Thermal Imaging of Aye-Ayes (*Daubentonia madagascariensis*) Reveals a Dynamic Vascular Supply During Haptic Sensation

Gillian L. Moritz · Nathaniel J. Dominy

Abstract Infrared thermography (IRT) is used to visualize and estimate variation in surface temperatures. Applications of IRT to animal research include studies of thermofunctional anatomy, ecology, and social behavior. IRT is especially amenable to investigations of the somatosensory system because touch receptors are highly vascularized, dynamic, and located near the surface of the skin. The hands of aye-ayes (*Daubentonia madagascariensis*) are thus an inviting subject for IRT because of the prominent middle digit that functions as a specialized haptic sense structure during percussive and probative foraging. It is a vital sensory tool that is expected to feature a high density of dermal mechanoreceptors that radiate heat and impose thermal costs under cool temperatures. Here we explore this premise by acquiring IRT images of 8 aye-ayes engaged in a variety of passive and probative behaviors. We found that the middle digit was typically 2.3°C cooler than other digits when the metacarpophalangeal (MP) joint was extended, and that it warmed an average of 2.0°C when the MP joint was flexed during active touching behavior. These changes in digital surface temperature, which were sometimes as much 6.0°C, stand in sharp contrast with the profoundly invariant temperatures of the other digits. Although the physiological mechanisms behind these temperature changes are unknown, they appear to reveal a uniquely dynamic vascular supply.

Keywords Infrared imaging · Mechanoreceptors · Stenosis · Stenotic kinking · Thermography

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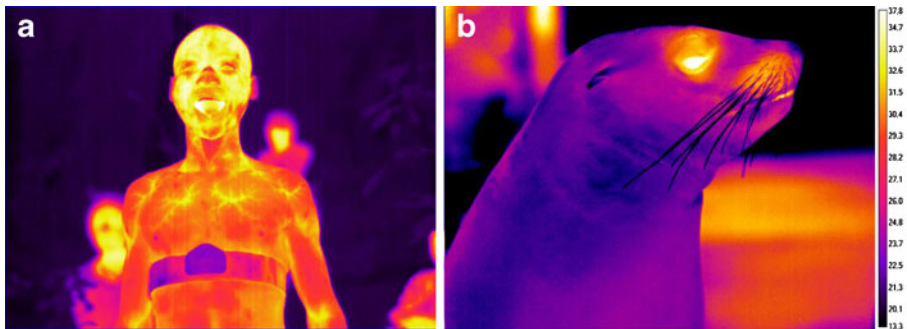Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA

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Introduction

Infrared thermography (IRT) is used to visualize and estimate variation in surface temperatures based on the physical laws of radiative transfer. For animals, surface temperatures vary as a function of vascular dilation and the emissivity of heat from skin, feathers, or fur (Fig. 1a). In the 1960s, the applications of IRT to animal research faced a variety of practical limitations, such as the need for large, liquid nitrogen-cooled detectors (Cena and Clark 1973; McCafferty *et al.* 2011). As a result, IRT was conceived mainly as noninvasive means of detecting disease among captive animals. At close range (<1 m), specific sites of heat transfer can point to the location and extent of infection. In other studies, IRT was employed at greater distances (>1000 m) to census wild populations (McCafferty 2007). By the 1990s, the development of handheld, electronically cooled cameras eased portability constraints and fueled a wider consideration of the energy costs faced by endothermic animals. As a result, the applications of IRT to animal research have surged in recent years to include studies of thermofunctional anatomy, ecology, and social behavior (Šumbera *et al.* 2007; Tattersall and Cadena 2010). For example, the thermal costs of sexual selection have been explored in species ranging from canaries to lions (Ward and Slater 2005; West and Packer 2002). IRT is therefore an established methodology that is undergoing a rapid and exciting practical expansion; yet, research applications focused on nonhuman primates are few (George *et al.* 1993; Glander *et al.* 2011; Nakayama *et al.* 2005).

