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How capuchin monkeys use their semi-prehensile tails

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Among primates, prehensile/semi-prehensile tails have evolved independently in the families Atelidae and Cebidae of the infraorder Platyrrhini (Neotropical monkeys). They facilitate maintaining stability during locomotion on thin, flexible branches and while reaching for food on challenging substrates. How a prehensile/semi-prehensile tail is coordinated with the hind limbs to facilitate controlled, flexible adoption of postures remains unknown. In an experimental set-up in the wild, we induced capuchin monkeys to adopt a tail-assisted, head-down tripod posture to reach for food, documenting from slow-motion video recordings (120 fps) both qualitative changes in the monkeys' positional behaviour – the relative orientation of their limbs and semi-prehensile tail – and quantitative changes in the left knee angle. The monkeys coordinated their tail and hind limbs in an online manner by preparing to anchor the tail over a substrate when beginning to adopt a tail-assisted, head-down, tripod posture, but anchoring it only at the moment when they extended their hand to grasp the food. Coordination of their semi-prehensile tail with their limbs enables these capuchin monkeys to adjust their posture more flexibly compared to anchoring their tail over a substrate in anticipation and subsequently changing posture.

Keywords: Left knee angle, locomotion, prehensility, *Sapajus libidinosus*, tail cantilever length, tripod posture.

A prehensile tail can support an animal's body completely, while a semi-prehensile tail can support it partially (prehensile implies 'able to grasp', from the Latin *prehendere*, to take hold of, to grasp)¹. Prehensile/semi-prehensile tails have evolved independently at least 14 times among 50 genera of 14 families of arboreal mammals. Among primates, prehensile/semi-prehensile tails have evolved independently in the families Atelidae (one of the five families of New World monkeys, including the howler,

spider, woolly and woolly spider monkeys) and Cebidae (also one of the five families of New World monkeys, but including capuchin and squirrel monkeys) of the infraorder Platyrrhini (Neotropical monkeys)^{1–3}. It is commonly accepted that prehensile/semi-prehensile tails function to maintain stability for locomotion on thin and flexible branches, and support the body during positional behaviour to access the food present on challenging substrates^{2,4–6}.

Several distinct morphological features render prehensile/semi-prehensile tails suitable for the mechanical demands of tail-assisted locomotion and positional behaviour. Prehensile/semi-prehensile tails have larger ventral (flexor) musculature with extrinsic tendons that cross fewer joint segments compared to nonprehensile tails. This is hypothesized to enable the tail tip to maintain contact with a substrate, facilitating the animal's movement in three dimensions⁷. Caudal vertebrae of prehensile/semi-prehensile tails also have a greater density of muscle attachments compared to those of nonprehensile tails, presumably enabling them to support larger proportions of body weight for longer periods^{8–10}.

Prehensile tails in atelids and semi-prehensile tails in cebids are distinguished by morphological features related to their independent evolutionary histories and different functions. Prehensile tails in atelids are longer compared to semi-prehensile tails in cebids¹⁰, accounting for a slightly greater proportion of body mass¹¹, thus allowing them to support a larger proportion of body weight for longer periods. Compared to prehensile tails in atelids, semi-prehensile tails in cebids have larger dorsal (extensor) musculature, resembling nonprehensile tails⁷, thus allowing the cebids to adopt a wider range of postures than the atelids. Prehensile tails in atelids have a hairless, glabrous friction pad on their ventrodorsal surface with four mechanoreceptors – Meissner's corpuscles, Pacinian corpuscles, Ruffini corpuscles and Merkel discs. In contrast, semi-prehensile tails in cebids are completely covered in hair, and only Ruffini corpuscles and Merkel cells are present in the ventrodorsal skin¹². Prehensile tail use in atelids and semi-prehensile tail use in cebids appear to reflect these

