The Company of
Biologists

RESEARCH ARTICLE

Thermal sensitivity of motor control of muscle-powered versus elastically powered tongue projection in salamanders

Jeffrey A. Scales[1], Mary Kate O'Donnell[2] and Stephen M. Deban[2,*]

ABSTRACT

Elastic-recoil mechanisms can improve organismal performance and circumvent the thermal limitations of muscle contraction, yet they require the appropriate motor control to operate. We compare muscle activity during tongue projection in salamanders with elastically powered, ballistic projection with activity of those with muscle-powered, non-ballistic projection across a range of temperatures to understand how motor control is integrated with elastically powered movements, and how this integration contributes to reduced thermal sensitivity. Species with ballistic tongue projection activated and deactivated their projector muscles significantly earlier than non-ballistic species, in a pattern consistent with a mechanism in which the muscle strains elastic tissue that subsequently recoils to power projection. Tongue projection was more thermally robust in ballistic species, but in both ballistic and non-ballistic species the projector muscles were activated earlier and for longer as temperature decreased. The retractor muscles showed a pattern similar to that of the projector muscles, but declined in a similar manner in the two groups. Muscle activity intensity also decreased at low temperatures in both groups, revealing that compensatory muscle activation does not account for the improved thermal robustness in ballistic species. Thus, relatively minor shifts in motor patterns accompanying morphological changes such as increased elastic tissue are sufficient to improve performance and decrease its thermal sensitivity without specialization of muscle contractile physiology.

KEY WORDS: Electromyography, Feeding, Temperature effects, Ballistic movement, Ectotherm

INTRODUCTION

Changes in temperature present a significant challenge to organisms, especially ectotherms; low temperature can result in substantial decreases in ecologically relevant performance such as predator escape and feeding (Huey and Bennett, 1987; John-Alder et al., 1989; Lutz and Rome, 1996; Wintzer and Motta, 2004; Devries and Wainwright, 2006; Herrel et al., 2007; Deban and Scales, 2016; Scales et al., 2016). Reductions in performance such as running and swimming velocities and jumping distances primarily result from lower muscle contractile rates that can decline by half over a 10°C drop in temperature (Bennett, 1984, 1985; Hirano and Rome, 1984; Bauwens et al., 1995; Lutz and Rome, 1996; Peplowski and Marsh, 1997; Navas et al., 1999;

Donley et al., 2007; Herrel et al., 2007; James, 2013). However, in movements powered by elastic recoil, these temperature effects are largely mitigated by temporally decoupling muscle contraction from the movement itself. For example, ballistic tongue projection in chameleons, toads and salamanders is thermally robust ($Q_{10}<2$) and even temperature independent in some cases (Deban and Richardson, 2011; Deban and Lappin, 2011; Anderson and Deban, 2012; Deban and Scales, 2016). In these systems, the reduced temperature sensitivity does not appear to result from compensatory muscle activity at low temperatures or atypical muscle contractile physiology (Deban and Lappin, 2011; Anderson and Deban, 2012; Anderson et al., 2014). Instead, the thermal robustness is the result of motor patterns that accommodate morphological specializations (e.g. elaborated series elastic elements) to take advantage of the weak effect of temperature on muscle contractile force (Herrel et al., 2007; Anderson and Deban, 2012; James, 2013) and the mechanical properties of elastic tissue (Alexander, 1966; Denny and Miller, 2006). But, how these motor control patterns differ from those associated with muscle-powered movements has received minimal attention. Consequently, our understanding of how motor control is integrated with morphological changes, and how this integration contributes to reduced thermal sensitivity, remains limited. To better understand this integration, we compare motor control and the effect of temperature on motor control between plethodontid salamanders with non-ballistic, muscle-powered tongue projection and those with elastically powered, ballistic tongue projection.

Based on electromyography (EMG) of muscle activity, elastically powered tongue projection shows consistent motor control features. Chameleons, toads and plethodontid salamanders activate the muscles responsible for tongue projection in advance of the tongue leaving the mouth (de Groot and van Leeuwen, 2004; Lappin et al., 2006; Deban et al., 2007; Anderson and Deban, 2012; Anderson et al., 2014). This early muscle activation relative to movement is consistent with a period during which muscle fibers contract to load elastic tissue with strain energy that later recoils to power tongue projection. Furthermore, in each of these systems at low temperatures, projector muscle activation begins earlier relative to tongue movement and remains active for longer compared with warmer temperatures (Deban and Lappin, 2011; Anderson and Deban, 2012; Anderson et al., 2014). Although we have begun to understand motor control in these elastically powered feeding systems, motor control of analogous muscle-powered systems has received less attention and we lack a full understanding of how motor control patterns are integrated with differences in morphology.

Plethodontid salamanders exhibit both elastically powered, ballistic tongue projection and muscle-powered, non-ballistic tongue projection, and both mechanisms share the same general tongue apparatus morphology. Tongue projection involves the articulated tongue skeleton and tongue pad being propelled out of the mouth by cylindrical projector muscles (paired subarcualis

[1]Department of Biological Sciences, One University Circle, California State University, Stanislaus, Turlock, CA 95382, USA. [2]Department of Integrative Biology, 4202 East Fowler Avenue, Science Center 110, University of South Florida, Tampa, FL 33620, USA.

*Author for correspondence (sdeban@usf.edu)

S.M.D., 0000-0002-7979-4346

List of symbols and abbreviations	
EMG	electromyography
Q_{10}	temperature coefficient
QP	m. quadratopectoralis
RCP	m. rectus cervicis profundus
r.m.s.	root mean square
SAR	m. subarcualis rectus

rectus, SAR; Lombard and Wake, 1977). Each tongue projector muscle surrounds one of a pair of epibranchial cartilages that extend caudally from the buccal region (Fig. 1). Each epibranchial attaches rostrally to paired ceratobranchials, which then connect rostrally to the unpaired basibranchial that sits in the floor of the mouth and supports the tongue pad (Lombard and Wake, 1977; Wake and Deban, 2000; Deban, 2002). In muscle-powered, non-ballistic projection, the SAR is directly attached to the epibranchials, and little collagen is available in the SAR for energy storage (Lombard and Wake, 1977; Deban et al., 2007; Deban and Scales, 2016; Scales et al., 2016). Thus, during tongue projection, activation of the SAR coincides with tongue movement and the epibranchial does not leave the SAR (Deban and Dicke, 1999; Deban and Scales, 2016; Scales et al., 2016). Conversely, in species with elastically powered projection, the epibranchials lie within the lumen of the SAR, but are not directly attached to it (Deban et al., 2007; Deban and Scales, 2016; Scales et al., 2016), and early activation of the
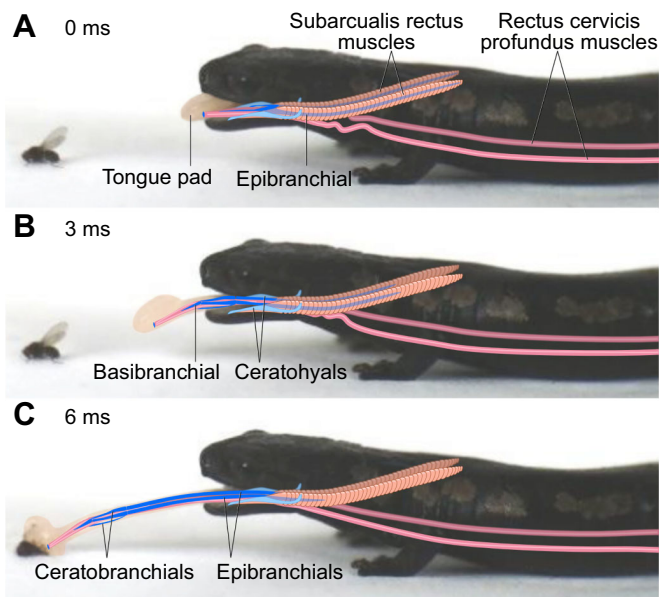

Fig. 1. Tongue projection in *Bolitoglossa franklini* with depicted morphological structures – the tongue skeleton (dark blue), the tongue projector muscles [m. subarcualis rectus (SAR), peach] and tongue retractor muscles [m. rectus cervicis profundus (RCP), pink)] – in their approximate configurations at three stages of tongue projection. (A) Start of ballistic projection at 0 ms, in which the epibranchials are within the SAR muscles, which originate on the paired ceratohyals (light blue) in the floor of the mouth; the slack RCP originates on the pelvis (not shown) and inserts into the tongue pad (highlighted in beige). (B) At 3 ms into projection, the tongue skeleton has been pushed rostrally and the tongue pad is accelerating out of the mouth. (C) At 6 ms, the epibranchials have been projected out of the SAR muscle and the tongue pad has reached the prey. Note that the ceratohyals and SAR muscles move little during projection. The RCP is now taut and prepared to pull the tongue back into the mouth and the epibranchials into the SAR muscles. Figure modified from Scales et al. (2016).

SAR muscle (80–200 ms prior to tongue launch) stretches collagenous aponeuroses within the muscles, which exert force on the epibranchials (Deban and Dicke, 1999, 2004; Deban et al., 2007; Anderson et al., 2014). The subsequent elastic recoil of these aponeuroses then accelerates the tongue out of the mouth (Deban et al., 1997, 2007; Deban, 2002; Deban and Scales, 2016) and the epibranchials completely separate from the SAR. Full tongue projection relies on momentum to carry the tongue skeleton and pad to the prey (Deban et al., 1997). Tongue retraction occurs via contraction of the long, paired retractor muscles (the rectus cervicis profundus, RCP), which originate on the pelvis in all plethodontids. Similarities in tongue projection apparatus, but vastly different tongue projection performance and thermal sensitivities, make the plethodontid feeding system an ideal model to examine how temperature affects motor control in elastic and muscle-powered systems.

We compare tongue projection and retraction performance and motor control between two species with elastically powered, ballistic tongue projection, *Bolitoglossa franklini* and *Ensatina eschscholtzii*, and two species with muscle-powered, non-ballistic tongue projection, *Desmognathus quadramaculatus* and *Plethodon metcalfi*. Previous morphological and kinematic studies show that *B. franklini* and *E. eschscholtzii* have elaborated collagen aponeuroses in the SAR, no direct myofiber attachment to the epibranchials, and achieve high-powered, thermally robust tongue projection (Deban et al., 2007; Deban and Scales, 2016; Scales et al., 2016). *Desmognathus quadramaculatus* and *P. metcalfi*, in contrast, exhibit lower tongue projection performance that is highly temperature sensitive (Deban and Scales, 2016; Scales et al., 2016); both species have myofibers that attach directly to the epibranchials, and relatively low collagen content in the SAR (Deban and Scales, 2016; Scales et al., 2016). We predict that muscle activity in the projector muscles of ballistic species will occur earlier relative to tongue projection to allow time for the myofibers to store strain energy in elastic tissue. We also predict that thermal effects on motor control will be similar between ballistic and non-ballistic species; that is, we do not expect compensatory muscle activity or physiological specializations in the muscles of ballistic species that would account for the differences in the temperature sensitivity of performance.

MATERIALS AND METHODS
Specimens
Salamanders were collected from natural populations: (1) *Bolitoglossa franklini* (Schmidt 1936), Chiapas, Mexico, (2) *Desmognathus quadramaculatus* (Holbrook 1840) and *Plethodon metcalfi* Brimley 1912, North Carolina, USA, and (3) *Ensatina eschscholtzii* Gray 1850, California, USA. Salamanders were housed individually in plastic containers with a substrate of moist paper towels at 14–19°C. *Desmognathus quadramaculatus* and *E. eschscholtzii* were maintained on a diet of gut-loaded crickets, while *B. franklini* and *P. metcalfi* were fed fruit flies. Six *B. franklini*, four *E. eschscholtzii*, four *D. quadramaculatus* and six *P. metcalfi* that fed readily under observation were implanted with EMG electrodes and used for feeding experiments. All procedures were approved by the Institutional Animal Care and Use Committee of the University of South Florida.

Electromyography
Bipolar patch electrodes were made from formvar-coated nichrome wire and silicone tubing as previously described (Anderson et al., 2014). Salamanders were anesthetized prior to electrode

implantation by one of two methods: immersion in a $1\,\mathrm{g\,l^{-1}}$ buffered aqueous solution of MS-222 (3-aminobenzoic acid ethyl ester; Sigma-Aldrich, St Louis, MO, USA) for 15–40 min (*E. eschscholtzii* and *D. quadramaculatus*), or by exposure to 0.2 ml of isoflurane evaporated in a sealed 15×11×5.5 cm plastic container for 15–40 min (*B. franklini* and *P. metcalfi*). Electrodes were implanted through two small incisions in the skin. The SAR electrodes were placed against the SAR at the level of the gular fold; however, the exact placement of electrodes varied by species. SAR electrodes were placed more caudal and dorsal in *B. franklini* and *E. eschscholtzii* on their longer SAR muscles. In *D. quadramaculatus*, much of the SAR is covered superficially by the quadratopectoralis (QP) muscle. Therefore, the fibers of the QP muscle were gently teased apart and the electrode was placed under the QP rostral from the incision so that it was positioned between the SAR and the QP. A second electrode was placed against the RCP between the fourth and fifth costal grooves.

Electrode leads were glued together using modeling glue and attached to the salamander's back near the pectoral girdle with a loop of suture to prevent the electrodes from being pulled loose or the animal becoming entangled in the leads. The insulation was stripped from the end of the electrode leads and soldered into a plug that inserted into a socket on the amplifier probe. EMG signals were amplified 500–1000 times using a differential amplifier (A-M Systems 3500) and filtered to remove 60 HZ line noise. All signal output was adjusted to 1000 gain to permit within-individual comparisons of signal amplitude. Conditioned signals were sampled at 10 kHz and digital images were synchronized via a common trigger as previously described (Anderson et al., 2014).

Feeding trials

After recovery from surgery (3–10 h), salamanders were presented with either crickets (*D. quadramaculatus* and *E. eschscholtzii*) or fruit flies (*B. franklini* and *P. metcalfi*). Feeding events were imaged in dorsal view at 6 kHz frame rate and 1/12,000 s shutter speed while salamanders rested on the surface of a temperature-controlled platform and EMG recordings were made, using previously described methods (Anderson et al., 2014; Deban and Scales, 2016).

Feeding trials were conducted across a range of experimental temperatures (5, 10, 15, 20 and 25°C) by varying the surface temperature of the feeding platform. Each salamander was allowed to acclimate at the experimental temperature for a period of at least 15 min prior to feeding trials. The salamander rested with its ventral surface against a moistened paper on the temperature platform, so its body temperature closely matched the temperature of the platform (±1°C). Body temperature was measured by directing a calibrated infrared thermometer (Sixth Sense LT300, Williston, VT, USA; ±1°C accuracy) at the dorsal surface of the head following each feeding event. The temperature sequence of feeding trials for each individual was randomized, with one to three feedings recorded per experimental temperature before attempting a different, randomly selected temperature. Salamander body temperatures ranged from 4.6 to 25.3°C.

Kinematic and dynamic analyses

Digital image sequences were used to quantify movements of the tongue during prey capture with respect to the upper jaw tip. The *x*, *y* coordinates of the tongue tip and the upper jaw tip were recorded from the image sequences as previously described (Anderson et al., 2014). The times of two events in the image sequences were measured relative to the start of tongue projection at time zero:

(1) maximum tongue projection, the time at which the leading edge of the tongue pad was the greatest distance from the tip of the upper jaw, and (2) the end of tongue retraction, the time at which the tongue pad was fully withdrawn into the mouth following tongue projection. The duration of tongue projection is equivalent to time of event 1 and the duration of tongue retraction was calculated as time of event 2 minus time of event 1. Average velocity of tongue projection and tongue retraction were calculated as the tongue projection distance divided by these durations, respectively.

