

1 **Title: Range of rotation of thoracolumbar vertebrae in Japanese macaques**

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25 **Abstract**

26 In humans, the range of thoracic vertebral rotation is known to be greater than that of the  
27 lumbar vertebrae due to their zygapophyseal orientation and soft tissue structure.  
28 However, little is known regarding vertebral movements in non-human primate species,  
29 which are primarily quadrupedal walkers. To understand the evolutionary background of  
30 human vertebral movements, this study estimated the range of axial rotation of the  
31 thoracolumbar spine in macaque monkeys. First, computed tomography was performed  
32 while passively rotating the trunk of whole-body cadavers of Japanese macaques, after  
33 which the motion of each thoracolumbar vertebra was estimated. Second, to evaluate the  
34 influence of the shoulder girdle and surrounding soft tissues, specimens with only bones  
35 and ligaments were prepared, after which the rotation of each vertebra was estimated  
36 using an optical motion tracking system. In both conditions, the three-dimensional  
37 coordinates of each vertebra were digitized, and the axial rotational angles between  
38 adjacent vertebrae were calculated. In the whole-body condition, the lower thoracic  
39 vertebrae had a greater range of rotation than did the other regions, similar to that  
40 observed in humans. In addition, absolute values for the range of rotation were similar  
41 between humans and macaques. However, in the bone–ligament preparation condition,  
42 the upper thoracic vertebrae had a range of rotation similar to that of the lower thoracic  
43 vertebrae. Contrary to previous speculations, our results showed that the mechanical  
44 restrictions by the ribs were not as significant; rather, the shoulder girdle largely restricted  
45 the rotation of the upper thoracic vertebrae, at least, in macaques.

## 46 **1 Introduction**

47           The role of trunk movements during locomotion has changed with the evolution  
48 of locomotion in vertebrates. Notably, lateral bending plays a significant role in the  
49 propulsion of fish, amphibians, and reptiles (Schilling, 2011); flexion and extension  
50 contribute significantly to running in quadrupedal mammals (Hildebrand, 1959; Schilling  
51 & Hackert, 2006); and axial rotation plays a major role in maintaining whole-body  
52 angular momentum among upright bipedal humans (Herr & Popovic, 2008; Umberger,  
53 2008). Previous studies using magnetic resonance imaging in living humans have shown  
54 that axial rotation of the trunk while laying down is mainly generated by rotations of the  
55 thoracic vertebrae, especially the lower thoracic vertebrae, which have a greater range of  
56 rotation than the upper thoracic vertebrae (Fujii et al., 2007; Fujimori et al., 2012, 2014;  
57 Ochia et al., 2006; Panjabi et al., 1980, 1994; Shin et al., 2013; Yamamoto et al., 1989).  
58 This corresponds to the structure of the thorax and the shape of the vertebrae that form  
59 the central axis of the trunk. Fujimori et al. (2012) attributed this to the lower ribs' smaller  
60 contribution to thoracic stability, based on studies by Brasiliense et al. (2011) and Watkins  
61 et al. (2005). While all thoracic vertebrae articulate with the ribs in humans, the eighth  
62 to tenth ribs (false ribs) fuse with the costal cartilage of the seventh rib (in humans) instead  
63 of the sternum, and the ventral ends of the eleventh and twelfth ribs (floating ribs) do not  
64 articulate with anything, leading them to believe that the restriction imposed on the lower  
65 thoracic vertebrae by the ribs is small. However, other factors, such as the scapula, could  
66 also be limiting factors for thoracic rotation, which means that this remains speculative.

67           Meanwhile, it is easily postulated that the shape of vertebrae, particularly the  
68 orientation of the articular facets of the zygapophyses, significantly influences spinal  
69 movement. In thoracic vertebrae, the articular facets are relatively flat and oriented more

70 coronally. As a result, lateral flexion and rotation are to some extent possible, but flexion  
71 and extension are significantly restricted. On the other hand, the articular surfaces of the  
72 prezygapophyses in lumbar vertebrae face dorsomedially, allowing for flexion and  
73 extension, but limiting lateral flexion and rotation (Panjabi et al., 1980; Russo, 2010;  
74 Shapiro & Russo, 2019). **Specific vertebrae with prezygapophyses that have articular**  
75 **surfaces facing coronally, and postzygapophyses that have articular surfaces facing**  
76 **ventrolaterally, are known as transitional vertebrae.** In humans, the twelfth thoracic  
77 vertebra is an example of this type of vertebra. The transitional vertebra is also called  
78 “diaphragmatic vertebra” (e.g., Slijper, 1946), but for the sake of clarity and to align with  
79 the recent trends (Haeusler et al., 2002) the term "transitional vertebra" is used here.

