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The penguin waddling gait pattern has a more consistent step width than step length

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Abstract

Previous research has indicated that the sagittal plane gait dynamics of humans are more stable and less dependent on active neural control, while the frontal plane dynamics are less stable and require greater neural control. The higher neural demands of the frontal plane dynamics are reflected in a more variable step width than step length. Greater variability in the step width occurs because humans modulate their foot placement for each step to ensure stability and prevent falls. Compared to other terrestrial animals, penguins appear to have excessive amount of frontal plane motion in their gait that is characterized as waddling. If excessive frontal plane motion requires additional neural control and is associated with falls, it would seem that evolutionary pressures would have eliminated such locomotive strategies. Here we measured the step length and width variability to determine if waddling results in a less stable gait. Remarkably, the variability of the step width was less than the variability of the step length. These results are directly opposite of what has been reported for humans. Hence, our data indicate that waddling may be an effective strategy for ensuring stability in the frontal plane dynamics. © 2008 Elsevier Ltd. All rights reserved.

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1. Introduction

Although walking is easy to observe, it is quite difficult to understand how a stable gait emerges from all degrees of freedom present in the neuromuscular system. Globally, the control of the bipedal gait pattern can be divided into neural strategies during the stance and swing phase. During the stance phase, the center of mass moves just outside of the base of support and creates a dynamically unstable condition (Alexander, 2003; Winter, 1991). Few control strategies are available during the stance that influences the trajectory of the center of mass. Rather to maintain stability, the nervous system adjusts the step length and width to redirect the center of mass to remain within the base of support of the locomotive system (Winter, 1991).

McGeer (1990) suggested that much of the sagittal plane stability and selection of a step length is governed by the mechanics of the locomotive system. This has been demonstrated in passive dynamic walking robots that have no on-board control algorithm that selects the step length. Remarkably, these walking robots are capable of producing human-like stable gaits that are passively stable to slight perturbations. However, these walking robots are not stable in the frontal plane, and an active feedback control algorithm must be employed to prevent falls if the frontal plane motion is not constrained (Kuo, 1999; McGeer, 1990). Several control algorithms have been suggested for insuring stability in the frontal plane of motion of the robot's gait. Such control algorithms include actively modifying step width, and moving the torso from right to left for each step (Kuo, 1999).

The concepts from passive dynamic robots can be extended to how humans control gait. Similar to passive dynamic walking robots, the sagittal plane gait dynamics are more stable and less dependent on active neural control, while the frontal plane motion appears to be less stable and requires a greater amount of neural control (Bauby and Kuo, 2000; Grabiner and Troy, 2005; Owings and Grabiner, 2004). The higher neural demands of the

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frontal plane dynamics are reflected in the more variable step width than step length (Bauby and Kuo, 2000; Grabiner and Troy, 2005; Owings and Grabiner, 2004). Greater variability in the step width occurs because humans modulate the medial–lateral placement of their foot for each step to ensure stability and to prevent falls (Bauby and Kuo, 2000; Winter, 1991). Interestingly, it has been demonstrated that if an external medial–lateral stabilizer is attached at the waist, the step width variability of the human gait is reduced (Dean et al., 2007; Donelan et al., 2004). All of these experimental results provide scientific evidence that the frontal plane motion of gait must be actively controlled by the nervous system for a stable gait.

Although animals demonstrate a remarkable ability to navigate complex terrains, the biomechanical variables that ensure stability have not received considerable attention. Historically, the number of legs present in the locomotive system has been used to quantify the stability of an animal's gait pattern (Alexander, 1991; Javes AS, 1980; Ting et al., 1994). A greater number of legs allow the animal to position itself in more of a sprawled-like posture where it can be more resistant to external (i.e., wind) or internal disturbances (i.e., neural errors) that occur during the gait pattern. Potentially, the higher number of legs may be an effective evolutionary adaptation that reduces the amount of neural control that is necessary for ensuring stability since the neural system only needs to ensure that three legs are on the ground at all times, and the center of mass lies within the boundaries (Ting et al., 1994).