The dynamics of tongue movements were calculated using published methods (Anderson et al., 2014; Deban and Lappin, 2011) by fitting a quintic spline to the distance–time data using the Pspline package in R statistical software (www.r-project.org). First and second derivatives of the spline function were computed to yield instantaneous velocity and acceleration, respectively. Tongue-mass-specific kinetic energy during tongue projection was then calculated as half the product of the squared maximum projection velocity. Muscle-mass-specific kinetic energy and maximum muscle-mass-specific power during tongue projection were calculated by multiplying these tongue-mass-specific values by the average ratio of the mass of the tongue projectile to the mass of the SAR muscles. Muscle-mass-specific power achieved during tongue retraction was calculated by multiplying the power by the average ratio of the mass of the tongue projectile to the mass of the RCP muscles. Mean and maximum values of velocity and acceleration, and kinetic energy and maximum power were used to examine the effects of temperature and projection distance in each species.

Analyses of electromyograms

The amplitudes and timing of muscle activity of the SAR and RCP relative to kinematic events were quantified from the rectified EMG signals using ADInstruments LabChart software running on an Apple iMac computer. The activity durations and latencies from the start of activity and peak activity intensity (measured as peak of r.m.s.) to associated kinematic events were measured in both the SAR and RCP. The start of muscle activity was defined as the time after which the EMG amplitude reached twice the background noise for a minimum of 10 ms, while the end of activity was defined as the time at which the signal dropped below twice the noise level for a minimum of 10 ms. Seven latency durations were measured (three for the SAR and four for the RCP): (1) the start of SAR activity to the start of tongue projection, (2) peak of SAR activity to the start of tongue projection, (3) the end of SAR activity to the start of tongue projection, (4) the start of RCP activity to the start of tongue projection, (5) the start of RCP activity to the time of maximal tongue projection, (6) peak of RCP activity to the time of maximal tongue projection, and (7) the end of RCP activity to the time of maximal tongue projection.

Amplitude and intensity variables were measured between the start and end of muscle activity. Intensity of the EMG bursts was measured in two ways: (1) the r.m.s. of the signal during the time of activity and (2) the integrated area (measured as the integral of the rectified signal over the activity time period) divided by the duration of the activity time period. The peak intensity of muscle activity was defined as the maximum r.m.s. value using a 20 ms time constant (i.e. the moving 20 ms time window over which the r.m.s. was calculated).

Statistical analyses

Species were separated into two groups for analyses based on previous studies of feeding kinematics, dynamics and morphology (Deban and Scales, 2016; Scales et al., 2016). Ballistic species are

those in which tongue projection is powered by an elastic-recoil mechanism and the tongue can act as a true projectile that reaches the prey under its own momentum: *B. franklini* and *E. eschscholtzii* in this study. Non-ballistic species, including *D. quadramaculatus* and *P. metcalfi*, are those in which tongue projection is powered directly by muscle contraction and the tongue does not act as a true projectile.

All performance and EMG data were $\log_{10}$ transformed before statistical analyses because biological rates are expected to have an exponential relationship with temperature. However, some EMG duration and latency data contained negative values because muscle activity events occurred both before and after the relevant kinematic events, making $\log_{10}$ transformations impossible. Because adding a constant value to the data to make all values positive can influence the estimates of slopes, and thus Q_{10} values, we used two methods to remedy the negative-value problem: (1) if fewer than 10% of data points for a given variable were negative, those few negative values were dropped from the analyses; (2) if the majority of the data points were negative (over 90%), all data were multiplied by −1, positivizing the data, and any newly negative data points were dropped from the analyses. If more than 10% of the data for a given variable was negative, these data are reported, but not statistically analyzed.

Data were divided into four overlapping intervals (5–15, 10–20, 15–25 and 5–25°C, each ±1°C) based on the body temperature at which the data were gathered in order to determine whether temperature effects varied across the full temperature range. An analysis of covariance (ANCOVA) was conducted on each subset of the data separately.

EMG and performance data were examined for three effects: (1) temperature, (2) projection distance and (3) individual. Measured body temperature as a continuous variable was included as a fixed effect to examine how muscle activity and kinematic and dynamic variables responded to changes in body temperature. Projection distance was included as a covariate because it has been found to correlate with performance measures in salamander feeding (Deban and Richardson, 2011; Deban and Scales, 2016), but was dropped from the model when not significant for a given variable. Individual was included in the model as a random effect to account for body size and other random individual differences, including EMG electrode characteristics.

Temperature coefficients (Q_{10}) were computed for each variable across each temperature interval (5–15, 10–20, 15–25 and 5–25°C) as the base 10 antilogarithm of the partial regression coefficients of the temperature effect in the ANCOVAs multiplied by 10 (Anderson et al., 2014). The ANCOVA models included effects of individual and projection distance (for relevant performance and EMG data) because these variables can influence the relationship between a given variable and temperature. Thus, calculation of Q_{10} values from the partial regression coefficients accounts for these effects as well. The temperature coefficients for durations were reported as inverse Q_{10} values (i.e. $1/Q_{10}$) to express them as responses of rates.

To test for differences in the effect of temperature on muscle activity and the feeding movements between the two groups, we used an ANCOVA including the same effects mentioned previously (i.e. individual and projection distance). However, a group×temperature interaction term was included in the model to test for differences in slopes (i.e. differences in temperature responses).

All statistical analyses were performed using R statistical software version 3.1.1 (www.r-project.org) on an Apple iMac computer. Significance levels were adjusted to control for false

discovery rate (Benjamini and Hochberg, 1995) when multiple comparisons were made within each temperature or temperature interval.

RESULTS
Feeding in ballistic and non-ballistic species
Individuals of all four species fed at all experimental temperatures (only one feeding at 25°C from *E. eschscholtzii*) using tongue projection. Species with ballistic, elastically powered projection (*B. franklini* and *E. eschscholtzii*) achieved significantly higher tongue projection performance than non-ballistic species (*D. quadramaculatus* and *P. metcalfi*) at all temperatures, with some kinematics and dynamics parameters 10-fold greater in ballistic species (Table S1, Fig. 2); this confirms previous findings (Deban and Scales, 2016; Scales et al., 2016). For example, ballistic tongue-projection velocity, acceleration and power reached 3.93 m s^{-1}, 1760 m s^{-2} and 3330 W kg^{-1}, respectively, compared with 0.72 m s^{-1}, 136 m s^{-2} and 77 W kg^{-1} in non-ballistic species. Tongue projection was also significantly less temperature sensitive in ballistic species. The Q_{10} values of almost all projection kinematic and dynamic variables were significantly lower in ballistic species at all temperature intervals.

Ballistic species achieved significantly higher retraction performance at all temperatures, but there was considerable overlap in the ranges of the kinematics and dynamics (Table S1, Fig. 2). Differences in the performance of tongue retraction between ballistic and non-ballistic species, when present, are greatly reduced compared with tongue projection. Furthermore, tongue retraction in ballistic and non-ballistic species showed similar temperature sensitivity. Temperature Q_{10} values significantly differed between the two groups only for maximum retraction power (at 5–15°C) and maximum retraction velocity (10–20°C). Thus, the thermal sensitivity of tongue retraction was similar between ballistic and non-ballistic species; any differences occurred at the lower temperature ranges.

Electromyographic activity
A total of 456 feedings with EMG recordings were captured: 215 feedings for *B. franklini* (*n*=146) and *E. eschscholtzii* (*n*=69), and 241 feedings for *D. quadramaculatus* (*n*=77) and *P. metcalfi* (*n*=164). The SAR was always activated prior to the start of tongue projection, with peak activity also occurring before the tongue left the mouth (Fig. 3). This activity burst typically ended after the tongue first became visible as it left the mouth, but occasionally ended before the start of tongue projection. The RCP was activated after the SAR and just before or after the tongue left the mouth. Peak RCP activity generally occurred just after, but sometimes prior to the tongue reaching maximum projection distance. The RCP commonly remained active throughout retraction until the tongue had returned into the mouth. Motor control of the SAR and RCP varied within the ballistic and non-ballistic species (Table 1, Figs 4, 5, Tables S2, S3). However, because our goal was to determine how motor control differs between tongue-projection mechanisms and because there was no significant difference in Q_{10} values for any variable between the two species within a group (Table S4, Figs 4, 5), we pooled the two species in each group for analyses.

Timing and duration of SAR activity
The activity of the SAR varied widely across temperatures in both ballistic and non-ballistic species, but it was always activated prior to tongue projection. However, the timing of SAR activity was
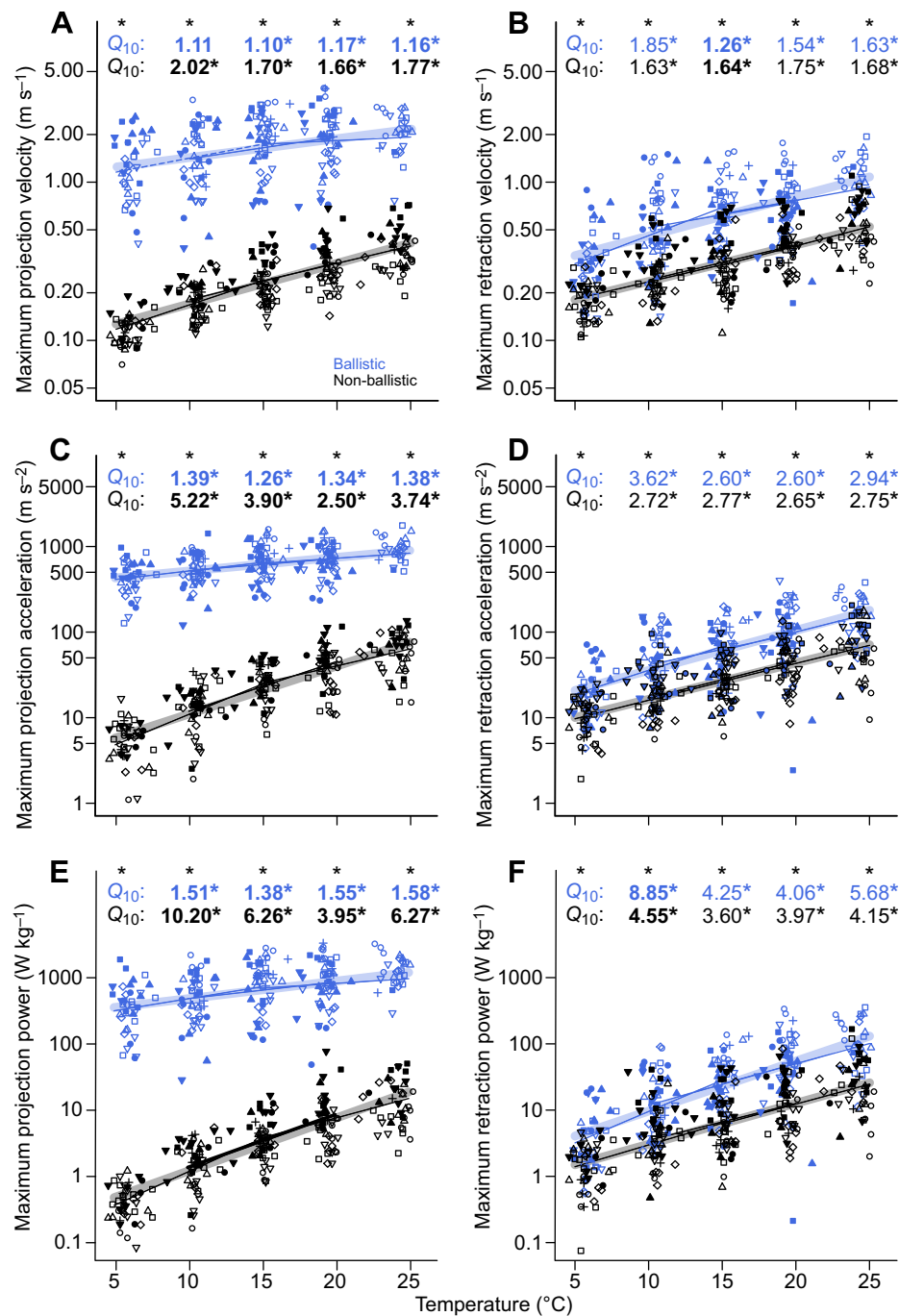
Fig. 2. Scatterplots of kinematic parameters versus body temperature including all feedings of ballistic (blue, *Ensatina eschscholtzii*, N=69, solid shapes; *Bolitoglossa franklini*, N=146, open shapes) and non-ballistic tongue projection (black, *Desmognathus quadramaculatus*, N=77, solid shapes; *Plethodon metcalfi*, N=164, open shapes). (A,B) Maximum projection and retraction velocity; (C,D) maximum projection and retraction acceleration; (E,F) maximum projection and retraction power. y-axes have log_{10} scales and are the same for a given parameter to facilitate comparison between projection and retraction. Note the significantly higher performance of ballistic tongue projection. Individual salamanders are represented by different symbols. Asterisks across the top of each graph indicate significant differences in performance between the two groups at each nominal experimental temperature. Regression lines from ANOVA including temperature and individual effects are shown for each temperature interval as solid lines when significant and as dashed lines when not significant; thicker lines are for the full 5–25°C range. Q_{10} values are shown for each temperature interval (5–15, 10–20, 15–25 and 5–25°C from left to right), with asterisks on Q_{10} values indicating a significant temperature effect. Bold Q_{10} values indicate significantly different thermal sensitivity between groups across each temperature interval.

shifted earlier in ballistic tongue projection (Table 1, Fig. 6, Table S5). For example, the SAR was activated 300 to 74 ms prior to the start of tongue projection in ballistic species, but only 133 to 60 ms before projection in non-ballistic species. The duration from the start of SAR activity to the start of tongue projection and the duration from SAR peak r.m.s. to the start of tongue projection were significantly longer in ballistic species at all temperatures (Table 1, Fig. 6, Table S5), and the duration from the end of SAR activity to the start of tongue projection was shorter. These timing differences indicate that the SAR is activated and deactivated earlier relative to tongue projection in ballistic species compared with non-ballistic species. The duration of SAR activity was also significantly longer in ballistic species at 5, 15 and 20°C.

