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RESEARCH ARTICLE

Cutaneous tactile sensitivity before and after tail loss and regeneration in the leopard gecko (*Eublepharis macularius*)

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ABSTRACT

Amongst tetrapods, mechanoreceptors on the feet establish a sense of body placement and help to facilitate posture and biomechanics. Mechanoreceptors are necessary for stabilizing the body while navigating through changing terrains or responding to a sudden change in body mass and orientation. Lizards such as the leopard gecko (*Eublepharis macularius*) employ autotomy – a voluntary detachment of a portion of the tail – to escape predation. Tail autotomy represents a natural form of significant (and localized) mass loss. Semmes–Weinstein monofilaments were used to investigate the effect of tail autotomy (and subsequent tail regeneration) on tactile sensitivity of each appendage of the leopard gecko. Prior to autotomy, we identified site-specific differences in tactile sensitivity across the ventral surfaces of the hindlimbs, forelimbs and tail. Repeated monofilament testing of both control (tail-intact) and tail-loss geckos had a significant sensitization effect (i.e. decrease in tactile threshold, maintained over time) in all regions of interest except the palmar surfaces of the forelimbs in post-autotomy geckos, compared with baseline testing. Although the regenerated tail is not an exact replica of the original, tactile sensitivity is shown to be effectively restored at this site. Re-establishment of tactile sensitivity on the ventral surface of the regenerate tail points towards a (continued) role in predator detection.

KEY WORDS: Mechanoreceptor, Monofilament, Skin, Reptile, Autotomy

INTRODUCTION

Adaptability in posture-gait control, body orientation and verticality is achieved using afferents from multiple sensory sources including vestibular, visual and somatosensory inputs (Meyer et al., 2004; Carver et al., 2006; Horak, 2010). Amongst tetrapods, control of balance is associated with somatosensory receptors within the skin known as cutaneous mechanoreceptors (Reed-Geaghan and Maricich, 2011; Schneider et al., 2016). Cutaneous mechanoreceptors on the palmar and plantar surfaces of limbs provide tactile perception and thus establish a sense of body placement with respect to the ground (Shumway-Cook and Horak, 1986; Quai et al., 2005). This sensory information is then relayed to the somatosensory cortex of the brain for processing (in conjunction with vestibular and visual inputs), to help achieve motor adaptability. In humans, reduced cutaneous feedback of the plantar surface of the foot (the sole) is correlated with diminished motor performance, postural instability and altered postural responses (Dhruv et al., 2002; Wang and Lin, 2008; Bent and Lowrey, 2013; Strzalkowski et al., 2015), resulting in compensatory motions in the ankles and hips (Meyer et al., 2004). These findings demonstrate that mechanoreceptors of the feet play an important role in governing postural responses and underscore their role as an important contributor to dynamic balance (Nurse and Nigg, 1999; Eils et al., 2002; Meyer et al., 2004; Strzalkowski et al., 2015).

Cutaneous mechanoreceptors in reptiles are known as sensilla (=corpuscles, tubercles, papillae; Jackson, 1977; Hiller, 1978; Bauer and Russell, 1988; Di-Poï and Milinkovitch, 2013; Crowe-Riddell et al., 2016). Although they primarily function as mechanoreceptors, sensilla may also participate as chemoreceptors, thermoreceptors, hygroreceptors and hydroreceptors (Siminoff and Kruger, 1968; Hiller, 1976, 1978; Jackson, 1977; Ananjeva et al., 1991; Di-Poï and Milinkovitch, 2013). Sensilla are widely distributed across the body of most lizards (e.g. Hiller, 1968, 1971; Matveyeva and Ananjeva, 1995; Russell et al., 2014), and hence are well positioned to participate in proprioception, tactile sensitivity, and the detection substrate-borne vibrations associated with locomotion, predator/prey detection and possibly communication (Lauff et al., 1993; Sherbrooke and Nagle, 1996; Barnett et al., 1999; Russell, et al., 2014; see also Hetherington, 1989; Virant-Doberlet et al., 2019). For example, the fossorial sandfish lizard (*Scincus scincus*) uses vibrational information to locate prey on or within a sandy substrate (Hetherington, 1989). Similarly, horned lizards (*Phrynosoma* spp.) may use sensilla to detect the approach of predators (Sherbrooke and Nagle, 1996). Sensilla have also been proposed as key mediators of tail autotomy (Russell and Bauer, 1987; Russell et al., 2014), a dramatic form of anti-predation behavior common to many species of lizard, as well as the tuatara, and some snakes, amphisbaenians and plethodontid salamanders (Jacyniak et al., 2017). During a predatory encounter, sensilla-mediated detection of skin deformation may induce tail autotomy (Maclean, 1980; Russell et al., 2014). Autonomous movements of the newly detached tail then serve as a distraction, enabling the lizard to escape capture (Higham and Russell, 2010; Lin et al., 2017). In most species, tail autotomy is followed by tail regeneration and the recreation of a structurally comparable replacement tail (e.g. McLean and Vickaryous, 2011; Fisher et al., 2012; Lozito and Tuan, 2016; reviewed in Bellairs and Bryant, 1985; Jacyniak et al., 2017). Underscoring the continued importance of mechanoreception, sensilla are regenerated during regrowth of the new tail (Russell et al., 2014).