Static stability may have its advantages at slow speeds; however, even polypedal animals such as the cockroach demonstrate dynamic stability at high speeds (Ting et al., 1994). During dynamic stability, the center of gravity may be positioned close to or even outside of the base of support (Ting et al., 1994; Winter, 1991). In this case, the animal must properly position the feet for the next step of the gait cycle to ensure that the movement system remains stable and does not topple over. Potentially in a dynamic system, the rules that govern where the feet must be positioned may be more flexible and allow for greater adaptability. Such flexibility has been suggested to be vital for animals to climb and adapt their locomotive pattern to an irregular terrain (Ting et al., 1994). Further explorations of a wide range of animals with bipedal and polypedal locomotive architecture are necessary to fully understand the tenets of static and dynamic gait stability.

Compared to other terrestrial animals, penguins appear to have an excessive amount of frontal plane motion in their bipedal gait that is characterized as waddling (Pinshow et al., 1977). The waddling gait of the penguin has previously been noted to have a higher metabolic cost than other terrestrial birds that are of similar mass (Dewasmes et al., 1980; Pinshow et al., 1977). Originally it was speculated that the higher metabolic cost was related to the waddling gait's inability to conserve mechanical energy. However, previous biomechanical experiments indicate that the lateral motion of the penguin is actually an effective method for conserving mechanical energy. In fact, penguins recover the highest amount of mechanical energy for any animal (Griffin and Kram, 2000). Currently, the higher metabolic cost of the penguin gait is speculated to be associated with their relatively short legs which may require the bird to walk with a higher stride frequency and generate faster muscular forces (Dewasmes et al., 1980; Griffin and Kram, 2000; Pinshow et al., 1977).

Superficially, the penguin's waddling gait pattern appears awkward and more susceptible to falls. Potentially, their gait may be less stable because the dynamics of the waddling gait pattern places the center of mass closer to or outside of the boundaries of stability. No efforts have been made to explore the dynamic stability of the penguin gait. Although penguins do spend much of their life in the water, terrestrial locomotion is a prominent feature of their reproductive success. During the breeding period, penguins walk long distances to the rookeries (Pinshow et al., 1976). This journey offers both a metabolic and stability challenge to the penguin's locomotive system. If the excessive frontal plane motion of the penguin gait requires additional neural control for ensuring dynamic stability, it would seem that evolutionary pressures would have eliminated such locomotive strategies. However, since previous investigations have provided evidence that waddling is an effective mechanism for conserving mechanical energy (Griffin and Kram, 2000), it is possible that it is also an effective strategy for ensuring a dynamically stable gait.

Quite often nature has already conducted many of the necessary scientific experiments for optimizing the stability of the locomotive system. Hence, investigating the locomotive patterns of species with diverse movement strategies can reveal new insights on the control properties for stable locomotion. Here we use a comparative approach to further understand the principles of stable bipedal locomotion by exploring the penguin's unique waddling gait pattern. We measured the step length and width variability of the penguin's gait to determine if waddling results in a less stable gait. Since waddling results in an increased amount of frontal plane movement, we hypothesized that a penguin's gait pattern would have greater step width variability than step length variability.

2. Methods

Ten king penguins (*Aptenodytes patagonica*; height: 68.1 ± 0.8 cm; weight: 11.1 ± 0.3 kg) from a local aquarium (Moody Gardens, Galveston, TX) participated in this investigation. All penguins were in good health with no gait altering musculoskeletal conditions. The research protocol was approved by the animal safety board for Moody Gardens and the University of Houston.

A custom-built walkway $(457 \text{ cm} \times 91.5 \text{ cm} \times 106.5 \text{ cm})$ was used to collect the penguins' walking trials. The floor



Fig. 1. The penguin walked down a custom-built walkway that had a *Gaitrite* pressure mat embedded in the walkway. The pressure mat registered the digital footprints for every step of the penguin's gait.

and walls of the walkway were made of plywood with two large Plexiglas viewing windows (Fig. 1). A *Gaitrite* pressure mat (Gaitrite, CIR Systems Inc., Havertown, PA) was embedded on the walkway floor and was used to collect the digital foot positions of the penguin gait as it walked down the walkway. The spatial resolution of the pressure mat was 1.27 cm (13,824 pressure sensors arranged in a 48×48 matrix), and the temporal resolution was 100 Hz. Previous research has demonstrated that the *Gaitrite* system is a reliable and valid instrument for measuring spatial temporal gait parameters (Bilney et al., 2003).

