# Planar Law of Intersegmental Coordination during Bipedal Walking in Japanese Macaques and Humans

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**Abstract:** We investigated covariation of the elevation angles of the lower limb segments during bipedal walking in bipedally-trained Japanese macaques and humans with a view to understand the mechanism underlying the origin and evolution of the planar law in human bipedal walking. Two highly trained Japanese macaques and two adult humans walking on a treadmill were recorded, and the time course of the elevation angles at the thigh, shank and foot segments relative to the vertical axis were calculated. Our analyses indicated that this planar law also holds true for macaque bipedal walking. However, the orientations of the plane are largely apart in the two species, indicating that the way the limb segments are kinematically coordinated is variable according to species, possibly due to the difference in the anatomy and mechanics of the foot segment.

**Keywords:** locomotion, kinematics, elevation angle, foot, *macaca fuscata*

## 1. INTRODUCTION

In human walking, the elevation angles of the thigh, shank, and foot segments, i.e., the orientations of the segments with respect to the vertical axis, are known to be stereotyped across subjects, and the temporal changes of these angles covary such as to form a regular loops lying close to a plane in a three-dimensional (3D) space [1,2]. This planar covariation of the elevation angle is suggested to be indicative of the coordinated neural control of bipedal locomotion, by reducing the degrees of freedom of variables to be controlled. However, it is also postulated that biomechanical factors such as strong correlation between the foot and shank elevation angles also play a part in emergence of the planar law [3].

In this study, we investigated the planar covariation of the elevation angles during bipedal walking in Japanese macaques to clarify if the same planar law holds true for bipedal walking in an inherently-quadrupedal primate. Differences in the planar covariations of the elevation angles in Japanese macaques, whose musculoskeletal system is not as adapted to bipedalism as that of humans, may hopefully provide valuable insight about the mechanism underlying the origin and evolution of the planar law in human bipedalism.

## 2. METHOD

Two highly-trained, adult Japanese macaques (KA, 12.3 kg; KU, 9.2 kg) walking bipedally on a treadmill at 3, 4, and 5 km/h were filmed using synchronized high-speed cameras at 125 frames/s and locomotor kinematics were analyzed [4]. Five landmarks on the right side of the body at 1) head of the fifth metatarsal, 2) lateral malleolus of the fibula, 3) lateral epicondyle of the femur, 4) greater trochanter, 5) acromion were manually digitized frame-by-frame. The coordinates of markers were calculated using 3D motion analysis software. The change in position of each coordinate over time was low-pass filtered at 12 Hz. For comparisons, two adult humans (K, 57 kg; M, 68 kg) walking on a treadmill at 3, 4, and 5 km/h were also recorded using a 3D optical motion capture system.

The elevation angles of the thigh, shank and foot segments were then calculated as the sagittally projected angles of the corresponding limbs with respect to the vertical axis. The calculated angle profiles were interpolated over cycle duration to fit a 100-points time base for normalization of the time.

To evaluate the inter-segmental coordination, the time courses of the elevation angles were plotted in a three-dimensional space and the trajectories were fitted by a plane using a least-square method. For this, principal component analysis of the covariance matrix of the elevation angles was performed and three eigenvectors were calculated. The first two eigenvectors describe the best-fitting plane and the third vector is the normal to the plane, representing the orientation of the plane. See literature for more details about the calculation method [1,2].

## 3. RESULTS

Figure 1 illustrates the 3D plot of the mean time-courses of the elevation angles of one human (M) and one macaque (KU) subjects walking at 3, 4, and 5 km/h, and the best-fitted planes of the corresponding loop trajectories. The % variance accounted for the first two eigenvectors was ~99% for all speeds and subjects in human bipedal walking, while that of macaque bipedal walking was <99%, indicating that the 3D trajectories of the elevation angles are essentially planar for both humans and macaques but the degree of planarity was comparatively low in macaques. The first eigenvector was very similar between the two species across and in all speeds. However, the second eigenvector was substantially different between humans and macaques. Therefore, the orientations of the best-fitted plane of angular covariation were substantially different between the two species. The mean % variance accounted for the first and second eigenvectors was 93.1% and 5.0%, respectively, in macaques and 87.4% and 11.5%, respectively, in humans. Figure 1 also shows that the orientation of the plane was more or less consistent with speed in human bipedal walking, but it was dependent of speed in macaque bipedal walking because the range of movement of the thigh elevation angle increased with speed in macaques.