Whereas tail autotomy provides an immediate means for evading predation, it can also dramatically alter total body mass (Jagnandan et al., 2014). In adult leopard geckos (*Eublepharis macularius*), maximum tail loss results in a re-distribution of weight across the limbs, and a cranial shift in the center of mass (Jagnandan et al., 2014). Even once the tail is completely regenerated, this repositioning of the center of mass is only partially recovered (Jagnandan et al., 2014). Interestingly, while there are transient changes in the ground

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reaction forces and joint angles of the hindlimb during running trials following tail autotomy, there are no significant changes in forelimb kinematics or running speed (Jagnandan et al., 2014). In humans, a link between sensory input from plantar surfaces in the feet and gait kinematics has been established (Magnusson et al., 1990; Nurse and Nigg, 1999; Eils et al., 2002), particularly following limb loss, which can cause increased skin sensitivity (lower tactile threshold) in residual limbs, affecting functional balance (Haber, 1955; Templeton et al., 2018). Whether the transient changes observed in leopard geckos are also associated with changes in tactile sensitivity remains unknown.

Here, we investigated cutaneous tactile sensitivity of the palmar and plantar surfaces of the feet and the ventral surface of the tail of the tail-autotomizing lizard *E. macularius* before and after tail loss. Previous research has demonstrated that sensilla are present across the body of *E. macularius*, including across the ventral surfaces of the feet and tail (Russell et al., 2014). We used monofilament testing to quantify sensitivity changes in response to immediate mass loss (following tail loss) and gradual mass gain (tail regeneration). Tail regeneration in the leopard gecko is a relatively rapid (~30 days), epimorphic (blastema-mediated) process that generates a structurally similar but non-identical replacement appendage (McLean and Vickaryous, 2011; Delorme et al., 2012; Jagnandan et al., 2014). We hypothesized that tactile sensitivity across the ventral surfaces of the limbs would temporarily change in response to tail loss, correlated with the redistribution of the center of mass. Further, we predicted that the regenerated tail would reacquire a high level of tactile sensitivity, associated with the regeneration of sensilla. We found that repeated testing resulted in the sensitization (increased sensitivity, decreased threshold) of both control (tail-intact) and tail-loss geckos in all regions of interest except the forelimbs, and tactile sensitivity was effectively restored in the regenerated tail.

MATERIALS AND METHODS

Animal model

A cohort of 15 captive bred subadult (less than 1 year in age with no signs of secondary sexual characteristics) leopard geckos, *Eublepharis macularius* (Blyth 1854), with original tails (average mass prior to autotomy, 22.16±0.35 g; average snout to vent length prior to autotomy, 177.8±2.36 mm; means±s.e.m.; Table S1) were obtained from a commercial supplier (Global Exotic Pets, Kitchener, Ontario, Canada). Animal utilization protocols were approved by the University of Guelph Animal Care Committee (protocols 1954, 3772) and followed the guidelines of the Canadian Council on Animal Care. Animal husbandry follows the work of McLean and Vickaryous (2011). Geckos were housed in a secure vivarium (Hagen Aqualab facility) at the University of Guelph, inside a temperature-controlled environmental chamber (average ambient temperature, 27.5°C). Geckos were housed individually in 18.9 liter (5 gallon) polycarbonate tanks, with a heat cable (Hagen Inc., Baie d'Urfé, Québec, Canada) set at 32°C and placed underneath one side of the enclosure to establish a thermal gradient. Each enclosure included two hide boxes and a water dish. Geckos had constant access to fresh drinking water and were fed three live larval mealworms (*Tenebrio* spp.) daily, dusted with powdered calcium and vitamin D3 (cholecalciferol; Zoo Med Laboratories Inc., San Luis Obispo, CA, USA). The environmental chamber was kept on a year-round 12 h:12 h light:dark photoperiod. All experiments were conducted during a 6-week span from November to December.

Experimental set-up

Geckos were randomly assigned into one of two groups: control (tail intact, n=5) or tail loss (n=10) (Fig. 1). Autotomy occurred on day 1 of the experiment. Five of the tail-loss geckos were randomly selected and euthanized at experimental day 9, and their brains were collected as part of a separate experiment investigating changes in brain cell neuromorphology. All remaining geckos (five tail loss and five controls) were euthanized at experimental day 32, 1 day after their last monofilament testing session (see below). Tail loss (autotomy) was performed by applying a firm pinch at the base of the tail (using the forefinger and thumb) of manually restrained and conscious geckos. Once the tail was self-detached, the gecko was released back into its enclosure. All autotomies occurred at roughly the same location along the tail (adjacent to the tail base), corresponding with maximal tail loss, and all geckos survived the autotomy procedure. Control geckos were manually restrained to simulate autotomy conditions but did not have their tails removed.

Monofilament testing

Geckos were placed in a clear plexiglass chamber (0.35×0.295×0.315 m) mounted on a raised, perforated (~10 mm diameter) platform (Fig. 2B). A mirror suspended at an oblique angle below the perforated platform was used to direct the monofilaments through the perforations (Fig. 2B,C). A video camera (Panasonic SDR-H85) was mounted outside the chamber to record the trials (see videos available from Dryad, https://doi.org/10.5061/dryad.8pk0p2nk7), and the front of the chamber was covered with a dark partition to blind the gecko to the presence of the experimenter. Geckos were acclimated to the testing chamber for 1 h prior to the start of each testing session.

