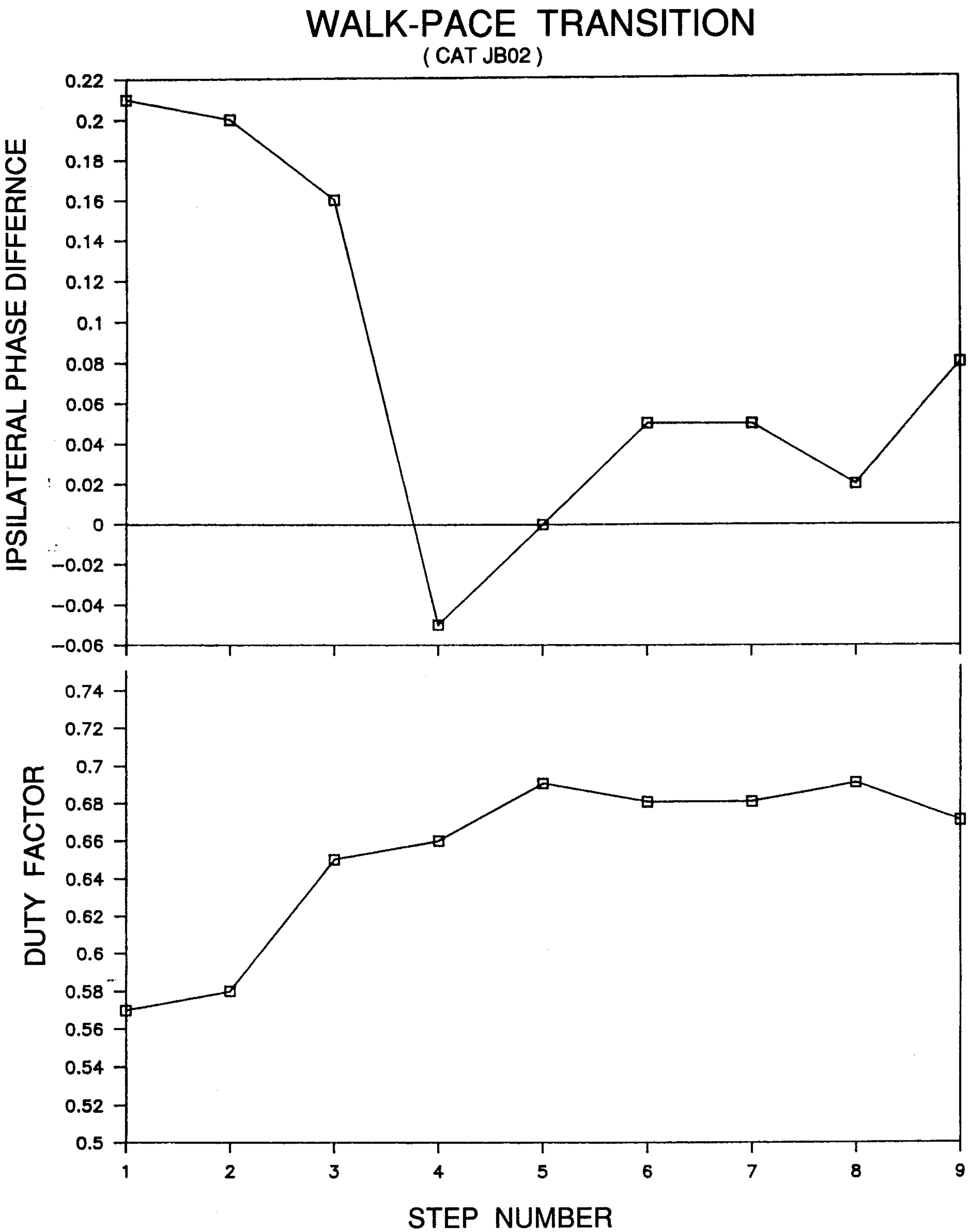

FIG. 3. Abrupt transition between diagonal and pacing walk at a relatively fast treadmill speed (1.46 m/s), showing sudden decline in one step cycle for the phase difference between the left hind- and forelimbs (top graph) associated with an increase in duty factor of the left hindlimb (bottom graph).