Temperature had the same effect on the timing and duration of SAR activity in ballistic and non-ballistic species. In ballistic species, the duration from the start of SAR activity to the start of tongue projection, the duration of SAR activity, and the duration of SAR peak amplitude to maximum tongue projection all significantly decreased at higher temperatures (Table S6, Fig. 6). The duration from the end of SAR activity to the start of tongue projection was independent of temperature over all of the individual temperature intervals, but there was a significant temperature effect over the whole temperature range ($1/Q_{10}=1.26$). Similarly, the duration from the start of SAR activity to the start of tongue projection, the duration of SAR activity, the duration from SAR peak activity intensity to the start of tongue projection, and the
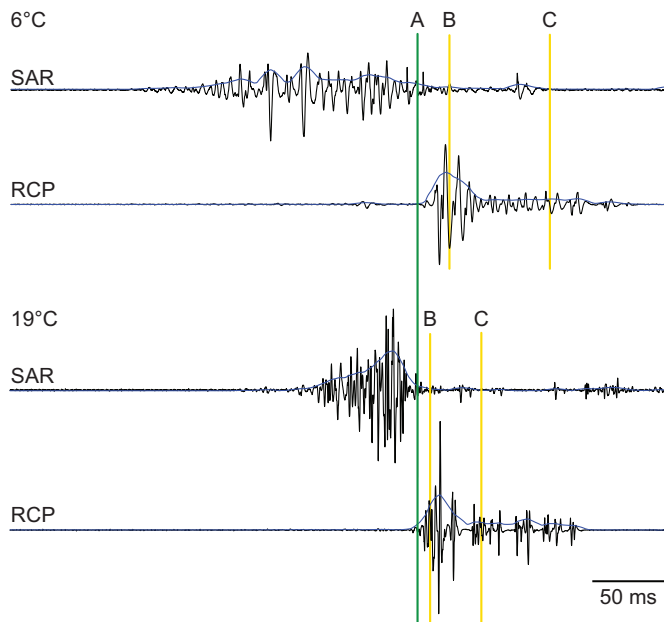
Fig. 3. Representative electromyographic (EMG) signals (black lines) and the root mean square (r.m.s.) of the signals (20 ms time constant, blue lines) from the m. subarcualis rectus (SAR) and m. rectus cervicis profundus (RCP) in an individual *Ensatina eschscholtzii* at 6°C (top) and 19°C (bottom). Traces are aligned at the start of tongue projection (A, green vertical line extending through all traces). The time of maximum tongue projection (B) and time of the end of tongue retraction (C) are indicated by vertical yellow lines. Note the earlier activation and longer activity duration of the SAR and the increased activity duration of the RCP at 6°C.

duration from the end of SAR activity to the start of tongue projection all decreased at higher temperatures in non-ballistic species. These trends were similar between ballistic and non-ballistic tongue projection as there was no significant difference in $1/Q_{10}$ values for any SAR activity durations (Table 2, Fig. 6).

Timing and duration of RCP activity

The timing of RCP activity was also variable across temperatures (Table 1). The start of RCP activity occurred both before and after the initiation of tongue projection and maximum tongue projection. Activity generally ceased after maximum tongue projection, but frequently continued until the tongue was completely withdrawn into the mouth. Although this general timing occurred in both ballistic and non-ballistic species, there were differences between the two groups. The duration from the start of RCP activity to maximum tongue projection was significantly longer in non-ballistic species at all temperatures except for 5°C (Table S5, Fig. 7), indicating that non-ballistic species activate the RCP earlier during tongue projection. Non-ballistic species also ceased RCP activity significantly later than ballistic species at all temperatures except 5°C. The earlier activation coupled with later deactivation of the RCP in non-ballistic species results in significantly longer RCP activity durations at temperatures above 5°C.

RCP activity generally showed similar temperature effects in ballistic and non-ballistic species. In ballistic tongue projection, the duration of RCP activity, duration from the start of RCP activity to maximum tongue projection, and duration from the end of RCP activity to maximum tongue projection all decreased with increasing temperature (Table S6, Fig. 7). These trends were mainly due to thermal sensitivity at lower temperatures as the same variables all significantly decreased with temperature at 5–15°C

and 10–20°C. In non-ballistic tongue projection, the duration of RCP activity, the duration from the start of RCP activity to maximum tongue projection, and the duration from the end of RCP activity to maximum tongue projection also all decreased as temperature increased. However, for the duration from the start of RCP activity to maximum tongue projection, this trend was due to changes across the 10–20°C interval. The temperature effects were similar in both groups. There was no significant difference in $1/Q_{10}$ values of RCP activity duration or the duration from the start of RCP activity to maximum tongue projection between the groups. However, ballistic species did have significantly higher $1/Q_{10}$ values for the duration from the end of RCP activity to maximum tongue projection at 5–15°C and 10–20°C, but not at 15–25°C. These differences at the smaller temperature intervals did not result in significantly different $1/Q_{10}$ values over the entire temperature range (Table 2, Fig. 7).

Muscle activity intensity

Muscle activity intensity generally increased with temperature. In ballistic species, SAR r.m.s. increased with temperature across all temperature intervals, whereas RCP r.m.s. significantly increased with temperature only at 5–15°C (Table S6, Fig. 8). The intensity of activity in the SAR and RCP showed similar temperature effects in non-ballistic species. SAR and RCP r.m.s. increased with temperature in the 5–15°C and 10–20°C intervals and the full temperature range, but were temperature independent from 15 to 25°C. The overall trend of increasing activity intensity with temperature in both ballistic and non-ballistic species results in similar temperature effects between the two groups. There was no significant difference in the Q_{10} values of SAR r.m.s. at any temperature interval, and RCP r.m.s. Q_{10} values only differed at 10–20°C (Table 2, Fig. 8).

DISCUSSION
Motor control of tongue projection

Bolitoglossa and *Ensatina* captured prey via ballistic tongue projection with high kinematic and dynamic values consistent with elastic power (Table S1, Fig. 2). The muscle activation patterns of the SAR in these species are consistent with a mechanism involving the loading and subsequent recoil of elastic tissues. The start of SAR activity occurred 49 to 300 ms prior to the start of tongue projection. Electromechanical delay from stimulation to increase in muscle tension in the SAR of plethodontids can be as short as 4 ms, and the SAR can reach 90% of peak tension within 50 to 200 ms of stimulations (Anderson et al., 2014). Thus, the timing of SAR activation observed here should be adequate to load strain energy in elastic tissue that can later recoil to power tongue projection. This timing is comparable to muscle activation preceding elastically powered feeding movements in other plethodontids (63–279 ms; Deban et al., 2007; Anderson et al., 2014), toads (150–250 ms; Lappin et al., 2006), chameleons (200–300 ms; Wainwright and Bennett, 1992; de Groot and van Leeuwen, 2004; Anderson and Deban, 2012) and other high-speed, elastically powered movements (Bennet-Clark and Lucey, 1967; Burrows, 2006; Patek et al., 2006; Van Wassenbergh et al., 2008; Roberts and Azizi, 2011; Kagaya and Patek, 2016). Interestingly, SAR activity frequently continued, often at low levels, well into tongue projection, suggesting that there is a muscular component to projection. How this muscle activity contributes to projection remains unclear, but was also observed in *Eurycea guttolineata* (Anderson et al., 2014), and a similar pattern of muscle activity combined with elastic recoil

Table 1. Summary statistics of motor control variables at each experimental temperature in ballistic and non-ballistic species

	5°C					10°C					15°C					20°C					25°C				
	Mean	s.e.m.	N	Min.	Max.	Mean	s.e.m.	N	Min.	Max.	Mean	s.e.m.	N	Min.	Max.	Mean	s.e.m.	N	Min.	Max.	Mean	s.e.m.	N	Min.	Max.
Ballistic																									
SAR activity duration (s)	0.212	0.010	36	0.098	0.340	0.170	0.007	49	0.096	0.285	0.151	0.006	51	0.061	0.276	0.129	0.006	52	0.070	0.273	0.104	0.005	27	0.069	0.187
SAR start to tongue projection start (s)	0.177	0.007	36	0.074	0.300	0.137	0.005	49	0.075	0.258	0.122	0.004	51	0.072	0.258	0.100	0.004	52	0.062	0.167	0.086	0.004	27	0.049	0.146
SAR max. amplitude to tongue projection start (s)	0.093	0.006	36	0.039	0.169	0.070	0.004	49	−0.005	0.155	0.053	0.004	51	−0.016	0.117	0.049	0.004	52	−0.019	0.143	0.046	0.005	27	0.002	0.111
SAR end to tongue projection start (s)	−0.035	0.008	36	−0.141	0.056	−0.033	0.005	49	−0.122	0.035	−0.030	0.004	51	−0.098	0.035	−0.030	0.004	52	−0.118	0.016	−0.018	0.002	27	−0.041	−0.006
RCP activity duration (s)	0.139	0.014	36	0.042	0.415	0.102	0.010	49	0.035	0.259	0.086	0.009	51	0.017	0.225	0.072	0.008	51	0.018	0.204	0.052	0.005	27	0.017	0.110
RCP start to tongue projection start (s)	0.065	0.011	36	−0.010	0.234	0.047	0.007	49	−0.004	0.156	0.040	0.007	51	−0.060	0.156	0.030	0.005	51	−0.015	0.124	0.016	0.005	27	−0.011	0.098
RCP start to max. tongue projection (s)	0.075	0.011	36	0.008	0.241	0.058	0.007	49	0.015	0.165	0.051	0.007	51	−0.052	0.200	0.040	0.005	51	0.003	0.132	0.024	0.005	27	0.005	0.105
RCP max. amplitude to max. tongue projection (s)	−0.002	0.003	36	−0.070	0.030	0.003	0.002	49	−0.056	0.020	0.005	0.003	51	−0.066	0.108	0.002	0.002	51	−0.051	0.022	0.001	0.003	27	−0.059	0.012
RCP end to max. tongue projection (s)	−0.063	0.005	36	−0.174	−0.021	−0.044	0.004	49	−0.111	−0.007	−0.034	0.003	51	−0.092	−0.001	−0.032	0.004	51	−0.096	0.005	−0.028	0.004	27	−0.062	−0.002
Non-ballistic																									
SAR activity duration (s)	0.163	0.007	43	0.084	0.284	0.165	0.008	56	0.080	0.340	0.126	0.005	52	0.070	0.246	0.111	0.005	51	0.064	0.181	0.097	0.004	39	0.055	0.158
SAR start to tongue projection start (s)	0.086	0.003	43	0.060	0.133	0.069	0.002	56	0.046	0.115	0.054	0.002	52	0.040	0.090	0.046	0.001	51	0.027	0.069	0.038	0.001	39	0.025	0.059
SAR max. amplitude to tongue projection start (s)	0.023	0.007	43	−0.118	0.071	0.006	0.006	56	−0.154	0.059	0.015	0.003	52	−0.092	0.059	0.017	0.001	51	0.001	0.033	0.010	0.002	39	−0.051	0.033
SAR end to tongue projection start (s)	−0.077	0.006	43	−0.180	0.002	−0.095	0.007	56	−0.282	−0.025	−0.071	0.005	52	−0.162	−0.018	−0.064	0.004	51	−0.139	−0.015	−0.058	0.004	39	−0.103	−0.015
RCP activity duration (s)	0.135	0.008	43	0.057	0.233	0.146	0.008	56	0.036	0.305	0.116	0.006	52	0.044	0.261	0.112	0.008	51	0.037	0.325	0.094	0.006	39	0.012	0.177
RCP start to tongue projection start (s)	−0.007	0.009	43	−0.096	0.107	0.031	0.007	56	−0.142	0.095	0.026	0.005	52	−0.068	0.096	0.025	0.007	51	−0.119	0.154	0.026	0.004	39	−0.042	0.064
RCP start to max. tongue projection (s)	0.069	0.008	43	−0.024	0.177	0.095	0.007	56	−0.013	0.219	0.072	0.005	52	0.009	0.219	0.068	0.007	51	−0.015	0.249	0.058	0.004	39	0.003	0.124
RCP max. amplitude to max. tongue projection (s)	−0.008	0.006	43	−0.091	0.117	−0.005	0.004	56	−0.063	0.103	−0.002	0.003	52	−0.046	0.075	−0.009	0.003	51	−0.049	0.076	−0.006	0.002	39	−0.047	0.021
RCP end to max. tongue projection (s)	−0.066	0.004	43	−0.134	−0.022	−0.051	0.003	56	−0.118	−0.009	−0.044	0.003	52	−0.100	−0.009	−0.044	0.002	51	−0.084	−0.009	−0.037	0.003	39	−0.086	−0.002

Positive values indicate that the electromyographic (EMG) event occurred prior to the associated kinematic event, while negative values show that the EMG event occurred after the associated kinematic event. RCP, m. rectus cervicis profundus; SAR, m. subarcualis rectus.
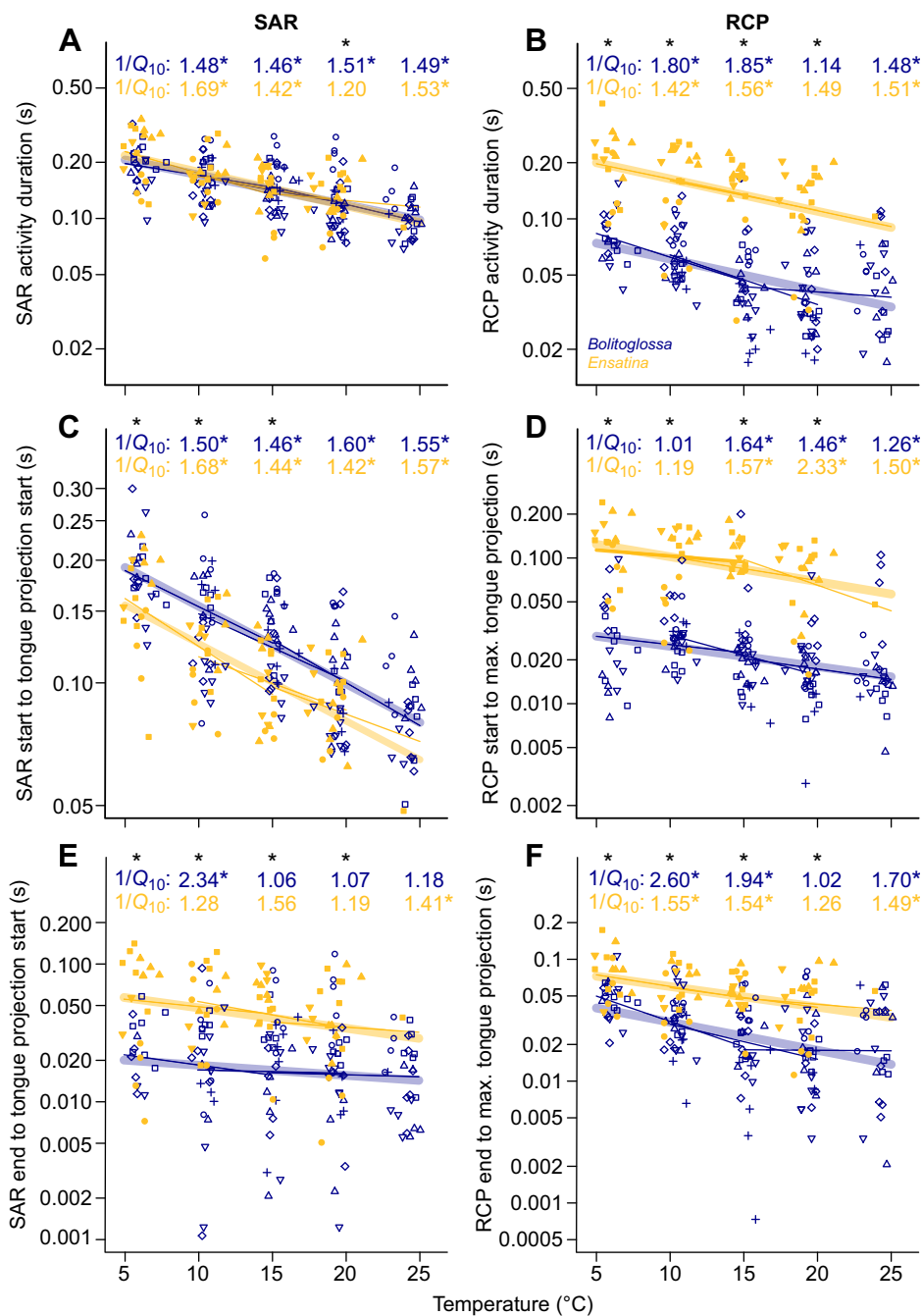
Fig. 4. Scatterplots of m. subarcualis rectus (SAR) and m. rectus cervicis profundus (RCP) activity timing versus body temperature for all feedings of *Bolitoglossa franklini* (blue, *n*=146) and *Ensatina eschscholtzii* (yellow, *n*=69). (A,C,E) SAR activity duration, start to tongue projection start and end to tongue projection start, respectively; (B,D,F) RCP activity duration, start to maximum tongue projection and end to maximum tongue projection, respectively. *y*-axes have $\log_{10}$ scales. Asterisks across the top of each graph indicate significant differences in performance between the two groups at each nominal experimental temperature. Regression lines from ANOVA including temperature and individual effects are shown for each temperature interval as solid lines when significant and as dashed lines when not significant; thicker lines are for the full 5–25°C range. $1/Q_{10}$ values are shown for each temperature interval (5–15, 10–20, 15–25 and 5–25°C from left to right), with asterisks on $1/Q_{10}$ values indicating a significant temperature effect. Bold $1/Q_{10}$ values indicate significantly different thermal sensitivity between groups across each temperature interval. *Bolitoglossa franklini* and *E. eschscholtzii* did show some differences in the timing of activation of the SAR and RCP, however, the effect of temperature on motor control was the same among the species with no significant differences in $1/Q_{10}$ values for any variable (See Tables S2, S3 also).

occurs in jumping frogs (Roberts and Marsh, 2003; Astley and Roberts, 2012).