All trials were collected on the same day with a room temperature of 1.1 °C. Prior to collecting the trials, the penguins were allowed to explore the walkway until an apparent comfort level with their surroundings was reached. Placing a zookeeper at the opposite end of the walkway was enough encouragement for the penguins to traverse through the walkway at a self-selected pace. We excluded any trials where a penguin hesitated or stumbled while walking through the walkway. All penguins performed 10 walking trials, which consisted of 15–20 steps per trial. Therefore, approximately 200 steps were analyzed for each penguin.

Custom laboratory software was created to determine the step lengths (X) and step widths (Y) of the penguin's gait by subtracting the right and left digital foot coordinate positions. Step length was calculated as the fore-aft displacement between the two feet, while the step width was calculated as the medial-lateral displacement between the two feet. The standard deviations of the step lengths and widths were calculated to determine the variability in the gait pattern. A correlated *t*-test with a 0.05 α level was used to determine if the step length variability was greater than the step width variability.

3. Results

The average velocity for the walking trials was 0.26 ± 0.05 m/s. This walking velocity is similar to previously reported speeds for penguins in the wild (Dewasmes et al., 1980). The mean and standard deviations of the step length and width of the penguins' gait patterns are presented in Figs. 2 and 3 respectively. Remarkably, our results indicate that the penguins' step width variability was significantly (p=0.0001) less than step length variability. These results indicate that penguins select a more consistent step width than their step length.

4. Discussion

The results presented here reject our hypothesis and indicate that penguin waddling results in the selection of a more consistent step width. Our conclusions are directly opposite of what has been found for humans, where step width is more variable due to the increased amount of neural control required for the frontal plane dynamics (Bauby and Kuo, 2000; Grabiner and Troy, 2005; Owings



Fig. 2. Means of the step length and step width of the penguins' gaits.



Fig. 3. Standard deviations of the step length and step width of the penguins' gaits.

and Grabiner, 2004). Hence waddling appears to result in a more stable gait than previously thought. The results presented here are aligned with the recent experiments that have determined that penguin waddling is an advantageous movement strategy for recovering mechanical energy (Griffin and Kram, 2000). The combined results of Griffin and Kram (2000) and ours suggest that modulation of the trunk with a waddling gait pattern may be a more efficient control strategy for ensuring stability than modulation of foot placement. It is alternatively plausible that the results presented here and Griffin and Kram (2000) may be related to the leg and trunk morphological difference between humans and penguins. In spite of this possibility, the experimental results presented here are intriguing and warrant further research on how the waddling gait may influence the dynamic stability of the gait pattern.

The experimental and theoretical grounds for this investigation were based on the notion that the amount of variability in the stepping pattern could be used to define the stability of the gait pattern. However, this notion should be observed with care because an increased amount of variability may not fully quantify the stability of the locomotive system (Li et al., 2005). It is possible that the larger amount of variations in the selected step lengths may be related to the fact that they were stable and did not require the nervous system to govern a precise foot placement. Alternatively, a more precise frontal plane foot placement may be required by the nervous system if the frontal plane dynamics are considerably less dynamically stable and more susceptible to perturbations. Our future projects are directed toward exploring these concepts with rocking rigid body models that are similar to the penguin's unique walking pattern. With these models we will be able to better define the stability of the walking pattern based on how the state variables of the system (i.e., angles and velocities) return back to their steady state after a perturbation (Full RJ, 2002), and how much additional control is necessary to ensure stability in the model's gait. These models will provide a stronger case as to how waddling influences the penguin's locomotive stability.

Insights from nature are often extended to scientific innovations and robotics. For example, many of the concepts from cockroach locomotion have been used for the development of robust hexapedal robots (Koditschek et al., 2004). Possibly, the insights from penguins may offer new inspirations for building stable bipedal walking robots that have improved mechanical efficiency. Many of the current passive dynamic walking robots have overcome frontal plane instabilities by incorporating a crutch-like gait or extra wide feet (Collins et al., 2005; Collins, 2001; McGeer, 1990). These mechanical solutions have no computational cost; however, they still lack much of the robust stability and flexibility demonstrated in nature. Alternatively, some bipedal walking robots have utilized over-engineered control algorithms to ensure stability (Collins et al., 2005). However, these robots lack efficiency and require extensive computational power that results in a limited battery life (Collins et al., 2005). Since a waddling gait appears to be stable and mechanically efficient, it may offer an alternative and simple control law that requires less battery power. Recently, a passive dynamic walking robot was constructed to incorporate a waddling-like gait for foot clearance and passive stability of the frontal plane dynamics (Collins et al., 2005; Tedrake, 2004). However, this walking robot still maintains the large feet that are characteristic of passive dynamic walking robots. No investigations have determined if a curve foot waddling pattern has the same mechanical efficiency and stability benefits noted in the penguin waddle. Additionally, no robotic designs have attempted to incorporate the torso waddling pattern noted in the penguin's gait. Future exploration of these concepts in computer simulations and walking robots may reveal new strategies for improved efficiency and stability.