80         The shape of the trunk and the formula of the vertebrae vary among primate  
81 species (Benton, 1967; Keith, 1923; Schultz, 1950; Shapiro, 1991; Slijper, 1946; Williams  
82 & Russo, 2015). In Hominoidea, the transitional vertebra is the vertebra that bears the last  
83 rib. In other primates, there are usually one to three additional ribs-bearing vertebrae  
84 caudal to the transitional vertebra (Shapiro, 1993; Williams, 2012a). For example, the  
85 most frequent transitional vertebra is T10 (the tenth thoracic vertebra) in macaques  
86 (Williams, 2019). Therefore, since Lanier's (1939) study, in addition to the traditional  
87 method based on the presence of ribs, a method based on the shape and orientation of the  
88 zygapophyseal facets has also been used to classify vertebrae when distinguishing  
89 between thoracic and lumbar vertebrae. According to this method, the vertebrae with the  
90 zygapophyses that possess relatively flat and more coronally oriented articular facets are  
91 defined as thoracic vertebrae, while the vertebrae with the **prezygapophyses** whose  
92 articular facets are concave and face dorsomedially are defined as lumbar vertebrae (e.g.,  
93 Washburn & Buettner-Janusch, 1952; Russo, 2010; Shapiro & Russo, 2019). **Previous**

94 studies have frequently utilized these factors as criteria to distinguish between the thoracic  
95 and lumbar spine, given the notion that the orientation and shape of the articular processes  
96 exert a substantial influence on spinal motion (Russo, 2010). Nevertheless, due to  
97 technical reasons mentioned later, in this study, vertebrae with ribs are referred to as  
98 lumbar vertebrae.

99         To gain insight into the evolutionary development of the functional morphology  
100 of the human trunk, it is necessary to conduct comparative studies using nonhuman  
101 primate species, identifying shared traits between humans and nonhuman primates, as  
102 well as derived traits unique to each group. This knowledge is also an essential foundation  
103 for using nonhuman primates as models for understanding humans. However, knowledge  
104 regarding the axial rotation of the trunk in non-human primates is limited. Previous  
105 studies have demonstrated the presence of trunk rotations similar to those in humans  
106 during bipedal walking in chimpanzees (Thompson et al., 2015) and macaques (Blickhan  
107 et al., 2021; Kinoshita et al., 2021; Ogihara et al., 2010). Unfortunately, however, the  
108 behavior of each vertebra in non-human primates during trunk rotation is not yet fully  
109 understood, both in vivo and in vitro (Shapiro & Russo, 2019). An exception to this is a  
110 biomechanical study that evaluated cynomolgus macaques (*Macaca fascicularis*) in order  
111 to compare the lumbar function of mammals (Gál, 1993a, 1993b). According to Gál  
112 (1993a), the lumbar vertebrae of cynomolgus macaques showed greater mechanical  
113 resistance and less mobility in flexion and extension in the sagittal plane than did the  
114 lumbar vertebrae of wallabies, tigers, jaguars, and seals. This study was valuable given  
115 that it was the first study to examine mammalian lumbar mechanical properties from a  
116 biomechanical perspective. However, data were limited to the lumbar vertebrae, and the  
117 data on axial rotation were not collected. Therefore, it remains unclear whether

118 differences in the range of axial rotation of the upper and lower thoracic and lumbar  
119 vertebrae exist among non-human primates and whether such variations exist among  
120 primate species.

121         The current study aimed to investigate whether variations in the range of the  
122 rotational motion among thoracolumbar vertebrae, as seen in humans, exist in other  
123 primate species and elucidate the reasons for the limited range of rotation in the upper  
124 thoracic vertebrae. Japanese macaques (*Macaca fuscata fuscata*), for which quantitative  
125 data on trunk rotation during bipedal walking have been reported (Blickhan et al., 2021;  
126 Kinoshita et al., 2021; Ogihara et al., 2010), were used as study subjects. The present  
127 study hypothesized that (1) based on the similar shape of the zygapophyses, the range of  
128 vertebral rotation would be similar in macaques and humans and (2) Rotation of the upper  
129 thoracic vertebrae is restricted by the presence of the ribs and/or the shoulder girdle. To  
130 test these hypotheses, experiments were conducted using two types of preparations: (1)  
131 whole-body cadavers and (2) bone–ligament preparation of the trunk. First, to estimate  
132 the range of rotation of the thoracolumbar vertebrae in the Japanese macaques, whole-  
133 body cadavers were scanned using a computed tomography (CT) scanner (Experiment 1).  
134 This aimed to test Hypothesis 1. Second, we measured the range of rotation after  
135 removing soft tissues to measure the range of rotation of the bone and ligament elements  
136 alone (thoracolumbar vertebrae, ribs, and pelvis) in macaques. In Experiment 2,  
137 conducted to test Hypothesis 2, the influence of the shoulder girdle will be eliminated.  
138 Therefore, if differences in the amount of rotation between the upper and lower thoracic  
139 vertebrae are observed, it is highly likely that the ribs are responsible for the difference.  
140 Conversely, if there are no differences in the amount of rotation, it can be inferred that  
141 the differences in rotation between the upper and lower thoracic vertebrae in vivo may be

142 due to the shoulder girdle.