Cutaneous sensitivity was tested using Semmes–Weinstein monofilaments at six sites of interest (Field et al., 1997): the palmar surface of each manus (forelimbs), the plantar surface of each pes (hindlimbs), and the ventral surfaces of the base (proximal)

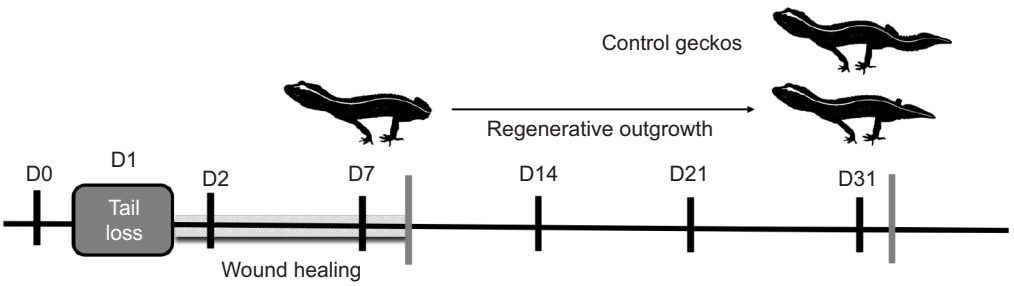

Fig. 1. Schematic illustration of experimental design for the monofilament assay. Black vertical lines correspond to monofilament testing days. Gray vertical lines correspond to euthanasia time points. Each group followed the same timeline, with a subset of the tail-loss group (n=5) being euthanized on day 9 (D9; as part of a separate study). The remaining tail-loss geckos (n=5) and all control geckos (n=4) were euthanized on D32. All monofilament testing was performed within 1.5 months.

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Fig. 2. Sites of interest for monofilament testing, and experimental chamber. (A) Schematic ventral view of a gecko. Monofilaments were applied to the palmar surfaces of the left and right manus (forelimbs) and the plantar surfaces of the left and right pes (hindlimbs), along with the ventral surfaces of the base of the tail and the tail tip (white dots). (B,C) The experimental chamber was a custom-built clear plexiglass enclosure (0.35×0.295×0.315 m) mounted on a raised and perforated (~10 mm diameter perforations) platform. An obliquely suspended mirror beneath the chamber enabled visualization of the sites of interest (C). A black partition (not shown) was placed along the front of the chamber, to blind the gecko to the presence of the experimenter. Application of a monofilament through a perforated hole is shown. Each monofilament was applied perpendicular to the skin until buckling.

and tip (distal) of the tail (Fig. 2A). Monofilaments each have a nylon fiber of varying diameters that are calibrated to buckle at a known force when applied perpendicularly to a surface. For each site, monofilaments were applied through the perforated platform in an area roughly corresponding to the middle of a testing site, until buckling occurred. After which, it was maintained in position for approximately 1 s, before being removed. To determine cutaneous sensitivity threshold, monofilaments were applied in an ascending series (Table S2) starting with a 0.091 g filament until a positive response was scored. A withdrawal response from the gecko was regarded as positive when the application of the monofilament resulted in lifting of the appendage from the platform during application. When no withdrawal response was observed, the application was deemed negative, and the subsequent gram monofilament was applied (Fig. S1). This process was repeated until a positive withdrawal response was observed. The smallest gram monofilament that evoked a positive response was recorded as the sensitivity threshold (hereafter, threshold). Threshold testing for each site was repeated (test and re-test) and averaged. The order of site testing was chosen opportunistically (pseudorandomly), as sites of interest could only be tested when they were placed over the perforations in the raised platform (within the chamber). Monofilament testing was only administered when the gecko was motionless, with all four feet contacting the platform.

Prior to autotomy (day 0 of the experiment), baseline thresholds of cutaneous sensitivity were established for all 15 geckos. Geckos were then tested on day 2 (1 day post-autotomy for the tail loss group), and then every 7 days thereafter, for 30 days. Daily feeding for geckos being tested took place only after all monofilament testing for the day was finished. One gecko from the control group did not react to monofilament testing, and thus was removed from the experiment.

Statistical analyses

Statistical analyses for the monofilament data were performed using SAS (SAS Institute Inc., Cary, NC, USA), with descriptive statistics reported as normalized means±s.e.m. Outliers (18/764 values) were calculated as values greater than ±2 s.d. from the mean for the entire dataset. If an outlier was removed, the second threshold testing value for that site was used instead of calculating the average. Data were then pooled by site and values outside of the mean±2 s.d. for each site were removed (forelimbs 1/276; tail tip 3/72), except if both the test and re-test values for a given site were from consecutive monofilaments. For each group, data were normalized to baseline values (i.e. day 0) and expressed as a ratio (Table 1). Data were

Table 1. Mean threshold values and percentage of baseline for each of the five sites of interest