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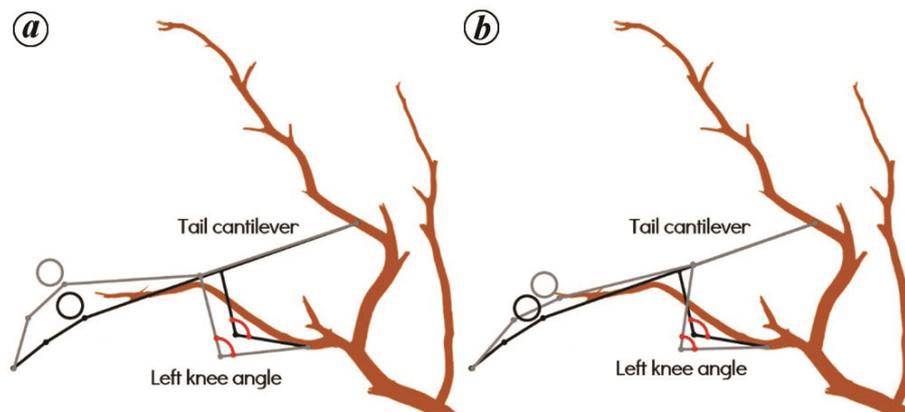


Figure 1. Left knee angle and tail cantilever length when the tail is coordinated in (a) anticipation – the monkey in grey is using a longer segment of its tail as a cantilever but larger knee flexion than the monkey in black, and (b) an online manner – the monkey in black uses a longer segment of its tail as a cantilever as well as smaller knee flexion than the monkey in grey.

morphological distinctions. Atelids use their prehensile tails primarily to suspend themselves completely or partially together with their hind limbs during locomotion and feeding^{13–18} (Figure 1 a). In contrast, cebids use their semi-prehensile tails primarily for feeding by anchoring it over a substrate to attain a head-up or a head-down tripod posture (Figure 1)^{13,19–22}.

The relationship between tail morphology and the dynamics of tail use in atelids or cebids may help in understanding the proximate – perceptual and sensorimotor – mechanisms underlying prehensile/semi-prehensile tail use. Therefore, our aim in the present study is to elucidate the dynamics of semi-prehensile tail use in bearded capuchin monkeys, *Sapajus libidinosus*, during feeding bouts in their natural habitat. Specifically, we documented qualitative and quantitative patterns of coordination of tail and limb use during transitions from above-branch to a head-down tripod posture.

Monkeys might coordinate their semi-prehensile tails with their limbs in two distinct ways. First, they might anchor their tail over a substrate in anticipation of postural changes. During this strategy, the geometrical relationships between the hind limbs and the tail imply that when the food is located at a constant distance, a longer ‘tail cantilever’ – the tail segment between the base of the tail and the anchoring substrate – should be associated with a greater flexion of the knee. For a given monkey, the tail cantilever length should not depend on the location of food. Second, monkeys might also coordinate their tail with their limbs in an ‘online’, dynamic manner by preparing to anchor it over a substrate during a postural transition, but finally anchoring it only at the moment which they grasp the food. Understanding this strategy, in inter-individual comparisons a longer tail cantilever should be associated with smaller knee flexion and, for a given monkey, the tail cantilever should be longer for food located at a greater distance (Figure 1 b).

Methods

Ethics statement

The present study was an offshoot of a long-term research project on bearded capuchin monkeys at Fazenda Boa Vista, Brazil, approved by the Institutional Animal Care and Use Committee (IUCAC) at the University of Georgia, Athens, USA (No. A2013 03-001-Y3-A2).

Subjects and study site

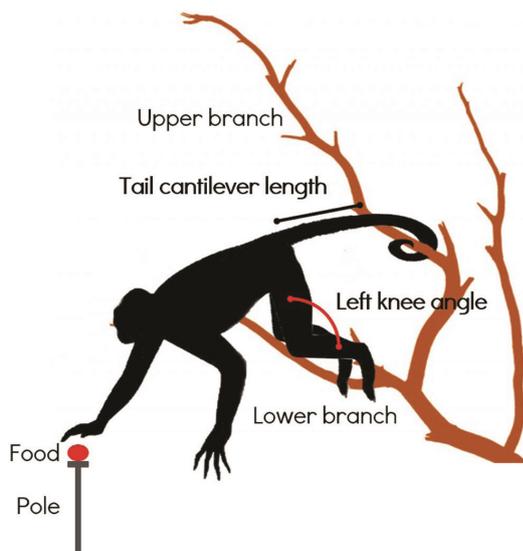
The subjects were seven individually recognized, wild, bearded capuchin monkeys at a privately owned open woodland, Fazenda Boa Vista, Piauí, Brazil (9°39’S, 45°25’W). The monkeys were habituated to human observers. The experiment was conducted in a flat area with several large trees frequented by the monkeys. These monkeys participated in several studies on nut-cracking using stone tools in the past^{23,24}, as well as biomechanics and motor control of stone-tool use^{25,26}.

