要約 Digest

Functional morphology of the trunk in primates: implications for the evolution of human bipedalism

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General background

Habitual bipedal walking is one of the key differences between humans and other primates. The transition to bipedal locomotion accompanies the difficulty of maintaining the upright posture of the trunk. Comparative research using primates including humans provides clues on how human ancestors developed the trunk control strategy during bipedal walking. However, at present, few studies have investigated trunk movement during bipedal walking in non-human primates, except for chimpanzees. Moreover, data on the relationship between vertebral morphology and range of motion among primate species are still lacking. To fill these gaps, this dissertation explores 1) the trunk movement during bipedal walking, 2) the range of axial rotation in thoracolumbar vertebrae, 3) the morphology of thoracolumbar vertebrae, especially focusing on humans, gibbons, and macaques.

Chapter 2

Methods: I analyzed the intra-trunk rotation during bipedal walking in the gibbon and macaque and compared them with those in humans using a three-dimensional motion capture system. **Results and discussion:** I found that both the gibbon and macaques exhibited intra-trunk rotation during bipedal walking. The fact that chimpanzees also showed intra-trunk rotation during bipedal locomotion (Thompson et al., 2015) suggests that the intra-trunk rotation during bipedal walking is not unique to the hominids, but is caused by the mechanical requirements of bipedal walking. However, the amount of pelvic rotation relative to the ground was significantly smaller in humans than in the other species, indicating that the "pelvic step" (i.e., the extension of stride length by pelvic rotation) is more effective in non-human primates than in humans.

Chapter 3

Methods: I examined the relationship between trunk list and step width during bipedal walking in the gibbon and macaques, and compared the results with those of humans in the same experimental system in chapter 2.

Results and discussion: The results showed that the safety ratio (the ratio between step width and the mediolateral motion of the CoM) was not significantly different among the four species, including chimpanzees (Thompson et al., 2018). Nevertheless, slight differences in trunk lists were found in chimpanzees (Thompson et al., 2018) vs. the gibbon and macaques. I suggest that strategies for generating stable bipedal locomotion may differ among non-human species depending on the musculoskeletal structure of the trunk and hindlimbs.

Chapter 4

Methods: To evaluate how the range of motion in each thoracolumbar intervertebral joint is related to the intra-trunk rotation during bipedal walking commonly observed in primate species investigated in Chapter 2, I measured the range of thoracolumbar rotation using cadaver specimens by CT scan and a custom-made jig.

Results and discussion: The results demonstrated that the range of rotation was greater in the lower thoracic vertebrae in intact macaque cadaver specimens, consistent with results in *in vino* humans (Fujii et al., 2007; Fujimori et al., 2012). However, when similar measurements were conducted using bone-ligament preparations (ribs, vertebrae, pelvis, sternum, and ligaments), the range of rotation was similar in the upper and lower thoracic vertebrae. Therefore, it was

suggested that the scapular girdle restricted the rotation of the upper thoracic vertebrae in intact whole-body cadaver specimens.

Chapter 5

Methods: Geometric morphometrics and traditional morphometric studies of the thoracolumbar vertebrae in 23 primate specimens from 7 species, including humans, chimpanzees, gibbons, and macaques, were conducted to investigate the relationship between thoracolumbar vertebral morphology and the range of trunk rotation.

Results and discussion: Compared to the cercopithecoids, hominoids and spider monkeys showed less intra-individual variation in the size and shape of thoracolumbar vertebrae. This suggests that the upright trunk posture/locomotion exhibited by the hominoids and spider monkeys requires relatively uniform thoracic and lumbar vertebrae. The angles of the articular processes in the transverse plane implied that pre-transitional vertebrae allow axial rotation more than post-transitional vertebrae. The shape of thoracolumbar vertebrae in humans was not unique among primates concerning axial rotation.

General conclusion

Although the longer lumbar region in humans as compared with that of great apes has been considered to be linked with intra-trunk rotation during bipedal walking (Bramble and Lieberman, 2004), this study rather showed that rotations tend to occur in the lower thoracic vertebrae rather than the lumbar vertebrae, at least in passive conditions investigated in Chapter 4. In addition, intra-trunk rotations during bipedal walking were found not only in chimpanzees but also in the gibbon and macaques (Chapter 2). Taken together, the findings of this study suggest that the trunk rotation necessary for efficient bipedal walking is based on morphology that was already present in the last common ancestor of the order Catarrhini. I postulate that the evolution of hominins' trunk morphology relevant to upright bipedalism may have proceeded smoothly, at least as to the axial rotation, without major modifications.