	Control		Tail loss	
	Threshold (g)	% of baseline	Threshold (g)	% of baseline
Hindlimbs				
D0	0.19503125	100	0.1849375	100
D2	0.1593625	81.7	0.1165625	63
D7	0.13859375	71.1	0.1325625	71.7
D14	0.1293125	66.3	0.1168	63.1
D21	0.13390625	68.7	0.13275	71.8
D31	0.1409375	72.3	0.1503	81.3
Forelimbs				
D0	0.14525	100	0.112026316	100
D2	0.100375	69.1	0.11375	101.5
D7	0.1095625	75.4	0.1095625	97.8
D14	0.10028125	69	0.106	94.6
D21	0.10496875	72.3	0.107875	96.3
D31	0.09803125	67.5	0.1003	89.5
Tail base				
D0	0.128125	100	0.105925	100
D2	0.1001875	78.2	0.09475	89.5
D7	0.1001875	78.2	0.091	85.9
D14	0.0956875	74.7	0.091	85.9
D21	0.0956875	74.7	0.1021	96.4
D31	0.0956875	74.7	0.091	85.9
Tail tip				
D0	0.1395	100	0.1375	100
D14	0.1050625	75.3	0.091	66.2
D21	0.11875	85.1	0.09475	68.9
D31	0.10975	78.7	0.091	66.2

Baseline taken at experimental day 0 (D0) and used to normalize each subsequent time point as a percentage of D0. Each threshold value represents the smallest (in g) monofilament that evoked a positive response, averaged across two technical tests for each of: n=4 biological replicates of control (tail intact) geckos; n=10 biological replicates of tail-loss geckos from experimental D0–7; and n=5 biological replicates of tail-loss geckos from experimental D14–31.

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log-transformed to meet assumptions of parametric testing. Normality and homogeneity of variance were tested using the Shapiro–Wilk and Brown–Forsythe tests, respectively. A three-way repeated-measures ANOVA (group×site×time) was performed to ensure there was no interaction. After determining there was no significant difference between groups prior to autotomy, an additional one-way repeated-measures ANOVA assessed the raw monofilament data (in grams) at baseline, pooling the gecko groups to identify any regional differences. Lastly, the data were separated into four regional site subsets (hindlimbs, forelimbs, tail base and tail tip) to examine the effect of tail loss and regeneration over time using a two-way repeated-measures ANOVA (group×time). All *post hoc* analyses examined pairwise comparisons using Fisher's least significant difference (LSD) test. Significance level for all analysis was determined as $P \leq 0.05$. Based on the research aims, *a priori* hypotheses were developed to examine specific *post hoc* comparisons for each ANOVA, outlined within the Results section. Only significant *post hoc* comparisons are reported.

RESULTS

All geckos continued to grow throughout the experimental time frame, including those undergoing tail autotomy, and none demonstrated any abnormal behaviors indicative of stress (e.g. aggression, anorexia, hyperactivity; Warwick et al., 2013). Comparable to a previous report (Jagnandan et al., 2014), autotomized geckos lost an average of 19.27% of their body mass, and an average of 39.76% of their body length (Table S1). At day 9 of the experiment, all geckos in the tail-loss group showed minimal signs of tail regeneration, either retaining a blood clot covering the site of autotomy or having lost the clot but with no evidence of new tail outgrowth. Tail tip testing began on day 14, when the first evidence of regenerative outgrowth of the new tail was visible. By day 32, all geckos in the tail loss group had fully regenerated tails (i.e. conical in shape and pigmented).

Monofilament test and re-test values were either the same for each site, or within ±2 logarithmic intervals (i.e. two consecutive monofilaments; see Table S2). Comparing all groups and all sites over time, there was a main effect of group ($F_{1,12}$=4.73, P=0.05), site ($F_{2,24}$=13.16, P=0.0001) and time ($F_{5,45}$=10.22, P<0.001). Additionally, an interaction effect existed between group and site ($F_{2,24}$=12.12, P=0.0002). Based on *a priori* hypotheses, *post hoc* comparisons for the group and time interactions were examined, to identify how tail loss and regeneration influenced regional differences in cutaneous sensitivity. *Post hoc* analyses revealed that there were no significant differences between left and right forelimbs and left and right hindlimbs (P>0.05). As a result, data for left and right were pooled for each of forelimbs and hindlimbs. *Post hoc* analyses also showed at day 0, there were no significant differences between the control and experimental group (P>0.05). Therefore, these groups were pooled to investigate differences in sensitivity prior to autotomy.

Prior to autotomy (day 0), the most sensitive site of interest (i.e. the site of interest with the lowest threshold) was the base of the tail (0.11±0.009 g), followed by the forelimbs (0.13±0.01 g), the original tail tip (0.14±0.001 g) and the hindlimbs (0.19±0.007 g) (one-way repeated-measures ANOVA, site effect: $F_{3,11}$=6.43, P=0.0089; Fig. 3). The threshold of the hindlimbs was significantly higher than the forelimbs (*post hoc* test, P=0.005) and tail base (*post hoc* test, P=0.003). Based on these regional differences in sensitivity, we used targeted ANOVAs to evaluate each site separately for the remainder of the analysis.