Experimental procedures

Figure 1 provides a schematic illustration of the experimental set-up. We placed pieces of a nut of the piaçava, *Orbignya* spp. palm – a preferred food – on the top of a vertical, 2.25 m high pole positioned at 0.9, 1.0 or 1.2 m horizontal distance from a branch bifurcating into a lower and an upper branch. Each monkey reached for food by gaining a tail-assisted, head-down tripod posture (Figure 2). Six monkeys individually reached for food placed at 1.0 m from the lower branch over multiple trials (Table 1). Monkey 7 reached for food placed at 0.9 m and 1.20 m from the lower branch over multiple trials (Table 1). We video-recorded the focal monkeys’ tail-use behaviour in a

Table 1. Number of trials, and mean \pm SD left knee angle and tail cantilever length across all trials for each monkey

Monkey	Number of trials	Left knee angle ($^{\circ}$)	Tail cantilever length (m)	Left knee angle ($^{\circ}$)	Tail cantilever length (m)
Food placed at 0.75 m					
1	12	139 \pm 9	0.30 \pm 0.02		
2	11	134 \pm 12	0.28 \pm 0.02		
3	11	134 \pm 6	0.28 \pm 0.01		
4	12	119 \pm 15	0.26 \pm 0.02		
5	12	126 \pm 11	0.27 \pm 0.01		
6	6	119 \pm 13	0.25 \pm 0.02		
Food placed at 1.0 m					
7	11	83 \pm 15	0.26 \pm 0.02	110 \pm 23	0.30 \pm 0.02

**Figure 2.** A schematic illustration of the experimental set-up.

calibrated 2D plane in slow motion at 120 fps and 640×480 pi resolution using a camera (Casio EXILIM EX-ZR700) mounted on a tripod placed at approximately 3.6 m from the plane of movement of the monkeys.

Data extraction

We documented the qualitative changes in the positional behaviour of the monkeys – changes in the relative orientations of their limbs and semi-prehensile tail – when adopting a head-down tripod posture. For each monkey for each trial, we measured from the video-recordings: (i) left knee angle at the time of grasping, and (ii) ‘tail cantilever length’ – the tail segment between the base of the tail and the anchoring substrate (Figure 2). We established intra- and inter-coder consistencies in measurements. Repeated measurements of both variables for 12 trials for monkey 1 by one of us (MM) over 15 days did not differ (left knee angle: mean \pm SD of absolute difference = $8.33 \pm 5.63^{\circ}$; paired sample *t*-test: $t = 1.32$, $df = 11$; $P = 0.214$; tail cantilever length: mean \pm SD of absolute difference = 0.01 ± 0.02 m, paired sample *t*-test:

$t = 0.11$, $df = 11$; $P = 0.917$). Repeated measurements for 12 trials for monkey 1 also did not differ between one of us (MM) and an undergraduate laboratory assistant (left knee angle: mean \pm SD of absolute difference = $9.8 \pm 7.0^{\circ}$, paired sample *t*-test: $t = 1.87$, $df = 11$; $P = 0.089$; tail cantilever length: mean \pm SD of absolute difference = 0.01 ± 0.01 m, paired sample *t*-test: $t = 0.46$, $df = 11$; $P = 0.658$).

Results

Table 1 describes the number of trials, mean \pm SD left knee angle and tail cantilever length across all trials for each monkey.

Figure 3 displays 15 snapshots from a representative video recording of a monkey in the act of adopting a tail-assisted, head-down tripod posture while reaching for food placed at a distance of 1.00 m from it. Initially, beginning from a quadrupedal posture, the monkey looped its tail around the upper branch contacting it with the ventral surface of the upper one-third of the tail (snapshots 1 and 2). Subsequently, it leaned forward, extended a forelimb forward and increased tail flexion about the substrate contact point (snapshot 3). Then it extended the other forelimb outward, reaching with both forelimbs towards the food and sliding the contact point of the tail towards the tip while wrapping it tightly around the branch (snapshots 4 and 5). At the moment when it grasped the food, the monkey had its tail anchored over the upper branch to prevent themselves from leaning forward further and falling below the level of the food (snapshots 6–8). In the first 0.75 sec of the second half of the behaviour (1.75–2.5 sec), with the most distal end of the tail anchored over the upper branch, the monkey flexed its knees to bring its body closer to the substrate (snapshots 9–11). In the remaining 1.00 sec (1.75–2.5 sec), the monkey flexed its tail, allowing the torso to swing back to the lower branch and regain a quadrupedal posture (snapshots 12–15).