143

144

## 145 **2 Material and Methods**

### 146 *2.1 Experiment 1: Whole-body cadaver*

#### 147 *Materials*

148 This study used non-formalin-fixed frozen cadavers of eight Japanese macaques  
149 (*Macaca fuscata fuscata*) (male: 5, female: 3) obtained from the collection of the Center  
150 for the Evolutionary Origins of Human Behavior at Kyoto University. According to the  
151 accompanying information, the five adult males (weighing 5.8–12.9 kg upon death) and  
152 three adult females (4.2–7.2 kg) had no deformity or disorder related to locomotion at the  
153 time of death. The cadavers had been preserved in a deep freezer at  $-20^{\circ}\text{C}$ .

154

#### 155 *Procedure*

156 Frozen cadaver specimens were thawed at room temperature for approximately  
157 2 days. After thawing, the specimens were fixed on two wooden boards. One was tied by  
158 the head and the other by the pelvis using strings. The specimen and wooden board were  
159 carried into the CT scanner (Asteion Premium 4, Toshiba Medical Systems, Japan), after  
160 which scanning was performed in two types of positions: natural and rotated. In the  
161 natural position, two boards were placed on the same plane of the CT scanner bed, and  
162 the trunk of the specimen was held tightly to prevent movement. In the rotated position,  
163 the trunk was rotated around the body axis by rotating the head side of the wooden board  
164 to the right by around  $45^{\circ}$  relative to the pelvis side of the wooden board (Figure 1). Thus,  
165 the cranium was rotated by around  $45^{\circ}$  relative to the pelvis. The imaging conditions were

166 as follows: slice thickness, 1.0 mm; the field of interest, 320 mm;  $512 \times 512$  matrices;  
167 and voxel size,  $0.625 \times 0.625 \times 1.0$  mm.

168 The CT image data were processed using three-dimensional image analysis  
169 software (Avizo, Thermo Fisher Scientific Inc., US). Ten landmarks were digitized on the  
170 reconstructed model of each thoracolumbar vertebra (Table 1). The  $xyz$  coordinates  
171 (dorsoventral, mediolateral, and craniocaudal, respectively) were defined from the  
172 landmarks to determine the local coordinate system specific to each vertebra (Figure 2).  
173 The  $y$ -axis was defined as the line connecting the most cranial point of the left and right  
174 inferior vertebral notch (landmarks 1 and 2, respectively). The  $x$ -axis was defined as the  
175 projection of the line between landmarks 9 and 10 to the vertebral articular surface, which  
176 was parallel to the cranial and caudal vertebral articular surface defined by landmarks 3–  
177 8. The  $z$ -axis was the cross-product between the  $x$ - and  $y$ -axes. Euler angles were used to  
178 represent the rotations of the cranial vertebral coordinate system relative to the caudally  
179 adjacent vertebral coordinate system (Figure 2). The rotation order of the Euler angle was  
180  $x$ ,  $y$ , and  $z$  (roll, pitch, and yaw, respectively), and rotation around the  $z$ -axis was used for  
181 analysis. The range of relative motion between two adjacent vertebrae was defined as the  
182 amount of rotation when the first vertebra was rotated by  $45^\circ$ . Accordingly, the value for  
183 the range of rotation is positive if the vertebra rotates in the same direction as the applied  
184 moment and negative if it rotates in the opposite direction. The package “Rspincalc”  
185 (Gama et al., 2015) in R. v.3.5.1 (R Core Team, 2019) was used for calculating the angles.

186 Previous research on human vertebrae was used as a reference to which  
187 macaques in the current study were compared. Data reported by Fujimori et al. (2012) on  
188 thoracic vertebrae and Fujii et al. (2007) on lumbar vertebrae were used given that they  
189 are relatively new and involved living subjects, not cadavers.



190

191 *2.2 Experiment 2: Bone–ligament preparations (vertebrae, ribs, and pelvis)*

192 *Materials*

193 Non-formalin-fixed frozen cadavers of macaques were obtained from the Center  
194 for the Evolutionary Origins of Human Behavior at Kyoto University, as in the case of  
195 Experiment 1, although the specimens used in Experiment 2 were partly different from  
196 those used in Experiment 1. The specimens included three adult males (weighing 11.8–  
197 15.1 kg upon death).

198

199 *Procedure*

200 Before dissection, the cadavers were thawed at room temperature for about 2  
201 days. After removing the cranial region, extremities, and soft tissues (including muscles)  
202 related to those regions, soft tissues of the trunk (skin, internal organs, trunk muscles such  
203 as the erector spinae, abdominal, psoas muscles, etc.) were removed. Finally, specimens  
204 consisting of the pelvis, vertebrae (C1 to the last caudal vertebra) with intact intervening  
205 ligaments and joint capsules, and ribs (with intercostal muscles) were obtained.