Our investigation of the hindlimbs revealed a significant main effect of time ($F_{5,45}$=5.34, P=0.0006), but no effect of group

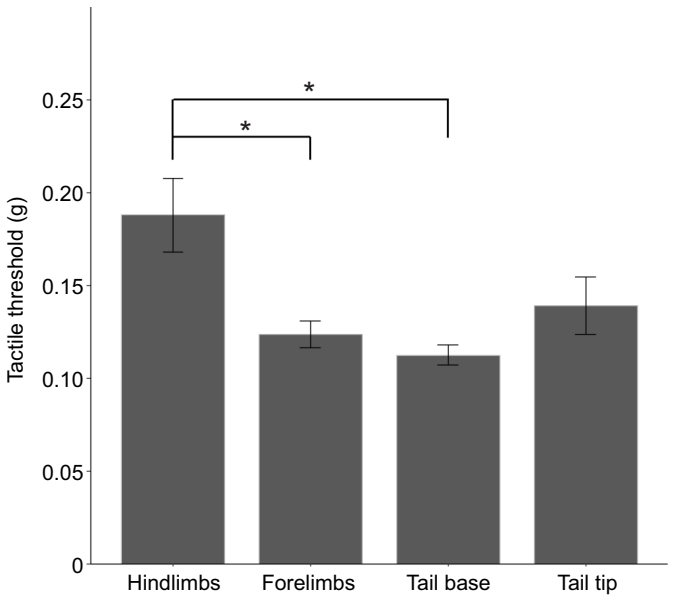

Fig. 3. Mean monofilament threshold values taken prior to autotomy (day 0). There were no significant differences between the left and right hindlimbs (pes) and left and right forelimbs (manus) (*post hoc* test, P>0.05); therefore, data from each of these regions were pooled. Each threshold value represents the smallest gram (g) monofilament that evoked a positive response, averaged across two technical replicates for each of n=14 biological replicates (mean ±s.e.m.) Asterisks (*) denote significance (one-way repeated-measures ANOVA and *post hoc* tests for multiple comparisons, $P \leq 0.05$).

($F_{1,12}$=0.24, P=0.6354) or interaction ($F_{5,45}$=0.74, P=0.597) was present (Fig. 4A). Overall, the hindlimb threshold decreased in both control and tail loss groups, which was maintained over time. Specifically, hindlimb thresholds of the tail-loss group were significantly lower than the baseline threshold by day 2 (*post hoc* test, P<0.001); however, the control threshold was not significantly lower than the baseline until day 7 (*post hoc* test, P=0.0275). This is indicative of a sensitization effect occurring following the administration of monofilament testing, following baseline (D0) testing in both gecko groups.

Monofilament testing of the forelimbs revealed a significant main effect of group ($F_{1,12}$=13.99, P=0.0028), time ($F_{5,45}$=4.59, P=0.0018) and group×time ($F_{5,45}$=2.77, P=0.0291) (Fig. 4B). Compared with baseline (day 0), the control group (tail intact geckos) showed a significant decrease in the forelimb threshold, beginning at day 2 (*post hoc* test, P<0.0002). In contrast, the forelimb thresholds of the tail-loss group were not significantly different from baseline at any time point. However, tail-loss geckos did have significantly higher thresholds than control geckos at each time point: day 2 (*post hoc* test, P=0.0002), day 7 (*post hoc* test, P=0.0081), day 14 (*post hoc* test, P=0.0056), day 21 (*post hoc* test, P=0.0101) and day 31 (*post hoc* test, P=0.0148).

At the tail base, we found a significant main effect of group ($F_{1,12}$=10.07, P=0.008) and time ($F_{5,45}$=4.91, P=0.0011), but no interaction effect ($F_{5,45}$=0.95, P=0.461) (Fig. 4C). Beginning at day 2, thresholds of the control (*post hoc* test, P=0.008) and tail loss (*post hoc* test, P=0.043) groups were significantly lower than baseline thresholds for all time points (sensitization), except for the tail-loss group at day 21 (*post hoc* test, P=0.484). At day 21, the threshold of the tail-loss group was also significantly higher than that of the control group (*post hoc* test, P=0.0079). Within the tail-loss group, all geckos responded to the smallest monofilament (=0.091 g) and therefore, the threshold values for both the test and