Non-ballistic species had low values for kinematic and dynamic performance parameters for both tongue projection and retraction (Table S1, Fig. 2), suggesting they result from the same mechanism – muscle power. Activation patterns of the SAR are also consistent with muscle-powered tongue projection in these species in two important ways. First, the latency of the start of SAR activity relative to the initiation of tongue projection is short, averaging only 59 ms and directly preceding tongue projection by as little as 25 ms. This latency is much shorter than those of elastic feeding systems (Wainwright and Bennett, 1992; Van Wassenbergh et al., 2008; Deban and Lappin, 2011; Anderson and Deban, 2012; Anderson et al., 2014) and may not allow sufficient time for the loading and recoil of elastic tissue (Table 1). Second, although peak muscle activity did occur prior to the

start of tongue projection, SAR activity frequently continued well into tongue projection, suggesting a significant muscular contribution during projection.

The difference in timing of SAR activity between the two groups reveals a mechanism of elastic energy storage in ballistic tongue projection, but not in the species exhibiting non-ballistic tongue projection. The duration of SAR activity did not consistently differ between the ballistic and non-ballistic species (Table S5), and even when there was a difference, activity durations showed substantial overlap (Table 1, Fig. 6, Table S5). However, the SAR activity of ballistic species typically starts and ends earlier relative to tongue projection compared with non-ballistic species. This shift to earlier muscle activity is consistent with muscle contraction loading elastic tissue with strain energy in ballistic species (Deban and Dicke, 1999; Deban et al., 2007; Anderson and Deban, 2012; Anderson
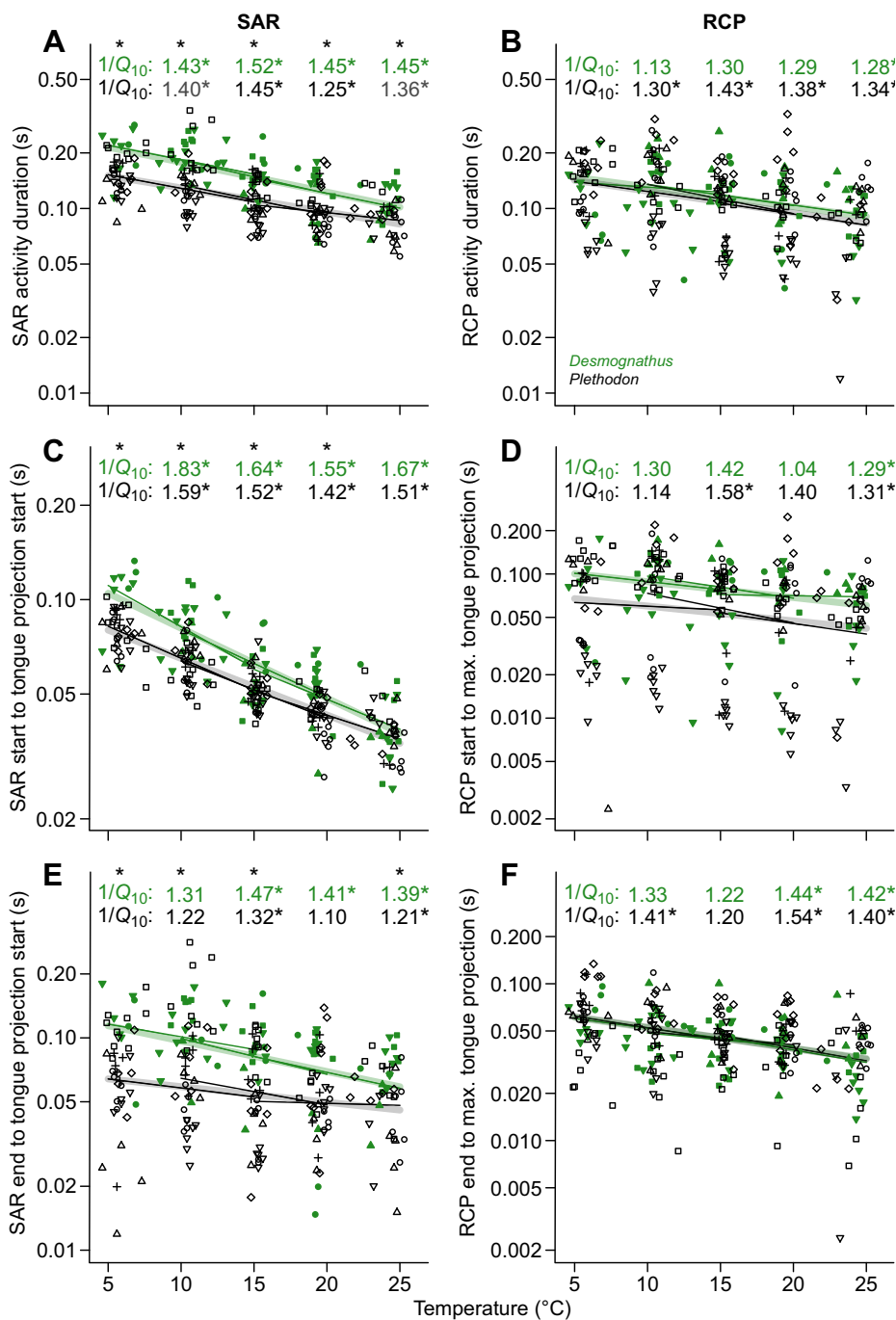
Fig. 5. Scatterplots of SAR and RCP activity timing versus body temperature for all feedings of *Desmognathus quadramaculatus* (green, *n*=77) and *Plethodon metcalfi* (black, *n*=164). (A,C,E) SAR activity duration, start to tongue projection start and end to tongue projection start, respectively; (B,D,F) RCP activity duration, start to maximum tongue projection and end to maximum tongue projection, respectively. For indications, see Fig. 4. Variation in motor control within the non-ballistic species was mainly concentrated in the SAR, with *D. quadramaculatus* activating the SAR earlier and deactivating later than *P. metcalfi*. Thus, *D. quadramaculatus* had longer SAR activity durations at all temperatures. In contrast, the timing and duration of RCP activity did not differ at any temperature and the effect of temperature on motor control did not significantly differ between the two species at any temperature (see Tables S2, S3 also).

et al., 2014). Conversely, the later activity observed in the non-ballistic species is consistent with tongue projection being powered directly by muscle. This shift in muscle activity timing suggests that subtle changes in morphology accompanied by rather simple modifications in motor control are sufficient to produce the radically different performances observed in muscle-powered and elastically powered tongue projection.

Changes in temperature had a significant and similar effect on the timing of SAR activity in ballistic and non-ballistic tongue projection. Both groups activated the SAR earlier and for longer durations at lower temperatures (Table 1, Fig. 6). The early activation and increased activity times likely result from the SAR taking longer to do the same work as a result of the reduced rates of contraction and force development of muscles at lower temperatures

(Ranatunga, 1982; Bennett, 1984; Rall and Woledge, 1990; Swoap et al., 1993; James, 2013) and are common responses of muscle activity to reduced temperatures (Jayne and Daggy, 2000; Deban and Lappin, 2011; Anderson and Deban, 2012; Anderson et al., 2014). The similar responses in motor control to temperature changes suggest that neural and muscular properties do not differ among these species despite their different tongue projection mechanisms. However, tongue projection performance was significantly more robust to temperature changes in ballistic species than non-ballistic species regardless of the thermal sensitivity of SAR activity (Table 2, Figs 2, 6). The maintenance of the high tongue projection performance at low temperature in ballistic species is therefore not the result of temperature-related changes in motor control. Additionally, the discrepancy between the

Fig. 6. Scatterplots of m. subcualis rectus (SAR) activity timing versus body temperature for feedings of ballistic and non-ballistic tongue projection. (A,B) Activity duration; (C,D) start to tongue projection start; (E,F) end to tongue projection start. y-axes have $\log_{10}$ scales and are the same for a given parameter to facilitate comparison ballistic and non-ballistic projection. Note the similar effects of temperature on muscle activity in both groups, but a significantly earlier start and end of SAR activity in ballistic tongue projection. Indications as in Fig. 2.

temperature effects on motor control and performance between ballistic and non-ballistic species suggests that the decreased temperature dependence of ballistic projection is also not the result of specializations in muscle physiology. Instead, the thermal robustness of ballistic species likely results from the low thermal sensitivity of the mechanical properties of elastic tissues (Alexander, 1966; Denny and Miller, 2006) and the relatively low thermal dependence of muscle work used to load the elastic tissues (as compared with the high thermal dependence of rate properties such as muscle contractile velocity and power).

We provide compelling evidence that morphological variation underlies the differences in motor control and temperature effects between ballistic and non-ballistic species. Yet, in the absence of phylogenetically informed analysis, we cannot rule out the

possibility that phylogenetic relationships also play a role. However, *Bolitoglossa* and *Ensatina* represent two independent evolutions of elastically powered tongue projection, and *Ensatina* is more closely related to *Desmognathus* and *Plethodon* than to *Bolitoglossa* (Vieites et al., 2011; Shen et al., 2016), suggesting that phylogenetic relationships likely do not play a primary role in explaining the differences observed here.

Motor control of tongue retraction
Activity patterns of the RCP are consistent with braking of the tongue at the end of projection along with tongue retraction in both ballistic and non-ballistic species. The RCP was activated subsequent to the SAR and frequently after the onset of tongue projection, but usually prior to maximum tongue projection in both

Table 2. Results of ANCOVA examining the effects of group × temperature interaction in each of the experimental temperature intervals for ballistic and non-ballistic species

Variable	5–15°C		10–20°C		15–25°C		5–25°C	
	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value
Projection distance	8.7	0.0035*	4.01	0.0462	1.9	0.1691	3.68	0.0559
Projection duration	27.86	**0.0000***	5.13	**0.0243***	5.44	**0.0205***	44.82	**0.0000***
Average projection velocity	24.65	**0.0000***	7.25	**0.0075***	4.91	**0.0276**	39.58	**0.0000***
Max. projection velocity	68.84	**0.0000***	41.22	**0.0000***	19.65	**0.0000***	143.5	**0.0000***
Max. projection acceleration	58.39	**0.0000***	56.58	**0.0000***	17.99	0.0000*	147.46	**0.0000***
Max. projection power	75.22	**0.0000***	59.65	**0.0000***	18.92	**0.0000***	169.36	**0.0000***
Projection kinetic energy	71.39	**0.0000***	41.36	**0.0000***	20.91	**0.0000***	145.59	**0.0000***
Retraction duration	3.03	**0.0828**	0.12	**0.7296**	0.05	**0.8155**	1.91	**0.1673**
Average retraction velocity	2.91	**0.0891**	1.37	**0.2426**	1	**0.3189**	0.4	**0.5297**
Max. retraction velocity	1.17	**0.2808**	5.84	**0.0163***	0.95	**0.3295**	0.13	**0.7207**
Max. retraction acceleration	2.09	0.1494	0.02	**0.8939**	0.08	**0.7758**	1.62	**0.2031**
Max. retraction power	5.33	0.0217*	0.39	0.5311	0	0.9937	4.49	0.0346
SAR activity duration	2.33	**0.1281**	0.1	**0.7571**	1.64	**0.2012**	5.45	**0.02**
SAR start to tongue projection start	0	**0.9977**	1.07	**0.3009**	0.29	**0.5937**	0.11	**0.7389**
SAR max. r.m.s. to tongue projection start	0	0.9608	0.28	0.5997	0.06	0.8062	0	0.9487
SAR end to tongue projection start	0.34	0.563	0.04	**0.8511**	0.03	0.8676	0.22	**0.6389**
SAR r.m.s.	0.04	0.8473	2.06	0.1522	5.33	0.0218	4.63	0.032
RCP activity duration	6.07	0.0143	4.69	**0.0312**	0.19	0.6629	5.1	0.0244
RCP start to max. tongue projection	0.24	0.6211	0.64	0.425	1.38	0.2407	1.42	0.2336
RCP end to max. tongue projection	9.59	0.0022*	9.48	**0.0023***	2.38	**0.1243**	7.46	**0.0066**
RCP r.m.s.	1.62	0.2041	15.07	0.0001*	1.54	0.2157	1.56	0.2119

Asterisks indicate a significant interaction after adjusting for false discovery rate (P<0.05). Full model includes individual as a random effect and projection distance as a covariate. Bold indicates a significant effect of projection distance. RCP, m. rectus cervicis profundus; r.m.s., root mean square; SAR, m. subarcualis rectus.

groups (Table 1). This timing of muscle activity indicates that the RCP plays a role in braking the tongue near the end of tongue projection. In some cases, the RCP was activated after maximum tongue projection, and the RCP often remained active throughout tongue retraction in a pattern consistent with the function of tongue retraction. Furthermore, although RCP activity was variable, initiation near the start of tongue retraction to immediately after peak tongue projection suggests that tongue retraction is muscle-powered, consistent with previous studies (Deban and Dicke, 1999; Deban et al., 2007; Anderson et al., 2014).

Despite the similarities in RCP activity, species with non-ballistic tongue projection activated the RCP earlier and turned it off later, resulting in longer activity durations compared with ballistic-tongued species. This is an intriguing result because all of the species included in this study use the same retraction mechanism (Lombard and Wake, 1977). Earlier RCP activation in non-ballistic tongue projection may occur to commence braking of the tongue quicker during the relatively shorter tongue projections. It is also possible that the higher velocity of projection in ballistic species may help load the RCP eccentrically and enhance force so that the RCP can turn on later.

Temperature effects on RCP activity were generally similar between ballistic and non-ballistic species, with earlier activation and later deactivation at lower temperatures resulting in longer activity durations (Tables 1, 2, Fig. 7). The later deactivation of the RCP relative to peak tongue projection likely indicates that it takes longer to retract the tongue at lower temperatures owing to reduced contractile rates of muscle at lower temperatures. The earlier activation of the RCP is somewhat surprising because the RCP may be limited in how early it can be activated without interfering with tongue projection. Relative thermal independence of the start of RCP activity has been observed in *Eurycea guttolineata* (above 5–10°C; Anderson et al., 2014) and chameleons (Anderson and Deban, 2012), suggesting that interference may be a problem. The earlier RCP activation observed in the present study suggests that

these species may activate the RCP sufficiently late in tongue projection at warmer temperatures so that shifting RCP activation earlier at colder temperatures still does not interfere with projection. However, based on the absence of a temperature effect on RCP activation at 5–15°C, this temperature range may be the limit where early RCP activation interferes with projection in non-ballistic species, restricting the range of activation times. It may also be that the RCP of the smaller *Eurycea* develops tension faster than the RCP of the larger species studied here, making interference with projection more likely in *Eurycea* (Anderson et al., 2014).