Active Touch, the Haptic Sense

IRT has also informed studies of the senses. It is especially amenable to the somatosensory system because touch receptors are highly vascularized, dynamic, and located near the surface of the skin (Fundin *et al*. 1997). For pinnipeds, haptic (active touch) perception with vibrissae can result in striking thermal increases of the

Fig. 1 a Thermograph of a man after 30 min of walking in the Bwindi Impenetrable National Park, Uganda (ambient conditions=19.7°C; relative humidity=97.4%). Evaporative cooling of the skin surface (mean temperature=30.3°C) reveals vasodilation and elevated surface temperatures of the perforating branches of the thoracic and thoracoacromial arteries (range=31.0–32.2°C). **b** Thermograph of a Steller's sea lion (*Eumetopias jubatus*) in Santa Cruz, CA (ambient conditions=14.4°C; relative humidity=85.0%). A rich arterial supply to the underlying mechanoreceptors of the whiskers results in a conspicuous thermal window; the mean mystacial surface temperature is 25.0°C, whereas the overall mean surface temperature is 21.8°C.
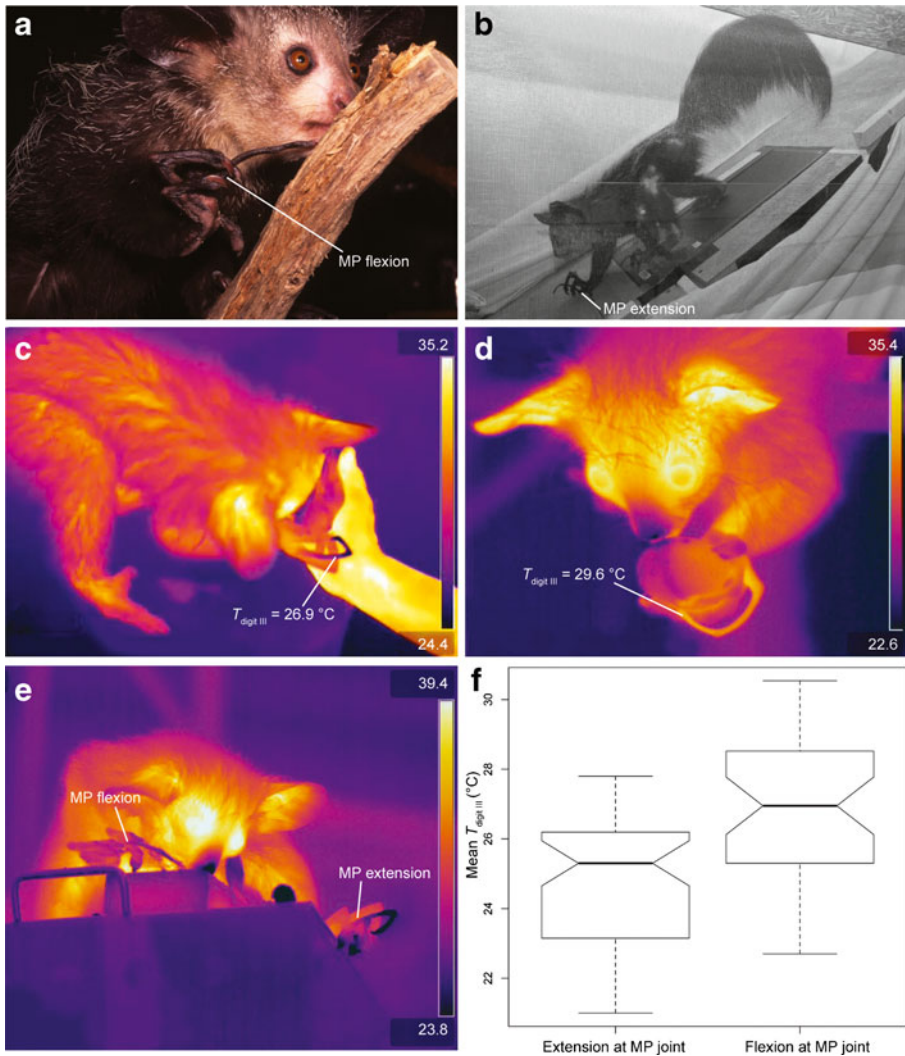
mystacial skin (Fig. 1b). Such a thermal window —or surface area associated with disproportionate heat loss due to increased peripheral blood flow (Mauck *et al.* 2003; Weissenböck *et al.* 2010)— is a testament to the adaptive value of whiskers (*cf.* Muchlinski 2008, 2010). The benefits of active touch for detecting prey must offset the cost of reduced heat retention in cold water (Dehnhardt *et al.* 1998; Mauck *et al.* 2000). Similarly, the egg-incubating feet of sleeping penguins (*Aptenodytes patagonica*) are exceedingly sensitive to egg movement (Dewasmes and Telliez 2000), yet also costly thermal windows in air temperatures of −15°C (McCafferty *et al.* 2011). For penguins the fitness advantages of mechanosensitive feet appear to override the high energetic costs.