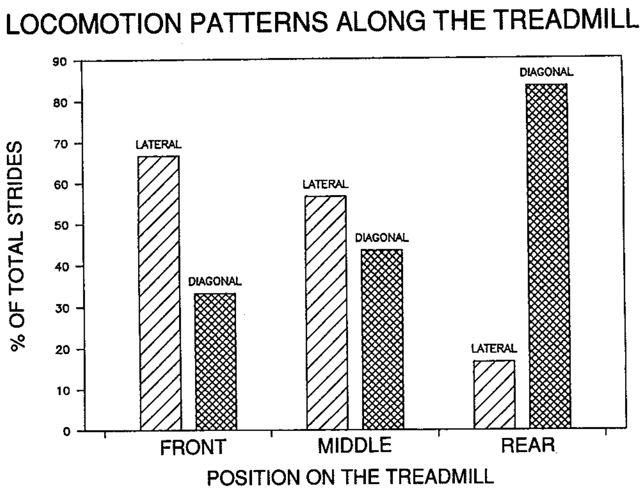

FIG. 4. Frequency of occurrence of lateral gait patterns (ipsilateral phase differences 0–0.12) vs. diagonal gait patterns (ipsilateral phase differences 0.13–0.5) when the cats were located in the front third of the treadmill (n = 72 step cycles), middle third (n = 51 step cycles), and rear third (n = 32 step cycles).

7. Making the cycle period shorter without decreasing the stance phase is difficult because the swing phase of locomotion tends to have a relatively constant duration regardless of gait pattern or speed (8), probably because it requires excessive force to drive this pendular motion much beyond its mechanically resonant frequency.
8. Points 5–7 suggest that the animal will adopt an unusually long stride length to achieve a particular velocity while maximizing the relative duration of the stance phase.
9. The cat is a quadruped whose leg lengths are balanced to its torso length and whose fore- and hindlimb girdles have the same width. It tends to place each hindfoot on the same point on the ground that its ipsilateral forefoot just occupied (which is useful for locomoting on irregular terrain).
10. If such an animal tries to increase its stride length during a diagonal gait, its hindfeet will immediately collide with its forefeet. Hildebrand (11) noted this problem in accounting for the tendency of certain long-legged breeds of dogs to utilize pacing gaits overground.
11. By switching to a lateral, pacing gait, the in-phase motion of the ipsilateral limbs avoids their entanglement, permitting large increases in stride length and, hence, increased mean support (duty cycle) for a given forward speed [see also (14)]. This would improve the animal's ability to adjust to sudden speed changes such as stopping the belt. It also accounts for the ability of pacing horses to go faster than trotting horses (10).
12. A lateral gait does result in a less stable posture in the frontal plane, which would make direction changes more difficult. However, the one thing that the animal can count on in a treadmill is that it will not need to change direction, only speed. Nevertheless, there may be some increased energetic cost associated with the extended, lateral gait.

Operationally, we propose that the cat adopts the gait that it believes will permit it to cope best with the most pressing motor control problem of the moment. As treadmill speed increases, the walking animal must decide whether to extend its walking stride in order to maintain contact with the treadmill or to break into a diagonal trot. It is more likely to elect increasing stride if it is near the front of the treadmill and if it is uncertain about the continued motion of the belt. As stride length increases in the diagonal walk, the hindfoot will eventually collide with the forefoot, forcing a conversion to a more lateral gait. As the speed increases, the extended pacing walk will become more awkward and the animal may convert to a pace or a trot. If it is in a trot, then further increases in the treadmill speed will eventually force another, similar decision. The animal must either break into a gallop, which further reduces mean contact time, or extend its stride, which requires a pace to avoid foot collision. At the fastest galloping speeds, long stride length can be combined with the large phase difference between fore- and hindlimbs by placing the hindfeet lateral to the forefeet to avoid collisions (12).