The left knee angle and tail cantilever length showed considerable inter-individual variation which is probably associated with the inter-individual variation in body dimensions (Figure 4). Across monkeys 1–6, the left knee

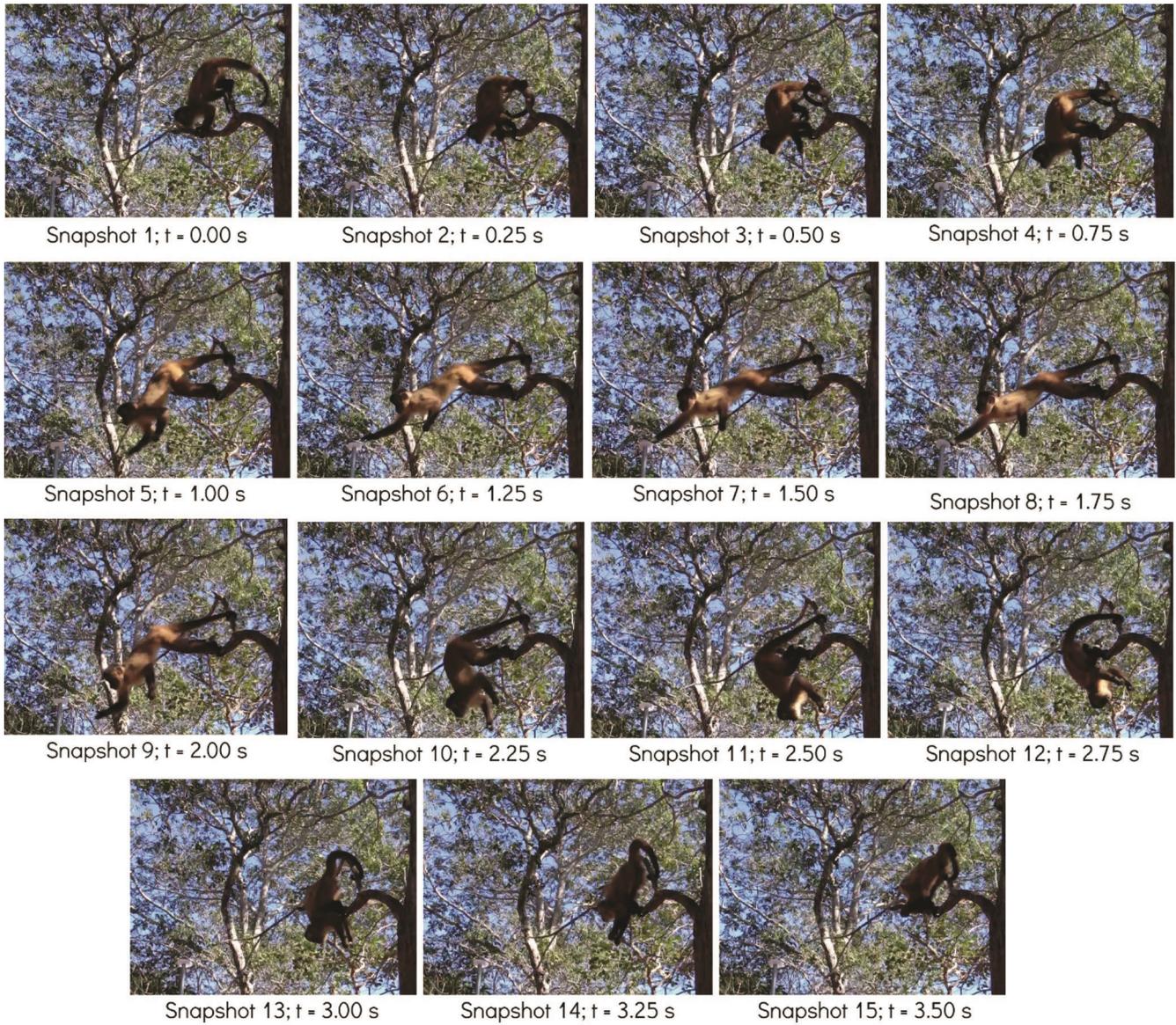


Figure 3. Fifteen snapshots from a video recording of a monkey in the act of gaining a tail-assisted head-down tripod posture to reach for food placed at a distance of 1.0 m from it.