206 To measure the three-dimensional positions and orientations of each vertebra,  
207 three round labels (3 mm in diameter) were attached to each thoracolumbar vertebra.  
208 These three labels represent the rigid body for each vertebra. The labels were located at  
209 the dorsal centers of the spinous processes and the dorsolateral tips of the transverse  
210 processes on both sides of the thoracic and lumbar vertebrae. Given that the pelvic  
211 entrapment prevented the transverse processes of the final lumbar vertebra, the labels for  
212 its transverse processes were attached to the bilateral anterior portions of the vertebral  
213 body instead. To define the reference position, additional labels were attached to the

214 dorsal center of the spinous process of the first sacral vertebra and the bilateral superior  
215 anterior iliac spines.

216           Relative motions between two adjacent vertebrae were measured using a jig  
217 specially designed and made for this study (Figure 3, Natsume Seisakusho Co., Ltd).  
218 Thereafter, the range of relative motion was estimated as the amount of rotation of the  
219 upper vertebra relative to the subjacent vertebra upon trunk rotation. The pelvis and  
220 cervical vertebrae were fixed to the jig, and trunk rotation around the longitudinal axis of  
221 the body was induced by rotating the cervical fixture, which fixed the first thoracic  
222 vertebra (Figure 3). An optical motion tracking system (Flex 3; OptiTrack Inc.,  
223 Corvallis, OR) and a Micron Series Digitizing Probe (Optitrack Inc., Corvallis, OR) were  
224 used for tracking the labels on the vertebrae. The labels were digitized when the cervical  
225 fixture was rotated by around 0° and 45°. Measurements were conducted during both right  
226 and left rotations. The *xyz* coordinates (dorsoventral, mediolateral, and craniocaudal,  
227 respectively) were defined from the labels to determine the local coordinate system fixed  
228 to each vertebra. The origin of the local coordinate system was the centroid of the three  
229 labels. Similar to Experiment 1, Euler angles were used to represent the rotations of the  
230 cranial vertebral coordinate system relative to the caudally adjacent vertebral coordinate  
231 system. The rotation order of the Euler angle was *x*, *y*, and *z* (roll, pitch, and yaw,  
232 respectively), and rotations around the *z*-axis were used for analysis. Accordingly,  
233 positive and negative values are obtained if the vertebra rotates in the same and opposite  
234 direction as the applied moment, respectively. The package “Rspincalc” (Gama et al.,  
235 2015) in R version 3.5.1 (R Core Team, 2019) was used for calculating the angles.

236

### 237 **3 Results**

238           Given the difficulty in precisely ascertaining the orientation and shape of  
239 zygapophyses in in vivo and bone-ligament preparations, for the convenience of this study,  
240 vertebrae with ribs are referred to as thoracic vertebrae, while those without ribs are  
241 referred to as lumbar vertebrae. All specimens utilized in this study consisted of twelve  
242 rib-bearing vertebrae. Among these, vertebrae whose ribs independently articulate with  
243 the sternum via the costal cartilage (T1-7) were classified as "upper thoracic vertebrae."  
244 The eighth through tenth ribs join together to form a single costal cartilage that articulates  
245 with the sternum, and the eleventh and twelfth ribs do not articulate with the sternum.  
246 The vertebrae with these ribs (T8-12) were defined as "lower thoracic vertebrae" in this  
247 study.

248           In Experiment 1 using whole-body preparations, Japanese macaques showed  
249 variations in the ranges of rotation that tended to be similar to that in humans [Figure 4,  
250 T1–T12: Fujimori et al. (2012); T12–L5: Fujii et al. (2007)]. In both species, the lower  
251 thoracic vertebrae showed greater rotation than did the lumbar and upper thoracic  
252 vertebrae. After dividing the thoracolumbar vertebrae into three segments, namely the  
253 upper thoracic vertebrae (T1–T7), lower thoracic vertebrae (T7–T12; although this region  
254 in macaques includes the transitional vertebra, it was categorized as such to compare  
255 species with the same number of vertebrae), and lumbar region (macaque: T12–L7,  
256 human: T12–L5), the range of motion of the upper thoracic vertebrae, lower thoracic  
257 vertebrae, and lumbar region was 8.0°, 16.7°, and 5.3° in macaques and 9.5°, 11.4°, and  
258 7.4° in humans, respectively (Figure 4). Although the sample size was too small to  
259 observe a significant difference between species, the results seemed to show that the  
260 lower thoracic vertebrae of macaques were capable of greater rotation than those of

261 humans, whereas the reverse was true for the upper thoracic vertebrae.

262           The results of Experiment 2 using the bone–ligament preparations differed from  
263 those of Experiment 1 using whole-body cadavers of Japanese macaques (Figure 5).  
264 Accordingly, upper thoracic vertebrae (T1–T7) had a similar or slightly greater range of  
265 rotation than did lower thoracic vertebrae (T7–T12). After the transitional vertebrae (T10),  
266 there was less rotation. The range of rotation of the upper thoracic vertebrae, lower  
267 thoracic vertebrae, and lumbar region was 18.3°, 12.0°, and 2.5°, respectively (Figure 5).  
268 In the bone–ligament preparations of macaques, the upper thoracic vertebrae had a greater  
269 range of rotation than did the lower thoracic vertebrae. When compared to whole-body  
270 preparations, the bone–ligament preparations had a greater range of rotation in the upper  
271 thoracic vertebrae but less range of rotation in the lower thoracic and lumbar vertebrae.  
272 Note that the results shown in Figures 4 and 5 contain negative values. This is presumably  
273 attributed to the coupled motions of the spine, as discussed later in the Discussion section.