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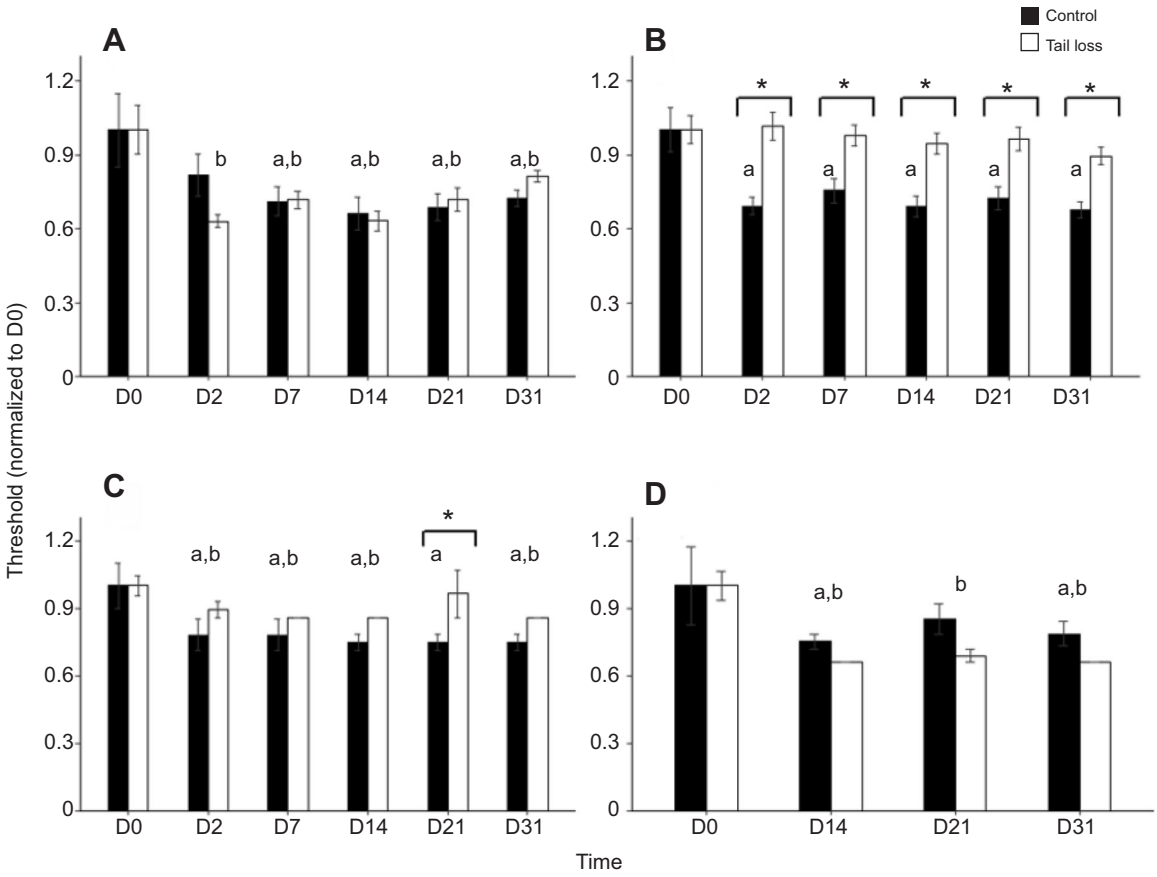

Fig. 4. Monofilament threshold values taken following autotomy, normalized to day 0. Tactile threshold of (A) hindlimbs, (B) forelimbs, (C) tail base and (D) tail tip of control (tail intact) and tail-loss groups over time. Data at experimental day 0 (D0) were normalized to 1.0. Each threshold value represents the lowest sensory response, measured in grams, averaged across two technical replicates for each of: n=4 biological replicates of control (tail intact) geckos; n=10 biological replicates of tail-loss geckos from experimental D0–7; and n=5 biological replicates of tail-loss geckos from experimental D14–31. Testing of the regenerated tail tip began on D14, when sufficient regenerative outgrowth had occurred to achieve an apical morphology. Asterisks (*) denote significance (one-way repeated-measures ANOVA and *post hoc* tests for multiple comparisons, $P \leq 0.05$). Different lowercase letters indicate significant differences from respective D0 values.

re-test did not vary within the group. This most likely represents a ceiling effect of the monofilament testing.

Tail tip data were collected at baseline, and then again once regenerative outgrowth had occurred (day 14) (Fig. 4D). We found a significant main effect of group ($F_{1,25}$=4.20, P=0.05) and time ($F_{3,25}$=6.44, P=0.002), but no interaction effect ($F_{3,25}$=0.62, P=0.606). Overall, thresholds for both groups decreased from baseline (sensitization), but time points were otherwise not significantly different from each other. Indeed, the regenerated tail tip consistently responded to the smallest monofilament (0.091 g), suggesting a ceiling effect of the monofilament testing.

DISCUSSION

The primary aim of this investigation was to determine whether tactile sensitivity across the palmar and plantar surfaces of gecko feet and ventral surface of the tail is altered in response to tail loss and regeneration. Prior to autotomy, geckos demonstrate significant site-specific (regional) differences in tactile sensitivity. Repeated monofilament testing sensitized all sites of interest in both control and tail-loss geckos with one important exception: the palmar surface of the forelimbs in geckos with autotomized tails. Our focus on tactile sensitivity of ventral surfaces (load-bearing, in the case of the feet) underscores the role of mechanoreception as it contributes to dynamic balance in small quadrupedal reptiles. In addition, our data reveal that tactile sensitivity of the tail tip is restored following tail regeneration, suggesting a continued mechanosensory role for the replacement appendage.