The concept of a thermal window is germane to nocturnal primates. The hands and feet of primates are richly and almost uniquely invested with Meissner corpuscles (MCs). MCs are rapidly adapting mechanoreceptors that respond to transient or phasic stimuli. Their distinctive morphology and location in the dermal papillae of glabrous skin, where they connect to and tightly abut the basal surface of the epidermis, indicate a primary role during haptic touch (Dominy 2009; Hoffmann *et al.* 2004). The location and complex innervation of MCs by 1 or 2 myelinated fibers from the subepidermal nerve plexus is expected to impose non-negligible energetic and thermal costs to primates active under cool temperatures. Such costs might even extend to the scalp in the form of localized thermal windows associated with somatocortical processing (George *et al.* 1993). To explore such possibilities, we captured infrared images of a nocturnal haptic specialist, the aye-aye (*Daubentonia madagascariensis*).

Aye-Ayes

Aye-ayes are a distinctive and enigmatic primate. They have elongated and ectaxonic hands with a disproportionately long, thin, and clawed 3rd digit that has been described as villiform, filamentous, gracile, and grotesquely attenuated (Fig. 2a) (Cartmill 1974; Jouffroy 1975; Oxnard 1981; Owen 1863). Digit III is not only independently mobile (Milliken *et al.* 1991), but also multiaxial because of a unique ball-and-socket metacarpophalangeal (MP) joint (Soligo 2005). As a result of this unique morphology, the digit is vulnerable to injury and poorly suited for bearing load during palmigrade locomotion; indeed, digit III is hyperextended at the MP joint, flexed at the interphalangeal joints, and "parked" to minimize loading during locomotion (Fig. 2b) (Kivell *et al.* 2010; Krakauer *et al.* 2002; Soligo 2005).

Such digital morphology functions to facilitate percussive foraging or tap-scanning (Erickson 1991, 1995, 1998; Erickson *et al.* 1998), a haptic-auditory behavior that contributes to the detection of embedded beetle larvae and to the material assessment of foods (Ancrenaz *et al.* 1994; Andriamasimanana 1994; Iwano 1991; Iwano and Iwakawa 1988; Lhota *et al.* 2008, 2009; Petter and Peyrieras 1970; Pollock *et al.* 1985; Sterling 1994; Sterling and McCreless 2006; Sterling *et al.* 1994). Accordingly, aye-ayes are described as having a well-developed sensorimotor intelligence (Gibson 1986; Sterling and Povinelli 1999) that is supported in part by a large and expanded somatosensory cortex (Kaufman *et al.* 2005). Such haptic specializations suggest that digit III might be richly innervated with MCs and

Fig. 2 a Metacarpophalangeal flexion of digit III during probative foraging (photograph by D. Haring, used with permission). **b** MP extension of digit III during palmigrade locomotion over a force plate (see Kivell *et al.* 2010; photograph by D. Haring, used with permission). **c** Thermograph of an aye-aye investigating a food object. The relatively cool middle digit ($T_{digit\ III}$=26.9°C, SD=1.1) is the result of preimage MP extension during palmigrady (*cf.* $T_{human\ skin}$=32.8°C, SD=0.6). **d** An aye-aye grasping a food object. The relatively warm middle digit ($T_{digit\ III}$=29.6°C, SD=0.2) is the result of MP flexion during haptic assessment. **e** The aye-aye Kali engaged in tap-scanning. The right flexed middle digit is substantially warmer ($T_{digit\ III}$=26.7°C, SD=0.8) than its extended counterpart ($T_{digit\ III}$=22.9°C, SD=1.4). **f** Notched boxplot of $T_{digit\ III}$ during MP extension and flexion. Boxes represent the interquartile range between the first and third quartiles and the line inside represents the median; nonoverlapping notches signify a difference at the 95% confidence level. Whiskers denote the lowest and highest values. On average, $T_{digit\ III}$ increased 2.0°C when the MP joint was flexed to accommodate haptic behaviors such as tap-scanning and probing (t=9.3, $p<0.0001$).

potentially a costly thermal window. Here we test this hypothesis by acquiring IRT images of aye-ayes engaged in a variety of passive and probative behaviors.