274

## 275 **4 Discussion**

### 276 *4.1 Comparison between humans and macaques in whole-body preparations*

277           Humans and macaques were similar in that they had a greater range of rotation  
278 in the lower thoracic vertebrae (Figure 4). Aside from variations in the range of rotation  
279 throughout the thoracolumbar vertebrae, absolute values for the range of rotation were  
280 similar between the two species. Given that the range of rotation between T1 and the last  
281 lumbar vertebra was similar in the two species (humans: 28.3°; macaques: 29.9°, Figure  
282 4), each vertebra may have a similar range of rotation. Thus, our results support  
283 Hypothesis 1, which states that “based on the shape of the zygapophyses, the range of  
284 vertebral rotation would be similar in macaques and humans.”

285           The orientation of the zygapophyses is associated with the overall differences in  
286 the range of rotation between the lower thoracic and lumbar vertebrae. Again, although  
287 humans and macaques have similar anatomical structures, the position of their transitional  
288 vertebrae is different. In mammals, the articular facets of the prezygapophyses of the pre-  
289 transitional vertebrae face dorsally or dorsolaterally (Russo, 2010; Shapiro, 1991), which  
290 allows lateral flexion and some rotation (Panjabi et al., 1980). In contrast, those of the  
291 post-transitional vertebrae direct dorsomedially (Russo, 2010; Shapiro, 1991), which  
292 allows anteroposterior flexion but limits rotation (Panjabi et al., 1980). This difference in  
293 the orientations of the zygapophyses may have promoted differences in the range of  
294 rotation of the thoracolumbar vertebrae in both humans and macaques (Figure 4).  
295 Therefore, the comparable values observed between humans and macaques generally  
296 support the idea that the orientation of the zygapophyses limits rotation.

297           Although the overall trends were similar, the position of the transitional vertebrae  
298 did not always correspond with the range of rotation. The typical position of the  
299 transitional vertebrae is T12 in humans and T10 in macaques (Williams, 2012a), which  
300 was consistent with our subjects. In humans, a change in range of motion would be  
301 expected between T11–12 and T12–L1. However, the actual change occurred between  
302 T10–11 and T11–12, which was more cranial than the transitional vertebra (Fujimori et  
303 al., 2012). One possible factor contributing to this discrepancy is that the change between  
304 the thoracic and lumbar type zygapophyses is gradual rather than abrupt. The  
305 prezygapophyseal angles relative to the sagittal plane in humans are reported to change  
306 gradually, with 100°–106°, 77°–81°, and 31°–32° at T11, T12, and L1, respectively  
307 (Masharawi, et al., 2004). According to Singer et al. (1988) and Shinohara (1997), 54%  
308 and 34% of all subjects, respectively, exhibited a gradual transition between the thoracic

309 and lumbar types rather than an abrupt one (however, for the interpretation of these results,  
310 refer to Williams et al., 2012b). In addition, Pal & Routil (1999) found that out of forty-  
311 four columns, forty-one (93%) showed a gradual change extending over either two or  
312 three successive vertebrae. No clear evidence has shown whether this gradual change in  
313 zygapophyseal orientation is related to the amount of rotation. In the macaques of  
314 Experiment 1, there was also no clear relationship between the range of rotation and  
315 zygapophyseal orientation. From the zygapophyseal orientation, an abrupt change would  
316 have been expected between T9–10 and T10–11, but the results showed that it seemed to  
317 occur between T11–12 and T12–L1, which was more caudal than the transitional vertebra  
318 (Figure 4). The reason for this change is unclear, since both T11 and T12 have lumbar-  
319 like zygapophyses. These inconsistent results suggest that the orientation of the  
320 zygapophyses is only one of the factors that determine the range of rotation of some  
321 vertebrae, even in the lower thoracic region (Haeusler et al., 2011, 2012). Other factors,  
322 such as the structure of the spinous and transverse processes or potential methodological  
323 differences, may also contribute to the observed differences in vertebral rotation, in  
324 addition to the angle of the zygapophyses. However, it is certain that there is some  
325 relationship between the position of the transitional vertebra and trunk motions during  
326 locomotion. Species that run and jump with flexible spines exhibit a cranial shift of the  
327 transitional vertebra by two to three elements (Williams, 2019). Given that the amount of  
328 flexion and extension is important in such locomotion, the position of the transitional  
329 vertebra, or the orientation and shape of the articular surface of the zygapophyses, may  
330 be more closely related to flexion/extension than rotation. Verification of this hypothesis  
331 is a topic for future research.