## 4. DISCUSSIONS

This study demonstrated that the planar low of the intersegmental coordination holds true for bipedal walking in Japanese macaques. However, the way the planar law is achieved during bipedal walking was found to be different between humans and macaques. In both species, the first eigenvector was headed in almost the same direction, but the % variance accounted for the first and second eigenvectors were much higher and lower, respectively, in Japanese macaques, indicating that the planarity of the 3D trajectory of the elevation angle is higher in humans but the leg movements in macaques seems to be relatively more confined to one component axis along the first eigenvector.

What distinguished human bipedal walking from that of macaques was the large component of the second eigenvectors. This difference may be attributed the time course of the elevation angle during the stance phase of bipedal walking. In human walking, the foot elevation angle remained almost constant in early to mid stance phase and the change in the elevation angle occurred mainly in the thigh segment. Therefore, the 3D trajectory of the elevation angle moved along the second eigenvectors to form the plane. On the other hand, in macaque bipedal walking, the foot elevation angle continued to decrease soon after the initial contact of the foot until the push-off, and hence the fluctuations of the elevation angle of the three segments resembled each other, resulting in the larger and smaller % variance accounted for the first and second eigenvectors, respectively. Therefore, the difference in the foot motion with respect to the ground between humans and macaques was considered to make a difference in the planar low of intersegmental coordination during bipedal walking in the two species.

This is possibly resulted from the difference in the anatomy and mechanics of the foot segment between human and macaque. The human foot is rigidly structured to form a longitudinal arch acting as an effective lever for push-off. However, the macaque's prehensile foot is a more flexible structure and bends at the midtarsal region in the stance phase (midtarsal break) [5]. As a result, the heel is gradually raised from the early stance phase, resulting in the continuous decrease in the foot elevation angle in the macaque bipedal walking. Consequently, the human foot segment specialized for terrestrial bipedalism seems to largely contribute to the emergence of the planar law in human walking.

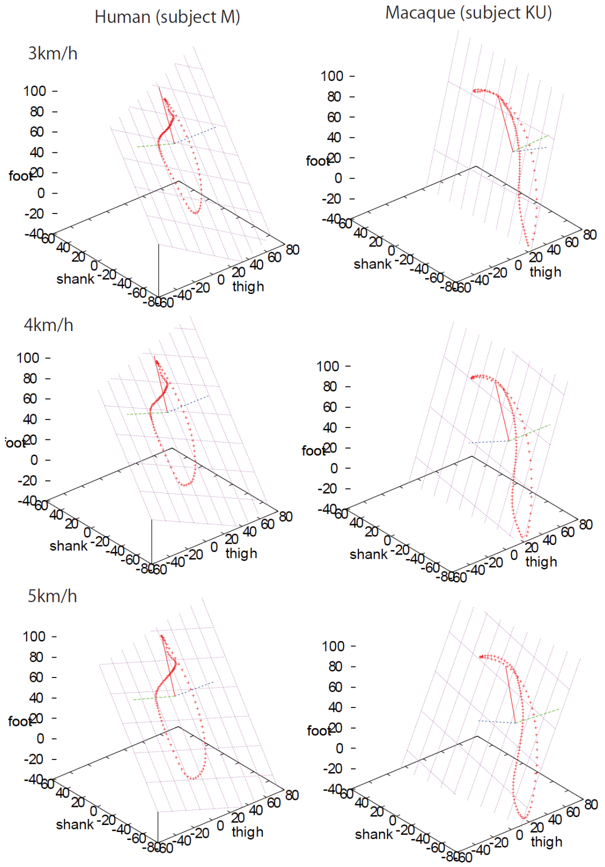


Fig. 1. 3D plot of the mean time courses of the elevation angles and the best-fitted planes of the corresponding loop trajectories. Trajectories progress counterclockwise. Foot-ground contact corresponds to the top of the loop.

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