Materials and Methods

Study Sites and Subjects

We studied 8 adult aye-ayes within the indoor, temperature-controlled enclosures of the Duke Lemur Center and San Francisco Zoo (*ca.* 25°C; Table I). We filmed the subjects from a distance of *ca.* 1 m during routine enrichment activities. Each activity motivated the aye-ayes to approach, evaluate, and extract prepared foods. Thus we filmed the middle digit when it was engaged in 3 sequential activities and positions: 1) locomotor approach resulting in a state of extension at the MP joint, 2) tap-scanning resulting in rapid flexion and extension at the MP joint, and 3) probing and removal of food resulting in full flexion at the MP joint. We defined states of MP flexion or extension as angular deviations >10º from a neutral position. The difficulty of the extraction tasks varied. Food rewards contained within cardboard or eggshells were extracted quickly, whereas foods embedded in bamboo sheaths were more challenging to excavate.

Thermal Imaging and Analysis

We estimated the surface temperatures of aye-ayes with a handheld infrared thermal imaging camera (ThermaCAM SC640; FLIR Systems, Boston, MA). The camera uses a 640×480 pixel focal plane array to produce 307,200-pixel thermographs (accuracy±1°C for objects 5–120°C). For each thermograph, we recorded the state of flexion of the MP joint and estimated the surface temperature of individual digits (T_{digit}) with commercial software that can calculate the temperature of selected pixels within a user-drawn polygon (ThermoVision ExaminIR Max v. 1.10, FLIR Systems). Here, T_{digit} is defined as the average temperature of all pixels within an irregular polygon extending from the MP joint to the distal apical pad of a given digit (excluding the nail or claw). This protocol was approved by the Duke Lemur Center Research Committee (approval no. O-9-137-08-5) and the Chancellor's Animal Research Committee of the University of California, Santa Cruz (approval no. 0811).

Table I Summary information for focal subjects

Name	Body mass (g)	Sex	Age (yr)	Provenance
Bellatrix	2620	F	5	DLC
Kali	2920	F	13	DLC
Lucrezia	2960	F	9	DLC
Medea	2470	F	6	DLC
Mephistopheles	2670	M	25	DLC
Nify	1910	M	2	SFZ
Sabrina	2750	F	7	SFZ
Warlock	2450	M	12	SFZ

DLC Duke Lemur Center; *SFZ* San Francisco Zoo

We estimated T_{digit} of each visible digit and used these values as independent sample points. To compare variation in T_{digit} within each test condition, i.e., state of MP extension or flexion, we used one-way ANOVAs and Tukey's *post hoc* test of honestly significant differences (HSD). To compare variation in T_{digit} between the 2 test conditions, we used a repeated-measures *t*-test. We performed all statistical tests using JMP v. 8.0.2 for Macintosh.

Results

We examined 81,345 pixels from 81 thermographs. Digit I (the pollex) was almost always obscured in our thermographs due to the grasping posture of the hand and the lateral vantage point of the camera operator. Accordingly, our results are limited to digits II-V. Among digits II, IV, and V, we found little variation in surface temperature regardless of whether the MP joint was flexed ($T_{digits\ II,\ IV,\ V}$: $F_{2,52}=1.3$, $p=0.88$) or extended ($T_{digits\ II,\ IV,\ V}$: $F_{2,129}=2.2$, $p=0.12$; Table II). Much more variable, however, was $T_{digit\ III}$ (Fig. 2c,d), which was typically 2.3°C cooler than the other digits when the MP joint was extended ($F_{3,184}=15.3$, $p<0.0001$, Tukey HSD, $P<0.05$; Fig. 2e). Yet $T_{digit\ III}$ increased significantly (an average of 2.0°C; repeated measures $t=9.3$, df=33, $P<0.0001$; Table II; Fig. 2f) when the MP joint was flexed to accommodate active tap-scanning and probing. We observed a similar change in digit V, but the difference was marginally significant and almost certainly the artifact of a small sample size ($n=3$ images in a state of MP flexion).