Interpretation of Locomotor Data

The above analysis can explain a number of observations and paradoxes presented by prior studies of treadmill locomotion. One of the most profound differences between treadmill and overground locomotion, identified by Wetzel et al. (21) and Coss et al. (4), was the tendency to pace on the treadmill, which they found surprising because of its presumed instability. Miller et al. (16) found a similar, puzzling tendency, along with the tendency to transit from a walking pace to a trot at faster speeds; they noted that both transitions tended to be abrupt. Lockard et al. (13) noted that pacing on the treadmill was more common in animals trained with food reward and least common in animals trained with electrical shocks, which produced a lowered body posture that would make it difficult to extend stride length. Vilensky and Patrick (20) noted an increased tendency to pace at all speeds, but with extended training over several weeks, cats decreased stride lengths at all speeds (computed by us from data in their Table 1). With training, cats tend to show less interest in the food and operator at the front of the treadmill, so they may have adopted shorter, diagonal steps at the back of the treadmill; they may also have developed an increased confidence that the belt would not be stopped suddenly. Interestingly, humans also exhibit a tendency to increase stride length and support time on a treadmill vs. overground locomotion at similar forward speeds, particularly for the faster speeds where the ability to stop may seem more critical (18).

If one assumes that all of these gait shifts reflect conscious, purposeful decisions by the subject, then it is difficult to account for the observations of occasional pacing in various reduced preparations including decerebrate and hindlimb deafferented animals and in swimming and air stepping (15). It may be that the parallel gaits are equally or more likely to be expressed than the diagonal gaits in reduced preparations. English (6) showed that lesions of the thoracic (but not cervical) dorsal columns (carrying proprioceptive information between the two limb girdles) resulted in a preponderance of parallel gait during overground locomotion. Vestibular information on lateral stability that might give preference for diagonal gaits under intact, overground conditions would be lacking in decerebrate and spinal preparations because the head is fixed mechanically.

It is possible that the mechanisms that trigger and control the changes in interlimb coordination in the gait transitions are primarily segmental, with descending commands producing only indirect influence on the probability of different transitions. Recently, Cruse and Warnecke (5) analyzed interlimb coupling during treadmill locomotion in normal cats and concluded that the strength of coupling between the ipsilateral limbs was lower than between contralateral limbs, which is consistent with the emergence of either diagonal or lateral gaits under a variety of circumstances. The ability of the limbs to extend their stride length and the propensity for the paws to collide will depend complexly on the posture adopted by or imposed on the animal and the nature of the substrate on which the behavior takes place [e.g., being held in the air or swimming in water; (16)]. We occasionally observed frank collisions between paws in association with the abrupt conversions between diagonal and lateral gaits. Given the usually close ipsilateral paw placements in diagonal gait, it is not possible to eliminate the possibility that such contacts were always associated with the abrupt gait conversions. Certainly such contact would be expected to result in vigorous discharge of both cutaneous and proprioceptive afferents that have strong interlimb reflex projections (19). However, English and Lennard (7) found a wider range of more gradual phase transitions in overground locomotion and concluded that several different neural systems probably modulated continuously the degree of coupling between the various limbs.

Somatosensory input has been used in another way by Blaszczyk and Dobrzecka (3) to induce lateral gait in puppies. A restraining tie between the ipsilateral feet produced perturbations at the points in the step cycle when the ipsilateral feet were furthest apart rather than closest together. Prolonged training (several months) resulted in a tendency to pace that persisted for several weeks after the restraints were removed.

The tendency of an animal to adopt parallel vs. diagonal gaits seems to depend on a complex mix of factors, not just the presence or absence of a moving belt. In intact, unrestrained animals, a variety of experiential and cognitive factors probably enter into their decisions. In reduced preparations, the factors probably include the position of the body over the treadmill as well as the neural changes produced by surgical and/or pharmacological interventions. Many of the relevant behavioral and postural factors are often not considered or specified by researchers concerned primarily with neuromuscular activity rather than kinematics. At the least, it would seem to be useful to identify which gaits the animals have actually adopted before comparing results between trials, animals, and studies.

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