In contrast to the SAR and tongue projection, decrements in retraction performance accompanied shifts in RCP activity at low temperatures in both ballistic and non-ballistic species. The similar relationships between temperature, motor control and tongue retraction in the two groups suggest that retraction is muscle-powered in both groups, and subject to the thermal limitations of muscle physiology (Bennett, 1984, 1985; James, 2013). A trend of muscle-powered tongue retraction strongly affected by temperature is observed in a variety of other feeding systems including tongue projection in *Eurycea* (Anderson et al., 2014), toads and true frogs (Deban and Lappin, 2011; Sandusky and Deban, 2012), and chameleons (Anderson and Deban, 2012).

Intensity of muscle activity
The intensity of activation of the both SAR and RCP decreased at lower temperatures in ballistic and non-ballistic species (Fig. 8), suggesting that the salamanders examined here either recruit fewer muscle fibers or activate each fiber at a lower frequency at low temperatures. Thus, ballistic-tongued species do not maintain their performance at lower temperatures by recruiting more muscle fibers, a mechanism that has been suggested for feeding systems (Devries and Wainwright, 2006). Muscle activity intensity displayed a similar trend in *Eurycea*, another plethodontid salamander (Anderson et al., 2014), but is independent of temperature during tongue projection in toads (Deban and Lappin, 2011) and

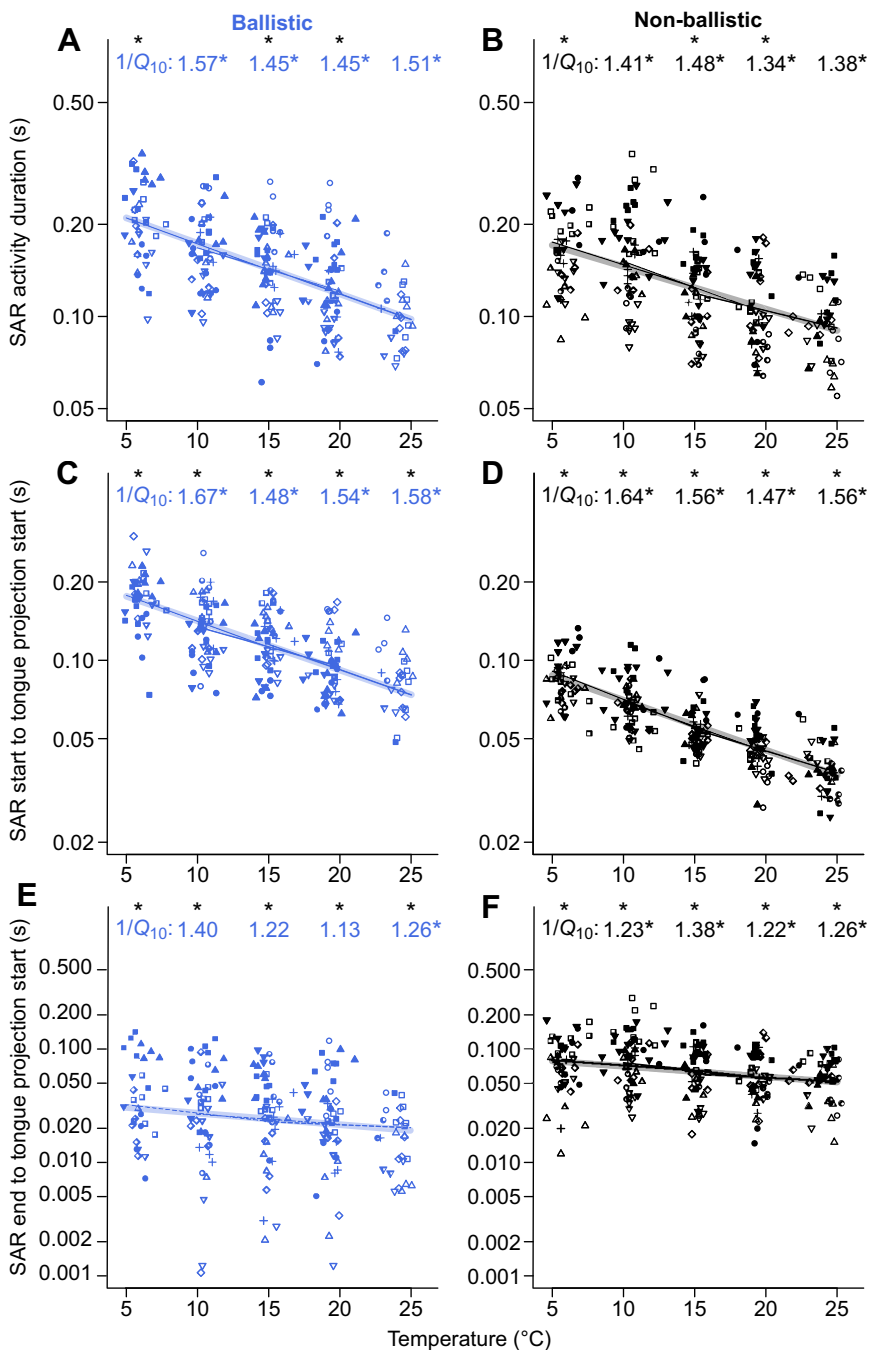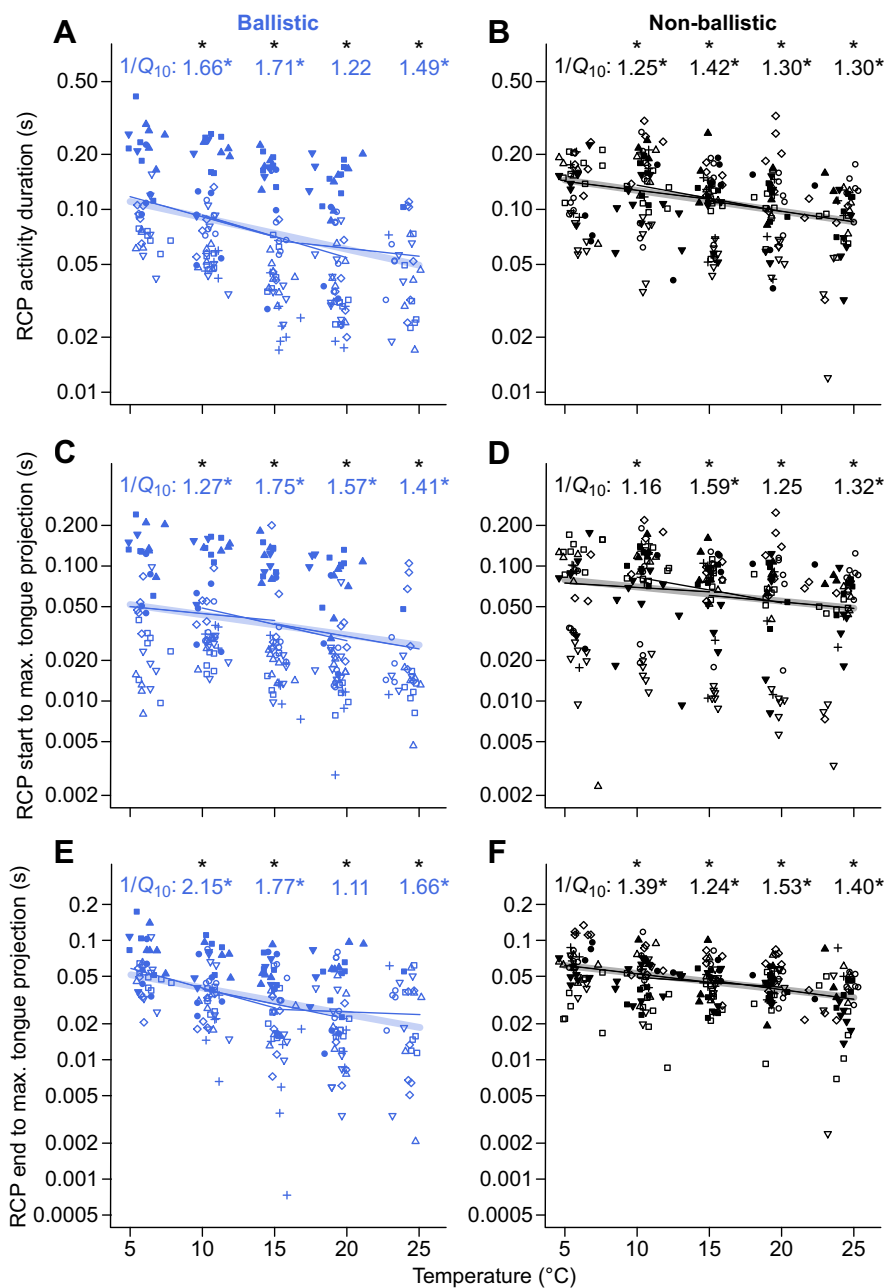**Fig. 7. Scatterplots of m. rectus cervicis profundus (RCP) activity timing versus body temperature for feedings of ballistic and non-ballistic tongue projection.** (A,B) Activity duration; (C,D) start to tongue projection start; (E,F) end to tongue projection start. Note the longer RCP activity durations in non-ballistic tongue projection that result from the earlier start and later end of RCP activity. Indications as in Fig. 2.

chameleons (Anderson and Deban, 2012). The precise physiological limitations underlying reduced muscle activity intensity at low temperatures in plethodontid salamanders is not known, but may stem from changes in motor unit recruitment or reduced nerve conduction at low temperatures (Abramson et al., 1966; Rome et al., 1984; Jayne et al., 1990; Hill et al., 2008).

Conclusions

The ballistic tongue projection of *Bolitoglossa* and *Ensatina* achieves significantly higher performance (e.g. velocity, acceleration and power) and increased thermal robustness (lower Q_{10} and $1/Q_{10}$ values) compared with the non-ballistic tongue projection of *Desmognathus* and *Plethodon*. This drastic difference in performance and thermal sensitivity is attributed to different mechanisms underlying tongue projection. Ballistic tongue projection is powered by elastic recoil, whereas non-ballistic tongue projection results from direct muscle power (Lombard and

Wake, 1977; Deban et al., 2007; Deban and Scales, 2016). The difference in mechanisms is reflected in the motor patterns of the SAR. Early activation and deactivation of the SAR in ballistic tongue projection is congruous with muscle loading elastic tissue with strain energy, which is then released rapidly to power tongue projection (Wainwright and Bennett, 1992; Deban et al., 2007; Van Wassenbergh et al., 2008; Deban and Lappin, 2011; Anderson and Deban, 2012; Anderson et al., 2014). Conversely, muscle activation in non-ballistic tongue projection occurred shortly before tongue projection, which is in accord with muscle directly powering projection. Thus, simple shifts in muscle activation coupled with relatively few morphological changes can result in extreme performance differences.

Elastically powered ballistic movements that display increased thermal robustness in performance have evolved independently multiple times in frogs, chameleons and salamanders (Anderson and Deban, 2010, 2012; Deban and Lappin, 2011; Deban and
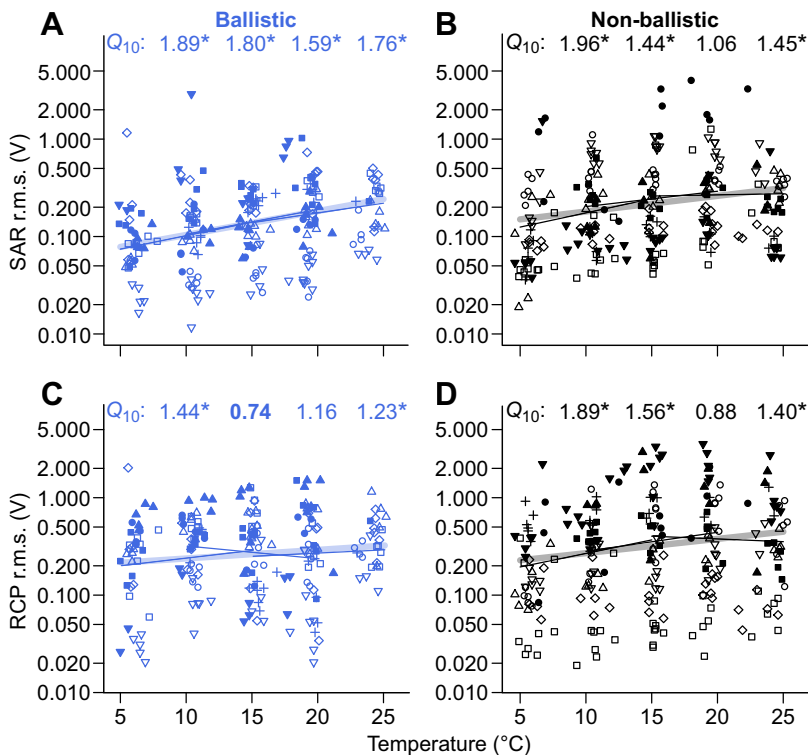
Fig. 8. Scatterplots of m. subarcualis rectus (SAR) and m. rectus cervicis profundus (RCP) activity intensity versus body temperature for feedings of ballistic and non-ballistic tongue projection. Note the reduced activity intensity at the lowest temperatures. Indications as in Fig. 2.

Richardson, 2011; Sandusky and Deban, 2012). However, whether motor patterns have converged is difficult to determine because the morphology of projection mechanisms varies widely. The taxa examined here, *Bolitoglossa* and *Ensatina*, represent two independent evolutions of elastically powered tongue projection within the Plethodontidae (Vieites et al., 2011; Shen et al., 2016), from an ancestrally similar non-elastic tongue apparatus (Deban and Scales, 2016; Scales et al., 2016). Although there are some differences between these taxa in motor control, they both show a shift to earlier activation and deactivation of the SAR compared with the presumed ancestrally conserved motor patterns of *Desmognathus* and *Plethodon*, suggesting that there has been a convergence of not only morphology, but also motor control.

Despite the changes in motor patterns, we find multiple lines of evidence that variation in muscle recruitment (i.e. level of excitation) does not explain the differences in the thermal sensitivity of tongue projection. First, muscle activity in species with ballistic and non-ballistic projection mechanisms show similar trends with temperature, with muscle activity increasing in duration at lower temperatures. Increased activity duration is a typical response of muscle to low temperatures in order to compensate for slower muscle contractile rates (Bennett, 1985; Jayne and Daggy, 2000; Anderson and Deban, 2012). Second, both the SAR and RCP exhibited increased duration of activity at lower temperatures in all species, but only tongue retraction showed large temperature-related decline in performance in ballistic species. Finally, muscle activity intensity decreased at lower temperatures regardless of tongue projection mechanism; therefore, compensatory changes in muscle recruitment, such as increased recruitment at low temperatures, do not occur and cannot account for the differences in thermal sensitivity of performance. These data provide evidence that the projector muscle of ballistic tongued species has no physiological specialization that would by itself account for increased thermal robustness. Thus, relatively subtle changes in morphology such as increased collagen and no muscular attachment to the epibranchials

(Deban and Scales, 2016; Scales et al., 2016), coupled with a shift in motor pattern, are sufficient to dramatically increase the thermal robustness of performance without specialization of muscle contractile physiology.

References
Abramson, D. I., Chu, L. S. W., Tuck, S., Jr, Lee, S. W., Richardson, G. and Levin, M. (1966). Effect of tissue temperatures and blood flow on motor nerve conduction velocity. *J. Am. Med. Assoc.* **198**, 1082-1088.

Alexander, R. M. (1966). Rubber-like properties of the inner hinge-ligament of Pectinidae. *J. Exp. Biol.* **44**, 119-130.