332

333 *4.2 Difference between whole-body and bone–ligament preparations*

334           While whole-body preparations of Japanese macaques showed less rotation in  
335 the upper thoracic vertebrae than in the lower vertebrae (Experiment 1), the bone–  
336 ligament preparations had a similar range of rotation for the upper and lower thoracic  
337 vertebrae (Figure 5). The restriction by the ribs has been thought to explain the difference  
338 in the amount of rotation between the upper and lower thoracic vertebrae based on the  
339 structure of the rib cage (Fujimori et al, 2012). It is based on the idea that the stiffness of  
340 the sternocostal and costovertebral joints at middle-lower thoracic segments was half,  
341 compared with those at upper thoracic levels (Schultz, 1974a, b). However, the upper and  
342 lower thoracic vertebrae had similar ranges despite the presence of the ribs in the bone–  
343 ligament preparations where the shoulder girdle was removed (Figure 5). These results  
344 indicate that the restrictions from the ribs do not largely influence the range of rotation,  
345 at least, in Japanese macaques. Rather, these results suggest that the shoulder girdle limits  
346 the motions of the upper thoracic vertebrae. Thus, the results of the present study partially  
347 support Hypothesis 2, which suggests that the rotation of the upper thoracic spine is  
348 constrained by the presence of ribs or the shoulder girdle. Specifically, our findings  
349 indicate that the shoulder girdle functions as a limiting factor for rotational movement in  
350 the upper thoracic vertebrae. The scapula and surrounding soft tissues, located  
351 posterior/lateral to the thorax, may enhance the stability of the upper thoracic vertebrae  
352 (Theodoridis & Ruston, 2002). Thus, our findings suggest that compared to the restriction  
353 caused by the ribs, that caused by the shoulder girdle had a greater influence on the  
354 difference in the range of rotation between the upper and lower thoracic vertebrae.

355           Conversely, low amounts of rotation were commonly observed in the lumbar  
356 vertebrae of whole-body and bone–ligament preparations, suggesting that the lumbar

357 vertebral shape, especially the orientations of the zygapophyses, strongly limits rotation  
358 regardless of the presence or absence of soft tissue. Although it remains yet uncertain why  
359 the position of the transitional vertebrae did not coincide with the abrupt change in the  
360 range of rotation, our findings support the notion that sagittally oriented zygapophyses  
361 limit the axial rotation (Panjabi et al., 1980).

362

#### 363 *4.3 The effects of coupled motion*

364 It remains unknown why some vertebrae rotated in the direction opposite to the  
365 applied moment in macaques (Figures 4 and 5). One possible reason could be that the  
366 motion was caused by the coupled motions of the vertebrae. The coupled motions  
367 between two adjacent vertebrae are a movement that occurs concomitantly with the  
368 primary motion (Lovett, 1905). In humans, lateral bending coupled with axial rotation  
369 was reported to occur in the same direction in the upper thoracic vertebrae, in the opposite  
370 direction in the lower thoracic vertebrae, and in the opposite direction in the lumbar  
371 vertebrae (Panjabi et al., 1994; Fujii et al., 2007; Fujimori et al., 2012). In experiments 1  
372 and 2, the cranial or cervical regions and the pelvis were fixed, and motions other than  
373 axial rotation (such as lateral bending and flexion/extension) are restricted. Thus, the total  
374 lateral bending in the thoracolumbar vertebra needs to be zero. When the axial rotation  
375 occurred in the vertebrae, the coupled lateral bending also occurred (Lovett, 1905).  
376 However, given that total lateral bending needs to be zero, the lateral bending must be  
377 canceled out somewhere in the vertebrae. For example, when right (+) axial rotation  
378 occurred, opposite left lateral bending occurred in the lower thoracic and upper lumbar  
379 vertebrae. To cancel the left lateral bending, right lateral bending occurred in the lower  
380 lumbar vertebrae, resulting in left (-) axial rotation in the lower lumbar vertebrae.



381 Another possible reason could be that the value below zero was a measurement error. In  
382 any case, our measurement methodology needs to be refined in the future.

383

#### 384 *4.4 Study limitations*

385 The current study has some limitations worth noting. First, in Experiment 1, the  
386 trunk was rotated with the body fixed to a wooden board, but the axis of rotation of the  
387 wooden board did not necessarily coincide with the axis of rotation of the vertebrae. Thus,  
388 forces might act in a different direction than the natural condition of living animals.  
389 Second, the maximum rotation of each specimen could be measured due to the  
390 mechanical limitations of the fixation device. Third, although this study focused primarily  
391 on zygapophyseal orientations, other portions of the vertebra may limit rotation. For  
392 example, the spinous process limits vertebral motion through the interspinous and  
393 supraspinous ligaments, and the transverse processes also restricts movement through the  
394 intertransverse ligaments (Bogduk, 2012). To clarify the form-function relationship  
395 among thoracolumbar vertebrae, it is necessary to investigate how these regions are  
396 associated with variations in the range of motion and how they differ among species.  
397 Finally, the coupled motion could not be controlled in the current experiments. Different  
398 results might have obtained had this been controlled. However, given that coupled motion  
399 is a natural movement of the vertebrae, it is necessary to consider whether controlling it  
400 would be reasonable.