In some individual cases, we recorded relatively extreme temperature differentials. For example, Fig. 2e of the female Kali shows that $T_{digit\ III}$ of the left hand was *ca.* 6.1°C cooler than $T_{digit\ II}$ and $T_{digit\ IV}$ (29.3° and 28.8°C, respectively), whereas the right middle finger, which is flexed at the MP joint and engaged in haptic tap-scanning of a sealed food container, is *ca.* 3.8°C warmer than its counterpart. Such warming occurred within 3 min of the onset of digital activity.

Table II Effects of MP joint extension and flexion on the mean surface temperature (±1 SD) of individual digits (T_{digit})

	Extension at MP joint		Flexion at MP joint			
Digit	N images	Mean T_{digit}[†]	N images	Mean T_{digit}[†]	Mean difference	p[‡]
II	42	27.8±2.5[a] (22.7–31.9)	20	28.5±1.8[a] (24.3–31.4)	0.7	0.253
III	55	24.9±1.7[b] (21.0–27.8)	34	26.9±2.1[b] (22.7–30.5)	2.0	<0.0001
IV	58	27.4±2.6[a] (23.0–30.8)	18	28.5±1.8[a] (23.8–31.4)	1.1	0.711
V	21	26.5±2.5[a] (22.3–29.9)	3	28.4±1.3[a,b] (25.1–30.8)	1.9	0.049

[†] Within-condition test, ANOVA Tukey's HSD: Values for individual digits that are statistically different from each other at the $p<0.05$ level are followed by different letters in superscript; values that are statistically indistinguishable from each other are followed by the same letter in superscript.

[‡] Between-condition test, repeated-measures *t*-test based on samples sizes in the flexion condition

Discussion

Here we report estimates of digital surface temperatures (T_{digit}) based on IRT. The middle digit of aye-ayes is a highly specialized haptic sense structure. It is a vital foraging tool that is expected to feature a high density of dermal mechanoreceptors and therefore radiate relatively more heat than other digits. We found that $T_{\text{digit III}}$ was typically 2.3°C cooler and sometimes as much as 6.0°C cooler than other digits when the aye-ayes were engaged in palmigrade locomotion. Yet $T_{\text{digit III}}$ warmed to near parity with the other digits when the metacarpophalangeal joint was flexed to accommodate percussive foraging and digital probing. These findings suggest a uniquely dynamic vascular supply to digit III during haptic sensation.

At least 3 compatible factors could account for the relatively cool temperatures of digit III during nonhaptic behaviors. First, the thin and elongate morphology of digit III results in a relatively high surface-to-volume ratio. Because such a ratio is unfavorable for heat retention, controlled vasoconstriction is expected to reduce thermal costs during inactivity or locomotion. Analogous examples of anatomical structures under thermal control include the tails of California ground squirrels (*Spermophilus beecheyi*: Rundus *et al.* 2007) and the bills of toco toucans (*Ramphastos toco*: Tattersall *et al.* 2009). Second, the importance of minimizing loading to digit III during palmigrade locomotion results in a high degree of extension at the MP joint (Fig. 2b; Kivell *et al.* 2010; Krakauer *et al.* 2002; Oxnard 1981). Such hyperextension might cause stricture of the palmar digital artery, termed stenotic kinking, that could result in cooler surface temperatures across the digit. Third, digit III has relatively reduced vascular requirements, as it is virtually devoid of subcutaneous fat. Moreover, the only muscle belly present (of the interossei palmaris) is diminished compared to its presence in the other digits (Soligo 2005). Taken together, such reduced metabolic demands are expected to contribute to relatively lower temperatures during nonhaptic activities, when digit III is practically functionless. Thus, although the underlying physiological mechanisms that drive the dynamic temperature changes reported here are unknown, our results highlight the potential thermal costs of a highly specialized sensory structure.

We believe that numerous potential applications of IRT exist within the field of primatology, a discipline with a long-standing interest in thermoregulatory behaviors (Brain and Mitchell 1999; Schmid 2011). For example, the few recent anthropological and primatological applications of IRT have had widely different aims, focusing on the effects of social signals, body size, and daily temperature changes on the surface temperatures of humans and nonhuman primates (Glander *et al.* 2011; Nakayama *et al.* 2005; Perry and Dominy 2009). Overall, our findings contribute to the expanding role of IRT in studies focused on animal functional physiology and anatomy.

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