Anderson, C. V. and Deban, S. M. (2010). Ballistic tongue projection in chameleons maintains high performance at low temperature. *Proc. Natl. Acad. Sci. USA* **107**, 5495-5499.

Anderson, C. V. and Deban, S. M. (2012). Thermal effects on motor control and in vitro muscle dynamics of the ballistic tongue apparatus in chameleons. *J. Exp. Biol.* **215**, 4345-4357.

Anderson, C. V., Larghi, N. P. and Deban, S. M. (2014). Thermal effects on the performance, motor control and muscle dynamics of ballistic feeding in the salamander *Eurycea guttolineata*. *J. Exp. Biol.* **217**, 3146-3158.

Astley, H. C. and Roberts, T. J. (2012). Evidence for a vertebrate catapult: elastic energy storage in the plantaris tendon during frog jumping. *Biol. Lett.* **8**, 386-389.

Bauwens, D., Garland, T., Jr, Castilla, A. M. and Damme, R. V. (1995). Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. *Evolution* **49**, 848-863.

Benjamini, Y. and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B* **57**, 289-300.

Bennet-Clark, H. C. and Lucey, E. C. (1967). The jump of the flea: a study of the energetics and a model of the mechanism. *J. Exp. Biol.* **47**, 59-67.

Bennett, A. F. (1984). Thermal dependence of muscle function. *Am. J. Physiol.* **247**, R217-R229.

Bennett, A. F. (1985). Temperature and muscle. *J. Exp. Biol.* **115**, 333-344.

Burrows, M. (2006). Jumping performance of froghopper insects. *J. Exp. Biol.* **209**, 4607-4621.

de Groot, J. H. and van Leeuwen, J. L. (2004). Evidence for an elastic projection mechanism in the chameleon tongue. *Proc. R. Soc. Lond. B Biol. Sci.* **271**, 761-770.

Deban, S. M. (2002). Constraint and convergence in the evolution of salamander feeding. In *Vertebrate Biomechanics and Evolution* (ed. J. P. Gasc and V. L. Bels), pp. 163-180. Oxford: BIOS Scientific Publishers.

Deban, S. M. and Dicke, U. (1999). Motor control of tongue movement during prey capture in plethodontid salamanders. *J. Exp. Biol.* **202**, 3699-3714.

Deban, S. M. and Dicke, U. (2004). Activation patterns of the tongue-projector muscle during feeding in the imperial cave salamander *Hydromantes imperialis*. *J. Exp. Biol.* **207**, 2071-2081.

Deban, S. M. and Lappin, A. K. (2011). Thermal effects on the dynamics and motor control of ballistic prey capture in toads: maintaining high performance at low temperature. *J. Exp. Biol.* **214**, 1333-1346.

Deban, S. M. and Richardson, J. C. (2011). Cold-blooded snipers: thermal independence of ballistic tongue projection in the salamander *Hydromantes platycephalus*. *J. Exp. Zool. A Comp. Exp. Biol.* **315A**, 618-630.

Deban, S. M. and Scales, J. A. (2016). Dynamics and thermal sensitivity of ballistic and non-ballistic feeding in salamanders. *J. Exp. Biol.* **219**, 431-444.

Deban, S. M., Wake, D. B. and Roth, G. (1997). Salamander with a ballistic tongue. *Nature* **389**, 27-28.

Deban, S. M., O'Reilly, J. C., Dicke, U. and van Leeuwen, J. L. (2007). Extremely high-power tongue projection in plethodontid salamanders. *J. Exp. Biol.* **210**, 655-667.

Denny, M. and Miller, L. (2006). Jet propulsion in the cold: mechanics of swimming in the Antarctic scallop *Adamussium colbecki*. *J. Exp. Biol.* **209**, 4503-4514.

DeVries, M. S. and Wainwright, P. C. (2006). The effects of acute temperature change on prey capture kinematics in largemouth bass, *Micropterus Salmoides*. *Copeia* **2006**, 437-444.

Donley, J. M., Shadwik, R. E., Sepulveda, C. A. and Syme, D. A. (2007). Thermal dependence of contractile properties of the aerobic locomotor muscle in the leopard shark and shortfin mako shark. *J. Exp. Biol.* **210**, 1194-1203.

Herrel, A., James, R. S. and Van Damme, R. (2007). Fight versus flight: physiological basis for temperature-dependent behavioral shifts in lizards. *J. Exp. Biol.* **210**, 1762-1767.

Hill, R. W., Wyse, G. A. and Anderson, M. (2008). *Animal Physiology*. Sunderland, MA: Sinauer Associates, Inc.

Hirano, M. and Rome, L. C. (1984). Jumping performance of frogs (*Rana pipiens*) as a function of muscle temperature. *J. Exp. Biol.* **108**, 429-439.

Huey, R. B. and Bennett, A. F. (1987). Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* **41**, 1098-1115.

James, R. S. (2013). A review of the thermal sensitivity of the mechanics of vertebrate skeletal muscle. *J. Comp. Physiol. B* **183**, 723-733.

Jayne, B. C. and Daggy, M. W. (2000). The effects of temperature on the burial performance and axial motor pattern of the sand-swimming of the Mojave fringe-toed lizard *Uma scoparia*. *J. Exp. Biol.* **203**, 1241-1252.

Jayne, B. C., Bennett, A. F. and Lauder, G. V. (1990). Muscle recruitment during terrestrial locomotion: how speed and temperature affect fibre type use in a lizard. *J. Exp. Biol.* **152**, 101-128.

John-Alder, H. B., Barnhart, M. C. and Bennett, A. F. (1989). Thermal sensitivity of swimming performance and muscle contraction in northern and southern populations of tree frogs (*Hyla crucifer*). *J. Exp. Biol.* **142**, 357-372.

Kagaya, K. and Patek, S. N. (2016). Feed-forward motor control of ultrafast, ballistic movements. *J. Exp. Biol.* **219**, 319-333.

Lappin, A. K., Monroy, J. A., Pilarski, J. Q., Zepnewski, E. D., Pierotti, D. J. and Nishikawa, K. C. (2006). Storage and recovery of elastic potential energy powers ballistic prey capture in toads. *J. Exp. Biol.* **209**, 2535-2553.

Lombard, R. E. and Wake, D. B. (1977). Tongue evolution in the lungless salamanders, Family Plethodontidae. II. Function and evolutionary diversity. *J. Morphol.* **153**, 39-80.

Lutz, G. J. and Rome, L. C. (1996). Muscle function during jumping in frogs. II. Mechanical properties of muscle: implications for system design. *Am. J. Physiol.* **271**, C571-C578.

Navas, C. A., James, R. S., Wakeling, J. M., Kemp, K. M. and Johnston, I. A. (1999). An integrative study of the temperature dependence of whole animal and muscle performance during jumping and swimming in the frog (*Rana temporaria*). *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **169**, 588-596.

Patek, S. N., Baio, J. E., Fisher, B. L. and Suarez, A. V. (2006). Multifunctionality and mechanical origins: ballistic jaw propulsion in trap-jaw ants. *Proc. Natl. Acad. Sci. USA* **103**, 12787-12792.

Peplowski, M. M. and Marsh, R. L. (1997). Work and power in the hindlimb muscles of Cuban tree frogs *Osteopilus septentrionalis* during jumping. *J. Exp. Biol.* **200**, 2861-2870.

Rall, J. A. and Woledge, R. C. (1990). Influence of temperature on mechanics and energetics of muscle contraction. *Am. J. Physiol.* **259**, R197-R203.

Ranatunga, K. W. (1982). Temperature-dependence of shortening velocity and rate of isometric tension development in rat skeletal muscle. *J. Physiol.* **329**, 465-483.

Roberts, T. J. and Azizi, E. (2011). Flexible mechanisms: the diverse roles of biological springs in vertebrate movement. *J. Exp. Biol.* **214**, 353-361.

Roberts, T. J. and Marsh, R. L. (2003). Probing the limits to muscle-powered accelerations: lessons from jumping bullfrogs. *J. Exp. Biol.* **206**, 2567-2580.

Rome, L. C., Loughna, P. T. and Goldspink, G. (1984). Muscle fiber activity in carp as a function of swimming speed and muscle temperature. *Am. J. Physiol.* **247**, R272-R279.

Sandusky, P. E. and Deban, S. M. (2012). Temperature effects on the biomechanics of prey capture in the frog *Rana pipiens*. *J. Exp. Zool.* **317A**, 595-607.

Scales, J. A., Stinson, C. M. and Deban, S. M. (2016). Extreme performance and functional robustness of movement are linked to muscle architecture: comparing elastic and nonelastic feeding movements in salamanders. *J. Exp. Zool. A Ecol. Genet. Physiol.* **325**, 360-376.

Shen, X.-X., Liang, D., Chen, M.-Y., Mao, R.-L., Wake, D. B. and Zhang, P. (2016). Enlarged multilocus data set provides surprisingly younger time of origin for the Plethodontidae, the largest family of salamanders. *Syst. Biol.* **65**, 66-81.

Swoap, S. J., Johnson, T. P., Josephson, R. K. and Bennett, A. F. (1993). Temperature, muscle power output and limitations in burst locomotor performance of the lizard *Dipsosaurus dorsalis*. *J. Exp. Biol.* **174**, 185-197.

Van Wassenbergh, S., Strother, J. A., Flammang, B. E., Ferry-Graham, L. A. and Aerts, P. (2008). Extremely fast prey capture in pipefish is powered by elastic recoil. *J. R. Soc. Interface* **5**, 285-296.

Vieites, D. R., Roman, S. N., Wake, M. H. and Wake, D. B. (2011). A multigenic perspective on phylogenetic relationships in the largest family of salamanders, the Plethodontidae. *Mol. Phylogenet. Evol.* **59**, 623-635.

Wainwright, P. C. and Bennett, A. F. (1992). The mechanism of tongue projection in chameleons. 1. Electromyographic tests of functional hypotheses. *J. Exp. Biol.* **168**, 1-21.

Wake, D. B. and Deban, S. M. (2000). Terrestrial feeding in salamanders. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 95-114. San Diego: Academic Press.

Wintzer, A. P. and Motta, P. J. (2004). The effects of temperature on prey-capture kinematics of the bluegill (*Lepomis macrochirus*): implications for feeding studies. *Can. J. Zool.* **82**, 794-799.

Table S1. Summary statistics of performance variables at each experimental temperature in ballistic (*Bolitoglossa* and *Ensatina*) and non-ballistic (*Desmognathus* and *Plethodon*) species.

Ballistic

	5°C					10°C					15°C					20°C					25°C				
	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max
Projection distance (mm)	8.8	0.7	36	2.9	19.1	9.4	0.7	49	2.9	21.7	11.5	0.7	51	3.8	20.8	12.0	0.8	52	1.4	26.8	10.4	0.8	27	4.0	21.2
Projection duration (ms)	15.6	0.7	36	9.3	26.3	14.6	0.6	49	7.7	29.3	14.9	0.7	51	7.6	26.2	13.3	0.5	52	6.5	23.2	12.2	0.6	27	7.8	20.6
Average projection velocity (m/s)	0.54	0.05	36	0.18	1.41	0.63	0.05	49	0.09	1.57	0.77	0.04	51	0.12	1.50	0.85	0.05	52	0.13	1.57	0.79	0.04	27	0.41	1.21
Max. projection velocity (m/s)	1.35	0.10	36	0.41	2.58	1.56	0.10	49	0.38	3.31	1.96	0.10	51	0.70	3.21	2.06	0.12	52	0.39	3.93	2.11	0.11	27	0.77	2.98
Max. projection acceleration (m/s/s)	465.9	32.7	36	127.0	972.0	565.6	33.7	49	121.0	1420.0	747.5	44.9	51	252.0	1590.0	754.8	41.7	52	234.0	1500.0	968.7	59.4	27	513.0	1760.0
Max. tongue-mass-specific projection power (W/kg)	470.46	65.01	36	61.40	1890.00	642.33	67.29	49	28.70	2200.00	1058.76	98.39	51	116.00	2810.00	1113.57	106.37	52	48.80	3330.00	1386.48	134.48	27	294.00	3250.00
Max. muscle-mass-specific projection power (W/kg)	744.01	147.11	36	46.37	4077.00	797.97	120.07	49	61.91	3882.86	1164.67	155.76	51	135.53	5263.43	1286.71	154.34	52	105.27	4724.14	1023.73	94.88	27	209.72	2318.33
Projection energy (J)	6E-05	1E-05	36	2E-06	3E-04	6E-05	1E-05	49	6E-06	3E-04	9E-05	1E-05	51	1E-05	3E-04	1E-04	1E-05	52	6E-06	4E-04	6E-05	6E-06	27	8E-06	1E-04
Tongue-mass-specific projection energy (J/kg)	1.074	0.144	36	0.084	3.328	1.431	0.164	49	0.074	5.478	2.193	0.203	51	0.246	5.152	2.486	0.265	52	0.077	7.722	2.373	0.228	27	0.293	4.440
Muscle-mass-specific projection energy (J/kg)	1.791	0.343	36	0.060	7.179	1.787	0.283	49	0.159	7.689	2.439	0.324	51	0.340	9.323	3.071	0.415	52	0.166	12.322	1.757	0.162	27	0.209	3.167
Retraction duration (ms)	56.0	2.7	36	25.6	101.3	36.1	1.8	49	12.6	65.3	34.0	2.1	51	12.2	92.8	30.2	3.3	51	4.7	169.4	19.3	1.7	27	6.2	41.4
Average retraction velocity (m/s)	0.15	0.01	36	0.05	0.31	0.26	0.02	49	0.08	0.60	0.35	0.02	51	0.06	0.61	0.43	0.03	51	0.10	0.92	0.57	0.05	27	0.17	1.09
Max. retraction velocity (m/s)	0.35	0.03	36	0.14	0.89	0.60	0.05	49	0.14	1.50	0.72	0.04	51	0.25	1.56	0.77	0.05	51	0.17	1.77	1.08	0.07	27	0.41	1.94
Max. retraction acceleration (m/s/s)	23.9	2.8	36	4.4	71.5	57.6	6.0	49	10.0	156.0	77.4	6.8	51	11.7	199.0	121.2	11.6	51	2.4	402.0	178.5	16.7	27	49.6	380.0
Max. tongue-mass specific retraction power (W/kg)	5.73	1.00	36	0.56	21.00	20.22	2.93	49	2.20	90.20	36.97	4.52	51	2.83	137.00	73.24	9.74	51	0.21	337.00	133.24	18.48	27	11.30	355.00
Max. muscle-mass specific retraction power (W/kg)	5.70	1.22	36	0.31	27.25	16.94	2.63	49	1.21	69.04	27.26	3.38	51	2.70	104.47	53.18	6.60	51	0.28	194.66	75.41	10.13	27	6.22	195.45