401

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406

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556



557 **Figure legends**

558

559 **Figure 1**

560 **The three-dimensional surface of the macaque skeleton used in Experiment 1.** The  
561 trunk was rotated around the body axis by around 45° relative to the pelvis.

562

563 **Figure 2**

564 **The third lumbar vertebra of the Japanese macaque is presented here as an example.**

565 a), b), and c) Landmarks used in Experiment 1. The positions of the landmarks are  
566 summarized in Table 1. d) Coordinate system defined by the landmarks. The  $x$ ,  $y$ , and  $z$   
567 axes were defined as dorsoventral, mediolateral, and craniocaudal, respectively, using all  
568 landmarks.

569

570

571 **Figure 3**

572 **The jig and specimen used in Experiment 2.** The pelvis and cervical vertebrae were  
573 fixed to the jig, after which rotation around the longitudinal axis of the body was induced  
574 by rotating the cervical fixture (red arrow).

575

576

577 **Figure 4**

578 **Box plots for the range of motion of each thoracolumbar vertebra in Japanese**  
579 **macaques from Experiment 1.** Vertical lines through a box represent median values.

580 The left and right sides of the box are the first and third quartiles, respectively. Both ends

581 of the horizontal line represent the minimum and maximum values. Triangles demonstrate  
582 average values of humans from T1–T12: Fujimori et al., 2012, T12–L5: Fujii et al., 2007.  
583 The angular displacement of the upper thoracic, lower thoracic, and lumbar regions,  
584 computed through summation of individual vertebral values, was 8.0°, 16.7°, and 5.3° in  
585 macaques and 9.5°, 11.4°, and 7.4° in humans, respectively. T: thoracic vertebra; L:  
586 lumbar vertebra.

587

588 **Figure 5**

589 **Box plots for the ranges of motion of thoracolumbar vertebrae in Japanese**  
590 **macaques from Experiment 2.** Plots involved right and left rotations in all specimens.  
591 Horizontal lines through a box represent median values. The angular displacement of the  
592 upper thoracic, lower thoracic, and lumbar regions, computed through summation of  
593 individual vertebral values, was 18.3°, 12.0°, and 2.5°, respectively.

Table 1. List of landmarks used for Experiment 1.

Number	Description
1	Most cranial point of the left inferior vertebral notch
2	Most cranial point of the right inferior vertebral notch
3	Most dorsal point of the cranial articular surface of the vertebral body in the midline
4	Most ventral point of the cranial articular surface of the vertebral body in the midline
5	Most left lateral point of the cranial articular surface of the vertebral body
6	Most dorsal point of the caudal articular surface of the vertebral body in the midline
7	Most ventral point of the caudal articular surface of the vertebral body in the midline
8	Most left lateral point of the caudal articular surface of the vertebral body
9	Most cranial point of the spinous process tip
10	Most dorsocranial point of the junction of the bilateral laminar arch in the midline