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References

- Alexander, R., 1991. The gaits of tetrapods: adaptations for stability and economy. Zool. Soc. Lond. 48, 269–287.
- Alexander, R., 2003. Animal Locomotion. Princeton University Press, Princeton, NJ.
- Bauby, C.E., Kuo, A.D., 2000. Active control of lateral balance in human walking. J. Biomech. 33, 1433–1440.
- Bilney, B., Morris, M., Webster, K., 2003. Concurrent related validity of the GAITRite walkway system for quantification of the spatial and temporal parameters of gait. Gait Posture 17, 68–74.
- Collins, S., Wisse, M., Ruina, A., 2001. A three-dimensional passivedynamic walking robot with two legs and knees. Int. J. Robot. Res. 20, 607–615.
- Collins, S., Ruina, A., Tedrake, R., Wisse, M., 2005. Efficient bipedal robots based on passive-dynamic walkers. Science 307, 1082–1085.
- Dean, J.C., Alexander, N.B., Kuo, A.D., 2007. The effect of lateral stabilization on walking in young and old adults. IEEE Trans Biomed. Eng. 54, 1919–1926.
- Dewasmes, G., Le Maho, Y., Cornet, A., Groscolas, R., 1980. Resting metabolic rate and cost of locomotion in long-term fasting emperor penguins. J. Appl. Physiol. 49, 888–896.
- Donelan, J.M., Shipman, D.W., Kram, R., Kuo, A.D., 2004. Mechanical and metabolic requirements for active lateral stabilization in human walking. J. Biomech. 37, 827–835.
- Full RJ, K.T., Schmitt, J., Holmes, P., Koditschek, D., 2002. Quantifying dynamic stability and maneuverability in legged locomotion. Integr. Comp. Biol. 42, 149–157.
- Grabiner, M.D., Troy, K.L., 2005. Attention demanding tasks during treadmill walking reduce step width variability in young adults. J. Neuroeng. Rehab. 2, 25.
- Griffin, T.M., Kram, R., 2000. Penguin waddling is not wasteful. Nature 408, 929.
- Jayes AS, A.R., 1980. The giats of chelonians: walking techniques for very low speeds. J. Zool., Lond. 191, 353–378.
- Koditschek, D.E., Full, R.J., Buehler, M., 2004. Mechanical aspects of legged locomotion control. Arthropod. Struct. Dev. 33, 251–272.
- Kuo, A., 1999. Sabilization of lateral motion in passive dynamic walking. Int. J. Robot. Res. 18, 917–930.

- Li, L., Haddad, J.M., Hamill, J., 2005. Stability and variability may respond differently to changes in walking speed. Hum. Mov. Sci. 24, 257–267.
- McGeer, T., 1990. Passive dynamic walking. Int. J. Robot. Res. 9, 62-82.
- Owings, T.M., Grabiner, M.D., 2004. Step width variability, but not step length variability or step time variability, discriminates gait of healthy young and older adults during treadmill locomotion. J. Biomech. 37, 935–938.
- Pinshow, B., Fedak, M.A., Battles, D.R., Schmidt-Nielsen, K., 1976. Energy expenditure for thermoregulation and locomotion in emperor penguins. Am. J. Physiol. 231, 903–912.
- Pinshow, B., Fedak, M.A., Schmidt-Nielsen, K., 1977. Terrestrial locomotion in penguins: it costs more to waddle. Science 195, 592–594.
- Tedrake, R., Zhang, T.W., Fong, M., Seung, H.S., 2004. Actuating a simple 3D passive dynamic walker. Proc. IEE Int. Conf. Robot. Automat. 5, 4656–4661.
- Ting, L.H., Blickhan, R., Full, R.J., 1994. Dynamic and static stability in hexapedal runners. J. Exp. Biol. 197, 251–269.
- Winter, D., 1991. The Biomechanics and Motor Control of Human Gait: Normal, Elderly and Pathological. University of Waterloo Press, Waterloo.