Non-ballistic

	5°C					10°C					15°C					20°C					25°C				
	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max
Projection distance (mm)	5.9	0.2	43	2.4	10.4	6.6	0.2	56	3.7	11.1	6.3	0.2	52	2.3	10.5	7.0	0.3	51	2.9	10.2	7.0	0.4	39	2.6	11.7
Projection duration (ms)	81.8	3.0	43	29.5	122.9	62.0	2.2	56	30.4	111.4	49.9	2.3	52	13.2	111.8	47.0	2.1	51	21.4	89.7	36.7	1.9	39	17.9	72.5
Average projection velocity (m/s)	0.07	0.00	43	0.04	0.12	0.10	0.00	56	0.05	0.20	0.12	0.01	52	0.05	0.26	0.15	0.01	51	0.05	0.26	0.19	0.01	39	0.06	0.39
Max. projection velocity (m/s)	0.12	0.00	43	0.07	0.19	0.19	0.01	56	0.11	0.31	0.24	0.01	52	0.12	0.47	0.31	0.01	51	0.14	0.68	0.39	0.02	39	0.19	0.72
Max. projection acceleration (m/s/s)	6.05	0.45	43	1.10	16.70	15.01	1.13	56	1.92	35.90	27.41	1.70	52	6.36	54.50	45.26	3.32	51	10.90	116.00	64.26	4.96	39	15.10	136.00
Max. tongue-mass-specific projection power (W/kg)	0.46	0.04	43	0.08	1.21	1.87	0.17	56	0.17	5.47	4.60	0.48	52	0.83	16.70	10.36	1.71	51	1.57	77.30	16.83	2.10	39	2.24	50.60
Max. muscle-mass-specific projection power (W/kg)	1.62	0.14	43	0.29	4.14	6.58	0.59	56	0.56	18.72	16.41	1.79	52	2.84	61.57	37.07	6.33	51	5.37	284.98	60.11	7.78	39	7.66	186.55
Projection energy (J)	4E-07	8E-08	43	8E-08	2E-06	1E-06	2E-07	56	2E-07	6E-06	3E-06	5E-07	52	2E-07	1E-05	5E-06	9E-07	51	3E-07	3E-05	7E-06	1E-06	39	6E-07	3E-05
Tongue-mass-specific projection energy (J/kg)	0.01	0.00	43	0.00	0.02	0.02	0.00	56	0.01	0.05	0.03	0.00	52	0.01	0.11	0.05	0.01	51	0.01	0.23	0.08	0.01	39	0.02	0.26
Muscle-mass-specific projection energy (J/kg)	0.03	0.00	43	0.01	0.07	0.07	0.00	56	0.02	0.18	0.11	0.01	52	0.03	0.41	0.19	0.02	51	0.03	0.86	0.30	0.04	39	0.06	0.95
Retraction duration (ms)	60.5	3.1	43	27.6	116.9	52.7	3.1	56	18.5	122.5	37.1	2.5	52	16.0	119.5	34.9	2.3	51	15.8	89.2	23.7	2.0	39	7.3	66.9
Average retraction velocity (m/s)	0.09	0.00	43	0.04	0.17	0.13	0.01	56	0.06	0.27	0.16	0.01	52	0.05	0.37	0.20	0.01	51	0.05	0.43	0.30	0.02	39	0.07	0.54
Max. retraction velocity (m/s)	0.18	0.01	43	0.11	0.33	0.27	0.01	56	0.13	0.59	0.32	0.02	52	0.11	0.69	0.42	0.02	51	0.23	0.76	0.54	0.03	39	0.23	1.10
Max. retraction acceleration (m/s/s)	11.28	0.85	43	1.92	25.00	23.2	2.2	56	5.6	95.4	30.5	2.5	52	6.1	98.5	51.3	3.7	51	8.5	134.0	79.8	8.1	39	9.5	206.0
Max. tongue-mass specific retraction power (W/kg)	1.72	0.18	43	0.08	5.00	6.8	1.1	56	0.47	40.9	9.7	1.5	52	0.7	43.2	18.1	2.3	51	1.9	83.9	34.5	5.5	39	2.0	167.0
Max. muscle-mass specific retraction power (W/kg)	1.84	0.19	43	0.09	5.51	6.4	1.0	56	0.37	31.6	9.3	1.4	52	0.8	44.9	18.0	2.3	51	2.2	99.9	33.7	5.0	39	2.4	142.9

Table S2. Summary statistics of motor control variables at each experimental temperature in ballistic and non-ballistic species.

Bolitoglossa

	5°C					10°C					15°C					20°C					25°C				
	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max
SAR activity duration (s)	0.196	0.011	20	0.098	0.321	0.166	0.008	32	0.096	0.267	0.154	0.007	34	0.085	0.276	0.124	0.008	34	0.074	0.273	0.105	0.005	26	0.069	0.187
SAR onset to tongue projection onset (s)	0.189	0.009	20	0.124	0.300	0.146	0.007	32	0.080	0.258	0.133	0.005	34	0.082	0.186	0.103	0.005	34	0.067	0.167	0.087	0.004	26	0.050	0.146
SAR peak amplitude to tongue projection onset (s)	0.108	0.006	20	0.047	0.160	0.078	0.005	32	-0.005	0.155	0.058	0.005	34	-0.016	0.117	0.057	0.005	34	0.019	0.143	0.046	0.006	26	0.002	0.111
SAR offset to tongue porjection onset (s)	-0.007	0.007	20	-0.058	0.056	-0.020	0.005	32	-0.093	0.035	-0.021	0.004	34	-0.090	0.025	-0.021	0.004	34	-0.118	0.016	-0.018	0.002	26	-0.041	-0.006
RCP activity duration (s)	0.081	0.006	20	0.042	0.156	0.066	0.004	32	0.035	0.133	0.051	0.006	34	0.017	0.165	0.041	0.004	34	0.018	0.097	0.051	0.005	26	0.017	0.110
RCP onset to tongue projection onset (s)	0.023	0.006	20	-0.010	0.086	0.020	0.003	32	-0.004	0.089	0.014	0.005	34	-0.012	0.180	0.008	0.002	34	-0.015	0.066	0.015	0.005	26	-0.011	0.098
RCP onset to max. tongue projection (s)	0.032	0.005	20	0.008	0.099	0.031	0.003	32	0.015	0.097	0.026	0.006	34	0.007	0.200	0.019	0.002	34	0.003	0.077	0.023	0.005	26	0.005	0.105
RCP max. amplitude to max. tongue projection (s)	-0.002	0.003	20	-0.037	0.017	0.007	0.001	32	-0.017	0.019	0.011	0.003	34	-0.010	0.108	0.003	0.002	34	-0.049	0.022	0.002	0.003	26	-0.059	0.012
RCP offest to max. tongue projection (s)	-0.049	0.004	20	-0.107	-0.021	-0.034	0.003	32	-0.084	-0.007	-0.023	0.003	34	-0.063	-0.001	-0.022	0.003	34	-0.080	0.005	-0.027	0.004	26	-0.062	-0.002

Ensatina

	5°C					10°C					15°C					20°C					25°C				
	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max
SAR activity duration (s)	0.232	0.018	16	0.119	0.340	0.178	0.012	17	0.103	0.285	0.146	0.011	17	0.061	0.211	0.140	0.009	18	0.070	0.212	0.090	NA	1	0.090	0.090
SAR onset to tongue projection onset (s)	0.162	0.011	16	0.074	0.230	0.121	0.007	17	0.075	0.166	0.099	0.005	17	0.072	0.138	0.094	0.005	18	0.062	0.128	0.049	NA	1	0.049	0.049
SAR peak amplitude to tongue projection onset (s)	0.075	0.008	16	0.039	0.169	0.053	0.006	17	0.002	0.108	0.043	0.004	17	0.020	0.070	0.033	0.005	18	-0.019	0.083	0.028	NA	1	0.028	0.028
SAR offset to tongue porjection onset (s)	-0.069	0.010	16	-0.141	-0.007	-0.056	0.009	17	-0.122	0.011	-0.047	0.007	17	-0.098	0.015	-0.046	0.007	18	-0.099	-0.005	-0.041	NA	1	-0.041	-0.041
RCP activity duration (s)	0.211	0.021	16	0.094	0.415	0.171	0.017	17	0.050	0.259	0.156	0.011	17	0.029	0.225	0.134	0.012	17	0.033	0.204	0.103	NA	1	0.103	0.103
RCP onset to tongue projection onset (s)	0.118	0.014	16	0.034	0.234	0.098	0.012	17	0.013	0.156	0.091	0.012	17	-0.060	0.171	0.074	0.009	17	0.008	0.124	0.041	NA	1	0.041	0.041
RCP onset to max. tongue projection (s)	0.130	0.014	16	0.045	0.241	0.108	0.012	17	0.023	0.165	0.101	0.012	17	-0.052	0.182	0.082	0.009	17	0.016	0.132	0.048	NA	1	0.048	0.048
RCP max. amplitude to max. tongue projection (s)	-0.003	0.007	16	-0.070	0.030	-0.004	0.005	17	-0.056	0.020	-0.005	0.006	17	-0.066	0.018	0.000	0.004	17	-0.051	0.014	-0.026	NA	1	-0.026	-0.026
RCP offest to max. tongue projection (s)	-0.081	0.010	16	-0.174	-0.034	-0.062	0.006	17	-0.111	-0.023	-0.055	0.005	17	-0.092	-0.017	-0.052	0.006	17	-0.096	-0.011	-0.055	NA	1	-0.055	-0.055

Desmognathus

	5°C					10°C					15°C					20°C					25°C				
	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max
SAR activity duration (s)	0.214	0.018	9	0.115	0.284	0.192	0.010	19	0.128	0.268	0.157	0.009	18	0.100	0.246	0.131	0.009	17	0.065	0.180	0.110	0.007	14	0.068	0.158
SAR onset to tongue projection onset (s)	0.106	0.008	9	0.061	0.133	0.083	0.004	19	0.055	0.115	0.060	0.003	18	0.041	0.090	0.054	0.003	17	0.028	0.069	0.038	0.002	14	0.025	0.055
SAR peak amplitude to tongue projection onset (s)	0.027	0.020	9	-0.118	0.071	0.027	0.005	19	-0.042	0.059	0.018	0.003	18	-0.040	0.041	0.018	0.002	17	0.010	0.033	0.006	0.003	14	-0.023	0.018
SAR offset to tongue projection onset (s)	-0.109	0.019	9	-0.180	0.002	-0.109	0.008	19	-0.174	-0.050	-0.097	0.007	18	-0.162	-0.037	-0.077	0.007	17	-0.110	-0.015	-0.072	0.005	14	-0.103	-0.031
RCP activity duration (s)	0.124	0.017	9	0.067	0.226	0.139	0.012	19	0.041	0.239	0.126	0.012	18	0.052	0.261	0.109	0.010	17	0.037	0.168	0.097	0.009	14	0.032	0.158
RCP onset to tongue projection onset (s)	-0.010	0.021	9	-0.094	0.107	0.030	0.012	19	-0.142	0.084	0.032	0.009	18	-0.068	0.096	0.032	0.010	17	-0.048	0.076	0.036	0.005	14	-0.005	0.064
RCP onset to max. tongue projection (s)	0.062	0.022	9	-0.024	0.177	0.090	0.010	19	-0.013	0.172	0.079	0.009	18	0.009	0.161	0.067	0.010	17	-0.011	0.124	0.062	0.006	14	0.018	0.098
RCP max. amplitude to max. tongue projection (s)	-0.018	0.007	9	-0.047	0.012	-0.011	0.004	19	-0.047	0.007	-0.004	0.006	18	-0.046	0.075	-0.004	0.006	17	-0.036	0.076	-0.009	0.003	14	-0.047	0.003
RCP offest to max. tongue projection (s)	-0.062	0.006	9	-0.096	-0.042	-0.049	0.004	19	-0.101	-0.024	-0.047	0.005	18	-0.100	-0.022	-0.041	0.003	17	-0.061	-0.019	-0.034	0.005	14	-0.085	-0.014

Plethodon

	5°C					10°C					15°C					20°C					25°C				
	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max	Mean	SEM	N	Min	Max
SAR activity duration (s)	0.150	0.006	34	0.084	0.220	0.151	0.010	37	0.080	0.340	0.109	0.005	34	0.070	0.163	0.100	0.005	34	0.064	0.181	0.089	0.004	25	0.055	0.137
SAR onset to tongue projection onset (s)	0.081	0.002	34	0.060	0.102	0.063	0.002	37	0.046	0.085	0.051	0.001	34	0.040	0.074	0.043	0.001	34	0.027	0.055	0.039	0.002	25	0.028	0.059
SAR peak amplitude to tongue projection onset (s)	0.022	0.008	34	-0.113	0.064	-0.004	0.009	37	-0.154	0.051	0.014	0.004	34	-0.092	0.036	0.017	0.001	34	0.001	0.032	0.013	0.003	25	-0.051	0.033
SAR offset to tongue porjection onset (s)	-0.068	0.005	34	-0.128	-0.012	-0.088	0.010	37	-0.282	-0.025	-0.058	0.005	34	-0.115	-0.018	-0.057	0.005	34	-0.139	-0.023	-0.051	0.004	25	-0.092	-0.015
RCP activity duration (s)	0.138	0.009	34	0.057	0.233	0.150	0.011	37	0.036	0.305	0.111	0.007	34	0.044	0.191	0.114	0.010	34	0.042	0.325	0.093	0.008	25	0.012	0.177
RCP onset to tongue projection onset (s)	-0.006	0.010	34	-0.096	0.096	0.032	0.008	37	-0.056	0.095	0.023	0.006	34	-0.044	0.077	0.022	0.009	34	-0.119	0.154	0.021	0.005	25	-0.042	0.050
RCP onset to max. tongue projection (s)	0.071	0.008	34	-0.016	0.171	0.098	0.009	37	0.012	0.219	0.068	0.006	34	0.009	0.128	0.068	0.009	34	-0.015	0.249	0.055	0.006	25	0.003	0.124
RCP max. amplitude to max. tongue projection (s)	-0.005	0.008	34	-0.091	0.117	-0.002	0.006	37	-0.063	0.103	-0.001	0.004	34	-0.042	0.052	-0.012	0.003	34	-0.049	0.027	-0.004	0.003	25	-0.033	0.021
RCP offest to max. tongue projection (s)	-0.067	0.005	34	-0.134	-0.022	-0.052	0.004	37	-0.118	-0.009	-0.043	0.004	34	-0.082	0.033	-0.046	0.003	34	-0.084	-0.009	-0.038	0.004	25	-0.086	-0.002

Table S3. Results of anova comparing motor control variables at each experimental temperature.

Bolitoglossa vs. *Ensatina*	5°C F ratio	5°C P value	10°C F ratio	10°C P value	15°C F ratio	15°C P value	20°C F ratio	20°C P value	25°C F ratio	25°C P value
SAR activity duration	3.48	0.0729	0.92	0.3434	1.54	0.2217	4.63	0.0374 *	0.45	0.5095
SAR start to tongue projection start	4.99	0.0337 *	6.59	0.0143 *	32.50	<0.0001 *	1.49	0.2288	7.63	0.0120
SAR max. r.m.s. to tongue projection start	12.72	0.0013 *	9.46	0.0039 *	9.64	0.0035 *	11.33	0.0017 *	0.09	0.7679
SAR end to tongue projection start	28.32	<0.0001 *	13.00	0.0010 *	12.25	0.0013 *	13.29	0.0008 *	4.21	0.0535
RCP activity duration	69.30	<0.0001 *	98.59	<0.0001 *	123.00	<0.0001 *	120.50	<0.0001 *	2.41	0.1359
RCP start to max. tongue projection	84.97	<0.0001 *	156.40	<0.0001 *	175.50	<0.0001 *	126.80	<0.0001 *	3.37	0.0812
RCP end to max. tongue projection	10.51	0.0031 *	22.17	<0.0001 *	32.22	<0.0001 *	33.80	<0.0001 *	1.11	0.3039

Desmognathus vs. *Plethodon*	5°C F ratio	5°C P value	10°C F ratio	10°C P value	15°C F ratio	15°C P value	20°C F ratio	20°C P value	25°C F ratio	25°C P value
SAR activity duration	22.40	<0.0001 *	29.25	<0.0001 *	44.27	<0.0001 *	13.33	0.0007 *	8.31	0.0072 *
SAR start to tongue projection start	15.53	0.0004 *	32.22	<0.0001 *	8.44	0.0058 *	23.60	<0.0001 *	0.10	0.7483
SAR max. r.m.s. to tongue projection start	3.37	0.0778	4.03	0.0528	0.25	0.6191	0.83	0.3690	0.88	0.3582
SAR end to tongue projection start	15.69	0.0004 *	19.41	0.0001 *	36.51	<0.0001 *	4.24	0.0460	10.61	0.0028 *
RCP activity duration	0.94	0.3397	0.20	0.6567	2.32	0.1352	0.01	0.9366	0.64	0.4297
RCP start to max. tongue projection	0.72	0.4013	1.45	0.2348	2.83	0.0997	1.66	0.2055	3.75	0.0621
RCP end to max. tongue projection	0.03	0.8692	0.00	0.9440	0.07	0.7995	0.37	0.5477	0.00	0.9843

* Significant difference between species after adjusting for false discovery rate.