Differences in thresholds observed between our regions of interest prior to autotomy may relate to the body-wide pattern of sensilla distribution. Previous research on geckos has shown that the density and spacing of sensilla vary across the body (Russell et al., 2014). In general, skin on the dorsal surface of the head, trunk, tail and limbs has a higher density of sensilla than skin of the ventral surfaces. The original tail is particularly rich in sensilla, and the density of sensilla increases towards the tip (mean density on the dorsal surface increases from 59.3 to 76.1 mm^{-2}, and on the ventral surface from 17.4 to 25.5 mm^{-2}; Russell et al., 2014). This pattern of distribution is consistent with the prediction of skin deformation playing a role as an initiating factor in autotomy (Maclean, 1980; Russell et al., 2014). Interestingly, at day 0, our data indicate that the ventral tail base, and not the tail tip, was more sensitive to tactile stimulation. A similar trend towards increasing sensitivity in proximal locations to the body is seen in the octopus, another species capable of appendage autotomy (Alupay, 2013). By way of explanation, we note that the tail base supports the load of the length of the tail, as well as facilitating pelvic rotation and stabilizing lateral undulations, acting as a counterbalance (Jagnandan and Higham, 2017). This suggests that, at least for geckos, receptor density alone may not be an accurate predictor of overall tactile sensitivity. The differences in threshold may result from variation in mechanoreceptor type. For example,

subepidermal Pacinian corpuscles bordering the toes of gekkonids are known to function as deep-touch, vibration-sensitive receptors (Hiller, 1977). In humans, the presence of Pacinian corpuscles in the hands (Johanson et al., 1982) and feet (Strzalkowski et al., 2017) increase sensitivity relative to other mechanoreceptors; this may hold true for ventral surfaces of gecko feet. Other features contributing to tactile sensitivity include sensory acuity, central processing and selective weighting of cutaneous feedback (Carver et al., 2006; Strzalkowski et al., 2015; Templeton et al., 2018).

Obstacles in the environment are evaluated using tactile detection and proprioception, resulting in adjustments facilitated by neuromuscular shifts. Thus, regional differences in tactile threshold are also influenced by limb and joint kinematics, appendage loading and predator detection (Foster and Higham, 2012; Jagnandan et al., 2014; Russell et al., 2014). In the context of locomotion, the asymmetrical sensitivity of the forelimbs and the hindlimbs (at baseline, prior to autotomy) is matched by differences in functional roles: hindlimbs are primarily involved in propulsion, whereas forelimbs participate as brakes, energy absorption and stability (Lee, 2010; Foster and Higham, 2012; Autumn et al., 2006). When faced with environmental challenges in arboreal and terrestrial environments, lizard species show differential responses between the forelimbs and hindlimbs, as a result of differences in function, anatomy, kinematics and behavior (Losos, 1990; Foster and Higham, 2012; Jagnandan et al., 2014).

Our data indicate that for most sites, sensitization is most likely a result of the monofilament assay itself, and not tail autotomy. Following their first exposure to the monofilaments, control and tail-loss geckos demonstrated a significant decline in tactile threshold at every site (except the forelimbs) when compared with the baseline (day 0). Sensitization, a form of non-associative learning that results in increased responsiveness to stimuli, may have occurred because the geckos were tested at frequent intervals (McSweeney et al., 1996). Although sensitization is often associated with avoidance or fear (Rau et al., 2005; Götz and Janik, 2011), it is worth nothing that none of the geckos demonstrated any abnormal or stress-related behaviors (Warwick et al., 2013). Further, while some geckos did assume an elevated body posture (a recognized form of gecko anti-predation behavior; Landová et al., 2016), similar postures were seen during routine handling not associated with monofilament testing. One intriguing but presently untested possibility is that sensitization could be associated with the monofilament testing protocol mimicking a predatory encounter. A sympatric predator of the leopard gecko is the red sand boa, *Eryx johnii*. Sand boas are subterranean predators that employ a sit-and-wait strategy (Landová et al., 2016): they remain buried until prey comes nearby before striking. A recent behavioral study demonstrated that even captive-bred and predator-naïve leopard geckos have an innate anti-predation reaction to the presence of sand boas (Landová et al., 2016). We speculate that monofilament testing, which involves unanticipated cutaneous contact from underneath the gecko, may imitate a sand boa encounter.

Unlike all other sites, sensitivity of the forelimbs did not change from baseline (day 0) following tail autotomy. As autotomy requires an immediate adaptation of the locomotor system to ensure survival, these findings appear to correlate with the unequal impact that tail loss – and the resulting cranial shift in the center of mass – has on forelimb and hindlimb kinematics and muscle recruitment (Table 2). Notably, the forelimbs become more load-bearing as a result of autotomy. Whereas the hindlimbs temporarily become more sprawled once the tail is detached, there is no change in the joint angle at the elbow (Jagnandan et al., 2014). And while the recruitment and activation of the propulsive muscles of the hindlimb (the caudofemoralis and gastrocnemius muscles) was significantly reduced post-autotomy, there was no comparable change by muscles of the forelimb (the biceps and triceps brachii; Jagnandan and Higham, 2018). A body-wide re-distribution of mass has been observed in mammals (Besancon et al., 2004; Browning et al., 2007; Munoz-Nates et al., 2017). For example, during human pregnancy, the substantial increase in anterior mass is compensated for by a proportional increase of opposing muscle force, such that overall gait patterns do not change (Mitternacht et al., 2013; Ogamba et al., 2016). In horses with forelimb lameness, increased mass and pressure are taken up by the opposite hindlimb (Weishaupt et al., 2004), while in quadrupeds carrying objects in their mouth (rostral weight gain), the peak vertical force and foot pressure contact increases at the forelimbs and decreases at the hindlimbs (Bockstahler et al., 2016).