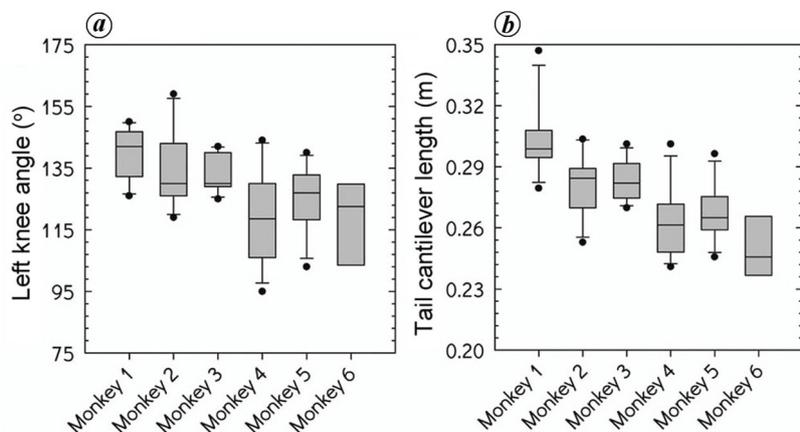


Figure 4. (a) Left knee angle and (b) tail cantilever length for six monkeys that reached for food placed at a distance of 1.0 m.

angle measured at the grasping moment predicted and explained a significant proportion of inter-individual variation in the tail cantilever length ($r^2 = 0.911$, $P < 0.001$; Figure 5). For monkey 7, the left knee angle measured at the grasping moment was greater (paired sample t -test: $t = 3.208$, $df = 20$, $P < 0.004$; Figure 6a), and the tail cantilever was longer (paired sample t -test: $t = 4.772$, $df = 20$; $P < 0.001$; Figure 6b) when it reached for food placed at 1.2 m than 0.9 m from the lower branch.

Discussion

In an experimental set-up in the wild, we induced capuchin monkeys to adopt a tail-assisted head-down tripod posture to reach for food placed at certain distance from them. Qualitative descriptions of changes in the relative orientation of their limbs and tail show that the monkeys coordinate their tail and hind limbs in an online, dynamic manner by preparing to anchor the tail over a substrate during the postural transition, but anchoring it only at the moment, or immediately prior to, grasping the food. Additionally, the observed correlation between left knee angle and tail cantilever length supports this assertion. This strategy of coordinating their semi-prehensile tail with their limbs enables the monkeys to adjust their posture more flexibly compared to anchoring their tail over a substrate in anticipation and subsequently bringing about changes in their posture.

The tail-assisted, head-down tripod posture of the monkeys in the present study is functionally equivalent to the arrangement of the overhead contact line equipment used for hanging electric wires for railways. The body parts of a monkey show functional equivalence with components of the equipment: (i) hind limbs + torso = bracket tube; (ii) forelimbs = register arm and (iii) tail = stay tube (Figure 7). The bracket tube and stay tube constitute a cantilever clamp assembly. Typically, the

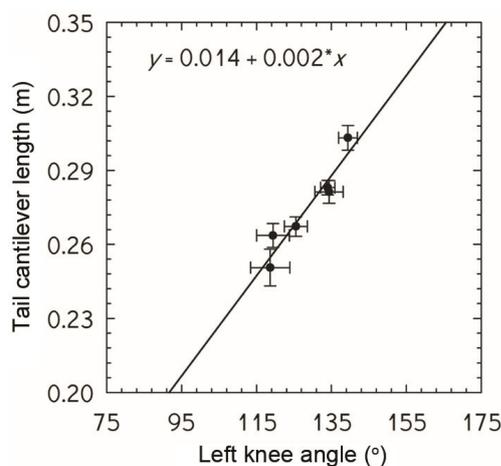


Figure 5. Relationship between tail cantilever length and left knee angle for six monkeys that reached for food placed at a distance of 1.0 m. Error bars indicate SEM.

stay tube is longer for hanging the wire at a greater distance from the pole. Analogously, a monkey's hind limbs and tail constitute a cantilever clamp assembly. The tail cantilever is longer while a given monkey reaches for food located at a greater distance from it. The tail thus appears to be functionally equivalent to a cantilever of adjustable length. However, given the small sample size of the present study – results limited to six individuals – further studies are required to confirm this interesting hypothesis.