Table S4. Results of ancova examining the effects of species x temperature interaction in each of the experimental temperature intervals within ballistic species (*Bolitoglossa* and *Ensatina*) and non-ballistic species (*Desmognathus* and *Plethodon*).

Bolitoglossa and *Ensatina*			*Desmognathus* and *Plethodon*		
Variable	Species x Temp F-ratio	Species x Temp P-value	Variable	Species x Temp F-ratio	Species x Temp P-value
5-15°C			**5-15°C**		
SAR activity duration	1.13	0.2909	SAR activity duration	0.04	0.8456
SAR start to tongue projection start	0.05	0.8265	**SAR start to tongue projection start**	2.47	0.1184
SAR max. r.m.s. to tongue projection start	0.52	0.4725	SAR max. r.m.s. to tongue projection start	1.66	0.1996
SAR end to tongue projection start	0.05	0.8313	SAR end to tongue projection start	0.15	0.6979
SAR r.m.s.	0.70	0.4047	SAR r.m.s.	4.46	0.0365
RCP activity duration	1.53	0.2184	RCP activity duration	0.41	0.5208
RCP start to to max. tongue projection	0.12	0.7258	**RCP start to to max. tongue projection**	0.32	0.5743
RCP end to max. tongue projection	4.37	0.0387	RCP end to max. tongue projection	0.09	0.7648
RCP r.m.s.	1.39	0.2410	RCP r.m.s.	4.52	0.0353
10-20°C			**10-20°C**		
SAR activity duration	0.16	0.6907	SAR activity duration	0.16	0.6869
SAR start to tongue projection start	0.91	0.3431	SAR start to tongue projection start	0.93	0.3367
SAR max. r.m.s. to tongue projection start	0.64	0.4233	**SAR max. r.m.s. to tongue projection start**	0.37	0.5429
SAR end to tongue projection start	0.84	0.3625	**SAR end to tongue projection start**	0.67	0.4158
SAR r.m.s.	1.49	0.2244	**SAR r.m.s.**	2.45	0.1194
RCP activity duration	2.14	0.1459	**RCP activity duration**	0.02	0.8835
RCP start to to max. tongue projection	1.65	0.2018	**RCP start to to max. tongue projection**	0.00	0.9589
RCP end to max. tongue projection	1.54	0.2162	**RCP end to max. tongue projection**	0.46	0.5004
RCP r.m.s.	0.42	0.5204	RCP r.m.s.	3.15	0.0779
15-25°C			**15-25°C**		
SAR activity duration	2.38	0.1258	**SAR activity duration**	3.52	0.0630
SAR start to tongue projection start	0.94	0.3333	SAR start to tongue projection start	1.26	0.2631
SAR max. r.m.s. to tongue projection start	0.01	0.9323	SAR max. r.m.s. to tongue projection start	0.65	0.4216
SAR end to tongue projection start	0.07	0.7866	**SAR end to tongue projection start**	3.00	0.0857
SAR r.m.s.	0.34	0.5611	SAR r.m.s.	0.48	0.4893
RCP activity duration	0.66	0.4177	**RCP activity duration**	0.00	0.9730
RCP start to to max. tongue projection	1.83	0.1789	RCP start to to max. tongue projection	1.41	0.2369
RCP end to max. tongue projection	0.27	0.6050	**RCP end to max. tongue projection**	0.00	0.9584
RCP r.m.s.	1.18	0.2804	RCP r.m.s.	7.46	0.0072
5-25°C			**5-25°C**		
SAR activity duration	0.07	0.7899	SAR activity duration	2.05	0.1538
SAR start to tongue projection start	0.17	0.6781	SAR start to tongue projection start	6.15	0.0139
SAR max. r.m.s. to tongue projection start	0.24	0.6228	SAR max. r.m.s. to tongue projection start	2.93	0.0884
SAR end to tongue projection start	0.58	0.4484	**SAR end to tongue projection start**	3.66	0.0570
SAR r.m.s.	0.50	0.4790	SAR r.m.s.	1.98	0.1603
RCP activity duration	0.00	0.9810	**RCP activity duration**	0.02	0.8984
RCP start to to max. tongue projection	0.31	0.5795	**RCP start to to max. tongue projection**	0.21	0.6463
RCP end to max. tongue projection	0.72	0.3979	**RCP end to max. tongue projection**	0.07	0.7903
RCP r.m.s.	0.02	0.8819	RCP r.m.s.	0.01	0.9430

*Significant interaction after adjusting for false discovery rate. Full model includes individual as a random effect and projection distance as a covariate. Bold indicates a significant effect of projection distance.

Table S5. Results of anova comparing motor control variables of ballistic and non-ballistic species at each experimental temperature.

	5°C		10°C		15°C		20°C		25°C	
	F ratio	*P value*	*F ratio*	*P value*	*F ratio*	*P value*	*F ratio*	*P value*	*F ratio*	*P value*
SAR activity duration	28.33	<0.0001 *	1.54	0.2185	26.24	<0.0001 *	10.95	0.0014 *	2.37	0.1299
SAR start to tongue projection start	262.50	<0.0001 *	294.60	<0.0001 *	565.80	<0.0001 *	441.60	<0.0001 *	268.70	<0.0001 *
SAR max. r.m.s. to tongue projection start	41.67	<0.0001 *	54.83	<0.0001 *	131.80	<0.0001 *	103.10	<0.0001 *	29.21	<0.0001 *
SAR end to tongue projection start	42.62	<0.0001 *	76.41	<0.0001 *	46.03	<0.0001 *	65.79	<0.0001 *	141.00	<0.0001 *
RCP activity duration	0.84	0.3618	44.76	<0.0001 *	52.67	<0.0001 *	64.23	<0.0001 *	31.18	<0.0001 *
RCP start to max. tongue projection	0.84	0.3641	62.19	<0.0001 *	28.30	<0.0001 *	40.51	<0.0001 *	58.35	<0.0001 *
RCP end to max. tongue projection	0.65	0.4244	6.01	0.0163 *	30.68	<0.0001 *	36.97	<0.0001 *	5.11	0.0269 *

* Significant difference between species after adjusting for false discovery rate.

Table S6. Results of ancova examining effects of temperature and projection distance on motor control variables in ballistic species (*Bolitoglossa* and *Ensatina*) and non-ballistic species (Desmognathus and Plethodon).

Bolitoglossa and *Ensatina*

Variable	Projection distance P-value	Temperature P-value	Temperature slope	Temperature intercept	Q_{10}	$1/Q_{10}$
5-15 °C						
SAR activity duration	0.0001 *	<0.0001 *	-0.0197	-0.64	0.64	**1.57**
SAR start to tongue projection start	0.0006 *	<0.0001 *	-0.0222	-0.69	0.60	**1.67**
SAR peak r.m.s. to tongue projection start	0.5607	<0.0001 *	-0.0286	-0.89	0.52	**1.93**
SAR end to tongue projection start	0.0967	0.15	-0.0148	-1.42	0.71	1.40
SAR r.m.s.	0.02	<0.0001 *	0.0276	-1.27	**1.89**	0.53
RCP activity duration	0.3848	<0.0001 *	-0.0219	-0.82	0.60	**1.66**
RCP start to to peak tongue projection	0.6637	0.0267 *	-0.0103	-1.25	0.79	**1.27**
RCP end to max. tongue projection	0.6888	<0.0001 *	-0.0331	-1.07	0.47	**2.15**
RCP r.m.s.	0.6275	0.0238 *	0.0157	-0.78	**1.44**	0.69
10-20°C						
SAR activity duration	0.0002 *	<0.0001 *	-0.0161	-0.68	0.69	**1.45**
SAR start to tongue projection start	0.0004 *	<0.0001 *	-0.0171	-0.76	0.67	**1.48**
SAR peak r.m.s. to tongue projection start	0.5433	0.0003 *	-0.0175	-1.03	0.67	**1.50**
SAR end to tongue projection start	0.134	0.3324	-0.0087	-1.49	0.82	1.22
SAR r.m.s.	0.0416	<0.0001 *	0.0254	-1.23	**1.80**	0.56
RCP activity duration	0.102	<0.0001 *	-0.0233	-0.80	0.59	**1.71**
RCP start to to peak tongue projection	0.0907	<0.0001 *	-0.0242	-1.07	0.57	**1.75**
RCP end to max. tongue projection	0.0167	<0.0001 *	-0.0249	-1.16	0.56	**1.77**
RCP r.m.s.	0.0497	0.0461	-0.0130	-0.37	0.74	1.35
15-25°C						
SAR activity duration	<0.0001 *	<0.0001 *	-0.0162	-0.69	0.69	**1.45**
SAR start to tongue projection start	<0.0001 *	<0.0001 *	-0.0187	-0.75	0.65	**1.54**
SAR peak r.m.s. to tongue projection start	0.5006	0.0018 *	-0.0188	-1.02	0.65	**1.54**
SAR end to tongue projection start	0.2709	0.5862	-0.0052	-1.56	0.89	1.13
SAR r.m.s.	0.6469	0.0001 *	0.0200	-1.16	**1.59**	0.63
RCP activity duration	0.1916	0.0866	-0.0087	-1.04	0.82	1.22
RCP start to to peak tongue projection	0.0162 *	0.0004 *	-0.0195	-1.02	0.64	**1.57**
RCP end to max. tongue projection	0.0346	0.5842	-0.0045	-1.51	0.90	1.11
RCP r.m.s.	0.0324	0.4271	0.0066	-0.70	1.16	0.86
5-25°C						
SAR activity duration	<0.0001 *	<0.0001 *	-0.0178	-0.66	0.66	**1.51**
SAR start to tongue projection start	<0.0001 *	<0.0001 *	-0.0200	-0.71	0.63	**1.58**
SAR peak r.m.s. to tongue projection start	0.7306	<0.0001 *	-0.0242	-0.93	0.57	**1.75**
SAR end to tongue projection start	0.0741	0.0209 *	-0.0101	-1.46	0.79	**1.26**
SAR r.m.s.	0.0239	<0.0001 *	0.0245	-1.23	**1.76**	0.57
RCP activity duration	0.3025	<0.0001 *	-0.0174	-0.87	0.67	**1.49**
RCP start to to peak tongue projection	0.0747	<0.0001 *	-0.0150	-1.21	0.71	**1.41**
RCP end to max. tongue projection	0.0977	<0.0001 *	-0.0221	-1.18	0.60	**1.66**
RCP r.m.s.	0.0623	0.0144 *	0.0088	-0.71	**1.23**	0.81

Desmognthus and *Plethodon*

Variable	Projection distance P-value	Temperature P-value	Temperature slope	Temperature intercept	Q_{10}	$1/Q_{10}$
5-15 °C						
SAR activity duration	0.5251	<0.0001 *	-0.0148	-0.68	0.71	**1.41**
SAR start to tongue projection start	0.0511	<0.0001 *	-0.0216	-0.93	0.61	**1.64**
SAR max. r.m.s. to tongue projection start	0.1172	<0.0001 *	-0.0288	-1.12	0.52	**1.94**
SAR end to tongue projection start	0.1042	0.0135 *	-0.0091	-1.17	0.81	**1.23**
SAR r.m.s.	0.4558	<0.0001 *	0.0292	-1.05	**1.96**	0.51
RCP activity duration	0.0845	0.0043 *	-0.0098	-0.80	0.80	**1.25**
RCP start to to max. tongue projection	0.0253	0.2759	-0.0065	-1.09	0.86	1.16
RCP end to max. tongue projection	0.0963	<0.0001 *	-0.0142	-1.14	0.72	**1.39**
RCP r.m.s.	0.7618	<0.0001 *	0.0278	-0.85	**1.89**	0.53
10-20°C						
SAR activity duration	0.0346	<0.0001 *	-0.0169	-0.65	0.68	**1.48**
SAR start to tongue projection start	0.7359	<0.0001 *	-0.0195	-0.96	0.64	**1.56**
SAR max. r.m.s. to tongue projection start	0.0368	0.0003 *	-0.0214	-1.40	0.61	**1.64**
SAR end to tongue projection start	0.0244	0.0002 *	-0.0138	-0.98	0.73	**1.38**
SAR r.m.s.	0.0406	0.0027 *	0.0157	-0.85	**1.44**	0.69
RCP activity duration	0.0014 *	<0.0001 *	-0.0153	-0.91	0.70	**1.42**
RCP start to to max. tongue projection	0.0021 *	<0.0001 *	-0.0202	-1.15	0.63	**1.59**
RCP end to max. tongue projection	0.0004 *	0.0048 *	-0.0094	-1.42	0.81	**1.24**
RCP r.m.s.	0.9858	0.0004 *	0.0194	-0.74	**1.56**	0.64
15-25°C						
SAR activity duration	0.0021 *	<0.0001 *	-0.0126	-0.85	0.75	**1.34**
SAR start to tongue projection start	0.0542	<0.0001 *	-0.0167	-1.01	0.68	**1.47**
SAR max. r.m.s. to tongue projection start	0.1673	0.0005 *	-0.0207	-1.40	0.62	**1.61**
SAR end to tongue projection start	0.0095 *	0.0303 *	-0.0087	-1.25	0.82	**1.22**
SAR r.m.s.	0.4371	0.6618	0.0024	-0.62	1.06	0.94
RCP activity duration	0.0016 *	0.003 *	-0.0115	-0.78	0.77	**1.30**
RCP start to to max. tongue projection	0.0442	0.0804	-0.0096	-1.07	0.80	1.25
RCP end to max. tongue projection	0.0021 *	0.0001 *	-0.0184	-1.26	0.65	**1.53**
RCP r.m.s.	0.9806	0.3098	-0.0056	-0.31	0.88	1.14
5-25°C						
SAR activity duration	0.058	<0.0001 *	-0.0139	-0.70	0.73	**1.38**
SAR start to tongue projection start	0.942	<0.0001 *	-0.0192	-0.96	0.64	**1.56**
SAR max. r.m.s. to tongue projection start	0.3412	<0.0001 *	-0.0238	-1.26	0.58	**1.73**
SAR end to tongue projection start	0.0279	<0.0001 *	-0.0099	-1.17	0.80	**1.26**
SAR r.m.s.	0.3543	<0.0001 *	0.0161	-0.90	**1.45**	0.69
RCP activity duration	0.0001 *	<0.0001 *	-0.0114	-0.78	0.77	**1.30**
RCP start to to max. tongue projection	0.0008 *	<0.0001 *	-0.0121	-1.30	0.76	**1.32**
RCP end to max. tongue projection	0.0001 *	<0.0001 *	-0.0147	-1.34	0.71	**1.40**
RCP r.m.s.	0.6423	<0.0001 *	0.0146	-0.72	**1.40**	0.71

* Significant effect after adjusting for false discovery rate. The coefficients and Q_{10} values for variables with projection distance p-values >.05 come from the model without projection distance included.