Studies investigating tactile sensitivity of the human foot have also addressed the relationship between somatosensation and biomechanics. For example, an increase in cutaneous sensitivity is associated with enhanced stability among distal limb amputees (Templeton et al., 2018). Tail loss in geckos represents a loss of sensory feedback from one-third of the body. Similar to humans, this may result in an upregulation in sensory systems (Templeton

Table 2. Summary of biomechanical and tactile sensitivity changes following tail loss and regeneration in the gecko *Eublepharis macularius*

Property	Immediately following autotomy	Following tail regeneration	Source
Body length	**40% loss**	**70% of original restored**	Present study
Body mass	**20% loss**	Resolved	Present study
Tactile sensitivity: hindlimbs	Decreased	Decreased	Present study
Tactile sensitivity: forelimbs	**Unchanged**	**Unchanged**	Present study
Tactile sensitivity: tail base	Decreased	Decreased	Present study
Tactile sensitivity: tail tip	Decreased	Decreased	Present study
Center of mass	**13% anterior shift**	**6% anterior shift**	Jagnandan et al. (2014)
Running speed	Unchanged	Unchanged	Jagnandan et al. (2014)
Peak vertical ground reaction force	**Reduced**	Resolved	Jagnandan et al. (2014)
Peak propulsive ground reaction force	**Increased**	Resolved	Jagnandan et al. (2014)
Posture: forelimbs	Unchanged	Unchanged	Jagnandan et al. (2014)
Posture: hindlimbs	**Sprawled**	Resolved	Jagnandan et al. (2014)
Joint angles: forelimbs	Unchanged	Unchanged	Jagnandan et al. (2014)
Joint angles: hindlimbs	**Femur depression, knee angle reduction**	Resolved	Jagnandan et al. (2014)
Muscle activity: forelimbs	Unchanged	Unchanged	Jagnandan and Higham (2018)
Muscle activity: hindlimbs	**Propulsive muscles reduced**	Resolved	Jagnandan and Higham (2018)

Parameters undergoing significant or notable changes are in bold.

et al., 2018), particularly closer to the area where the appendage is lost. In post-autotomy geckos, we suggest that the hindlimbs (and tail) remain more sensitive to enhance balance and gait, while forelimbs resisted sensitization as a result of the cranial transfer in weight distribution. An interesting future investigation would be to determine whether arboreal species of gecko capable of moving along vertical surfaces also demonstrate dissimilar responses to sensitization following tail autotomy.

Although tail regeneration does not structurally replicate the original appendage, it does restore somatosensory function. It is well understood that the regenerated tail of lizards (including geckos) is not a perfect replica of the original (McLean and Vickaryous, 2011; Fisher et al., 2012; Lozito and Tuan, 2016; Lynn et al., 2013; Russell et al., 2014, 2015; Gilbert et al., 2013; reviewed in Bellairs and Bryant, 1985; Jacyniak et al., 2017). For example, the regenerated tail differs from the original with respect to the tissue composition and organization of the axial skeleton (a series of bony vertebrae in the original, an unsegmented cone of cartilage in the regenerate) and the spinal cord [the original spinal cord has dorsal and ventral horns of grey matter (neuronal cell bodies), the regenerated does not], as well as the pattern of scalation (regenerated skin lacks the large cone-like tubercular scales present in the original) (Gilbert et al., 2013). Despite these obvious structural differences, we determined that the tactile sensitivity of the regenerated tail tip and tail base (except at day 21) is at least comparable with the original, underscoring the important functional role(s) of the replacement appendage. Like the original tail, the regenerated tail is used for counterbalance (Jagnandan et al., 2014) and predator detection (Maclean, 1980; Russell et al., 2014). Further, the regenerated tails of leopard geckos serve an important role as a lipid reserve (Bustard, 1967; Dial and Fitzpatrick, 1981; Doughty and Shine, 1998). Given that the regenerated tail tips uniformly responded to our lowest-weighted monofilament, it remains possible that regenerated tails have an even lower threshold than their original counterparts (i.e. regenerated tails are possibly more sensitive than the original appendages). That the original spinal cord and all the peripheral nerves are physically ruptured during autotomy makes this functional restoration all the more remarkable. The extent to which the regeneration of tactile sensitivity is modulated by changes (temporary or permanent) in central processing by the brain remains an important topic for future consideration.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: S.S.B., M.K.V.; Methodology: S.S.B., L.R.B., M.K.V.; Validation: S.S.B., E.H.; Formal analysis: S.S.B., E.H., L.R.B.; Investigation: S.S.B., M.K.V.; Resources: L.R.B., M.K.V.; Data curation: M.K.V.; Writing - original draft: S.S.B., M.K.V.; Writing - review & editing: S.S.B., E.H., L.R.B., M.K.V.; Visualization: S.S.B.; Supervision: L.R.B., M.K.V.; Project administration: M.K.V.; Funding acquisition: M.K.V.

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Data availability
Videos of monofilament testing have been uploaded to Dryad (Bradley et al., 2021): doi:10.5061/dryad.8pk0p2nk7.

Supplementary information
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