The tail-use behaviour described here suggests that in the capuchins when the tail is already in contact with a substrate, an increase in touch, pressure and stretching of the tail skin associated with the downward motion of the body might eventually trigger the anchoring of the tail over the substrate and prevent the body from falling further. While both slow-adapting and rapid-adapting mechanoreceptors – Meissner's corpuscles and Pacinian corpuscles – are present in the friction pad of prehensile tails in atelids, only slow-adapting mechanoreceptors – Ruffini corpuscles and Merkel cells – are present in the ventrodorsal skin of semi-prehensile tails in cebids¹². Meissner's corpuscles detect light touch, movement, and vibration; Ruffini corpuscles detect heavy touch, pressure and continuous skin stretching^{7,10,27}. Slow-adapting mechanoreceptors might be important for postural behaviours and rapid-adapting mechanoreceptors for locomotion. Further research is required to comprehensively comment on the function of mechanoreceptors in the tail skin during locomotion and postural behaviour in atelids and cebids.

The spatial relationships between the hind limbs and the capuchins tail embodied within the geometry of a given tail-assisted posture uniquely constrain tail–limb coordination during postural behaviour. However, the postural demands of locomotion supposedly do not constrain the tail–limb coordination in this manner. A previous study on the tail–limb coordination in woolly monkeys, *Logothrix logothricha* and black spider monkeys, *Ateles fusciceps robustus*¹⁶ indicates that, during locomotion, atelids anchor their tails on a substrate in anticipation of a subsequent step. Thus, prehensile tail–limb coordination in atelids seemingly contrasts with semi-prehensile tail–limb

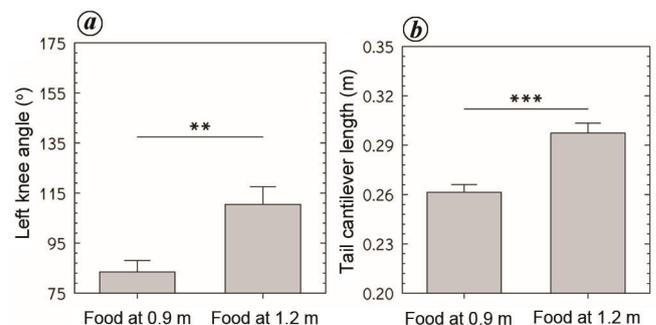


Figure 6. (a) Left knee angle and (b) tail cantilever length of a monkey that reached for food placed at 0.9 and 1.2 m from it. Error bars indicate SEM. *** $P < 0.001$.

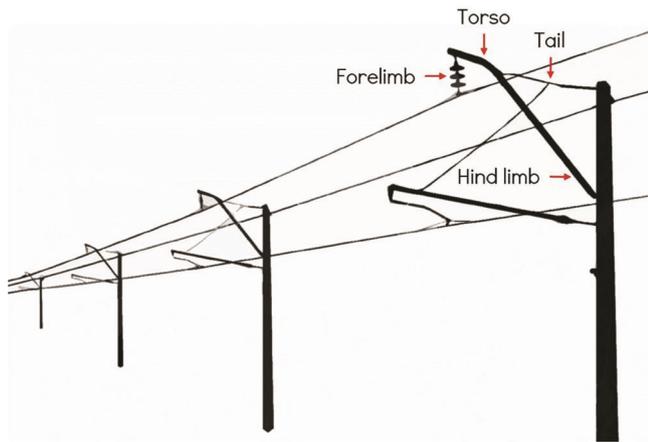


Figure 7. Illustration of the overhead contact line equipment used for hanging electric wires for railways, highlighting its resemblance with a monkey in a tail-assisted, head-down tripod posture (bracket tube = hind limb + torso; register arm = forelimb; stay tube = tail).

coordination in capuchins. However, for a meaningful comparison, further studies are required on (i) prehensile tail–limb coordination during postural behaviour in atelids although they do not always employ their tails like the cebids^{12,13,18} and (ii) semi-prehensile tail–limb coordination during locomotion in capuchins.

Further biomechanical analysis of prehensile/semi-prehensile tail-use behaviour is required to completely understand the coordination and control of tails in prehensile arboreal mammals. Distinct morphological features^{7,10–12} underlie distinct prehensile/semi-prehensile tail-use behaviour in Atelidae and Cebidae^{13–22}, making these animals ideal for identifying morphological features of prehensile/semi-prehensile tails adapted for both locomotion and positional behaviour versus those adapted exclusively for locomotion or positional behaviour.

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