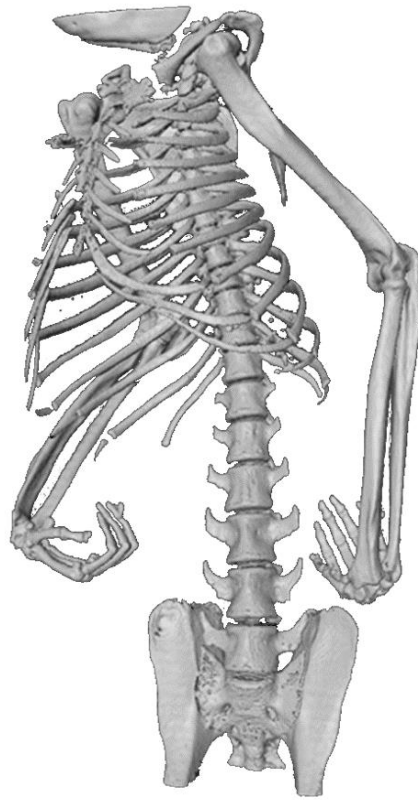


Figure 1

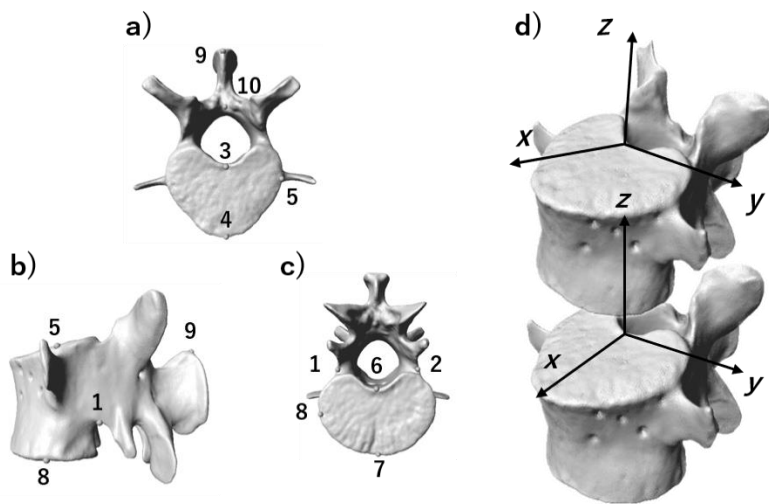


Figure 2



Figure 3

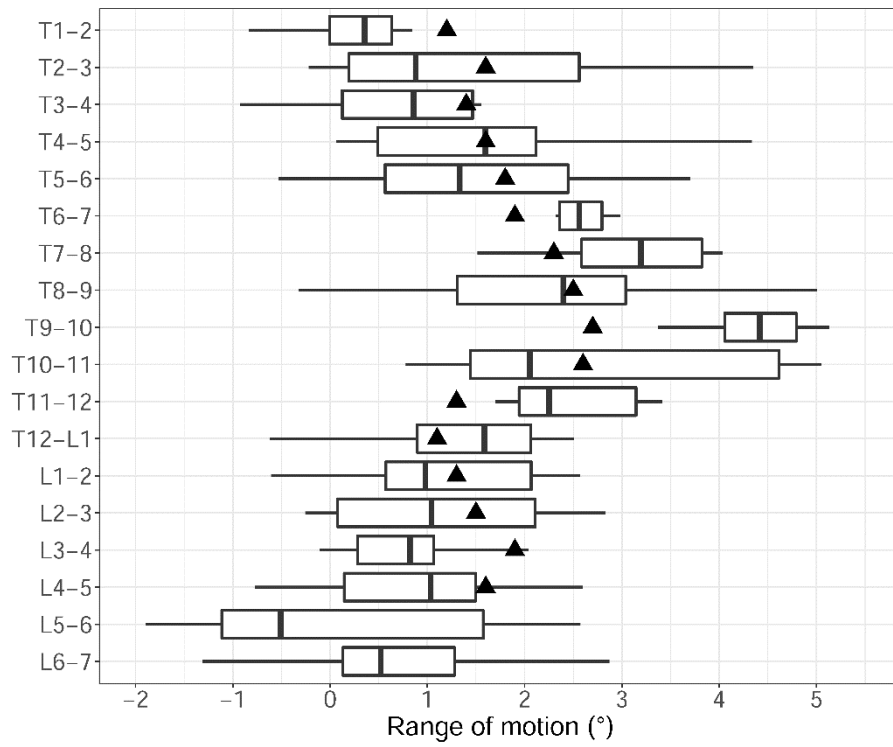


Figure 4

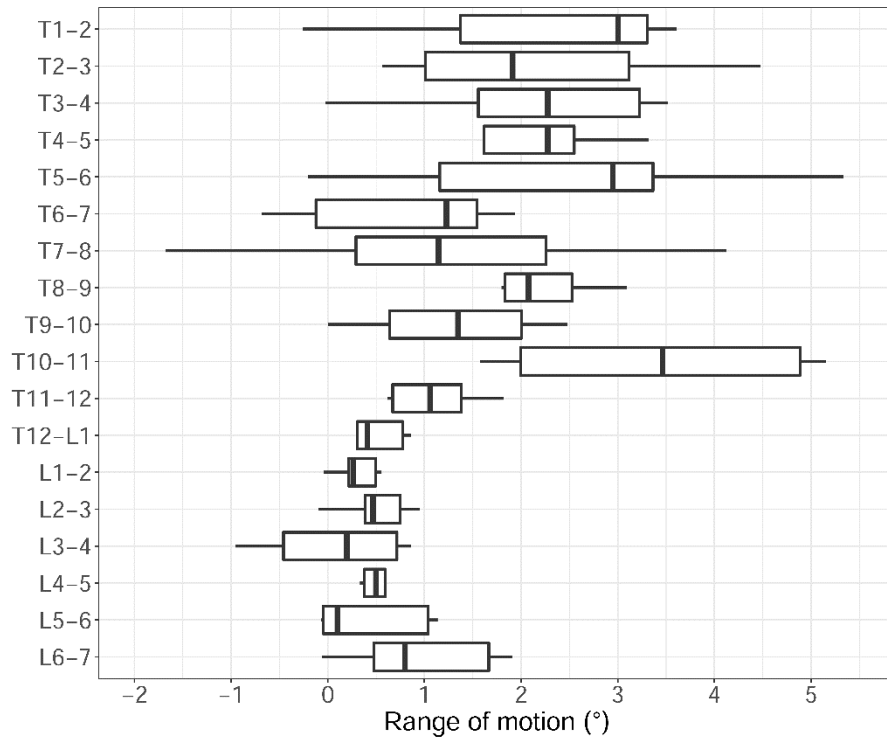


Figure 5