

Modulation, individual variation and the role of lingual sensory afferents in the control of prey transport in the lizard *Pogona vitticeps*

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SUMMARY

Most organisms feed on a variety of food items that may differ dramatically in their physical and behavioural characteristics (e.g. mobility, mass, texture, etc.). Thus the ability to modulate prey transport behaviour in accordance with the characteristics of the food appears crucial. Consequently, prey reduction and transport movements must be adjusted to the natural variation in material properties of the food, between and within feeding sequences and transport cycles. Here we describe an investigation of (1) the ability of the agamid lizard *Pogona vitticeps* to modulate prey transport kinematics when feeding on a range of food items differing in their physical characteristics and (2) the role of sensory feedback in controlling jaw and tongue movements by bilateral transection of the lingual trigeminal sensory afferents. Our findings demonstrate that *P. vitticeps* modulates the kinematics of its feeding behaviour in response to the mechanical demands imposed by different food types. In addition, transection of the trigeminal sensory afferents has an effect on the movements of jaws and tongue during transport, and increases the duration of transport cycles needed to process a given food type. However, after transection, transport cycles were still different for different food types suggesting that other sources of sensory information are also used to modulate prey transport in the lizard *P. vitticeps*.

INTRODUCTION

Feeding is important for energy acquisition as the feeding system delivers food to the digestive system where nutrients are assimilated. In terrestrial vertebrates, feeding behaviour is a complex activity involving capture, intraoral transport, reduction and swallowing of the food (Bramble and Wake, 1985). Intraoral transport is the movement of the food through the mouth following prey capture. Although food can be transported directly to the pharynx for swallowing, often movements of the upper and lower tooth rows (jaws) are used to reduce the food before swallowing (Reilly et al., 2001; Ross et al., 2007). Different kinds of vertebrates engage in intraoral food processing [e.g. fish, turtles, some birds, many lizards and most mammals (Bemis and Lauder, 1986; Mehta and Wainwright, 2007; Reilly et al., 2001)], and it is thought that intraoral processing is modulated to some degree in all these different lineages (Ross et al., 2007). In tetrapods, the hyolingual system also plays a major role in intraoral prey transport (e.g. Bels et al., 1994; Schwenk, 1995). Indeed, a tight coupling between the movements of the tongue and hyobranchium with those of the jaws is needed for efficient prey transport (Bramble and Wake, 1985; Schwenk, 2000). Among tetrapods, lizards are unusual as the function and morphology of the tongue differs in different clades that show different degrees of specialization of the tongue (Cooper, 1995; Schwenk, 2000).

Most organisms feed on a variety of food items differing in their mechanical properties (e.g. mobility, mass, texture, etc.). Thus, the ability to modulate prey transport and prey reduction behaviour in response to the characteristics of a food item appears to be crucial. Mammals and birds, because of their elevated metabolic rates

associated with endothermy, need to ingest more food than other vertebrates (Bennett and Ruben, 1979). In mammals, this is often thought to go hand-in-hand with a more efficient intraoral processing and more profound modulation of mastication to maximise energy gain and prevent damage to the teeth (e.g. Thexton and Hiiemae, 1997). Therefore, masticatory movements must be adjusted to the natural variation in material properties of the food, between and within feeding sequences and transport cycles (Ross et al., 2007). In contrast to what is often thought, most lizards also extensively reduce food items prior to swallowing. Moreover, like mammals, lizards modulate their feeding cycles in response to the mechanical properties of the food (e.g. Wainwright et al., 1991; Smith et al., 1999; Urbani and Bels, 1999).

Sources of sensory information that can be used to modulate a prey capture event are numerous (e.g. visual, chemosensory and tactile). However, during prey transport, tactile and chemosensory stimuli likely play the most important role in modulating intraoral transport as the tongue makes intimate contact with the food item and, in that way, may gather important sensory information about the food item. Which aspects of a food item specifically affect the coordination between jaws and tongue remains currently unclear, but size, mass, shape and mechanical resistance likely play an important role (e.g. Bels and Baltus, 1988; Herrel et al., 1996; Herrel and De Vree, 1999; Schwenk, 2000). Based on *a priori* mechanical reasoning we predict that (1) prey transport of hard and tough food items will take longer because of an increase in the slow closing phase where the teeth engage the food; (2) that large food items will be associated with larger gape distances to allow the passage of the tongue with adhering food; (3) that the transport of heavier

food items will be associated with an increased slow opening phase and total cycle duration as the larger adhesive forces needed to transport heavy food items are proportional to the contact area between tongue and food items achieved during the slow opening phase; and (4) that the transport of elusive food items would be associated with a decrease in the duration of the fast opening and/or fast closing phases and an increase in the jaw velocity, as these are the phases during which the teeth are not engaged with the food. Here we investigated the extent to which a generalized agamid lizard, *Pogona vitticeps*, is capable of modulating prey transport kinematics in response to different food types. To do so, we offered food types differing in their physical characteristics including size, hardness, mass and mobility. The food types used were chosen to reflect the natural diet of *P. vitticeps* (Kennerson and Cochrane, 1981; MacMillen et al., 1989).

As the control of feeding cycles and the sources of sensory information used to modulate prey transport remain poorly understood, we decided to investigate the role of lingual sensory feedback in the modulation of transport cycles. To do so, we used nerve transection experiments (e.g. Anderson and Nishikawa, 1993; Deban, 1997). We decided to focus on the sensory branch of the mandibular ramus of the trigeminal nerve as this branch innervates the anterior half of the tongue that comes into close contact with the food during prey capture and transport. Its superficial position and ease of access makes it an ideal candidate for nerve transection experiments. If no changes in the kinematics of prey transport are observed after transection, then this branch of the trigeminal nerve can be excluded as a source of sensory information during prey transport (e.g. Deban, 1997; Nishikawa, 2000). This would suggest that other sources of sensory information or other lingual sensory afferents (e.g. glossopharyngeal) are dominant during prey transport. In case transection effects are significant, this would suggest that the trigeminal nerve plays an important role in coordinating prey transport in *P. vitticeps*. If so, we predict an increase in the duration of prey transport cycles (see Herrel et al., 2001) and an increase in the duration of the slow opening and slow closing phases as the animals are lacking information to appropriately control their feeding movements to the characteristics of the food item.

MATERIALS AND METHODS

Experiments were carried out in the laboratory at the University of Antwerp on four commercially bred juvenile specimens of the species *Pogona vitticeps* Ahl (mean snout–vent length, SVL: 74.33±2.84 mm). The animals were housed in a glass vivarium on a 12 h:12 h light:dark cycle and offered mealworms, endive, crickets and waxworms *ad libitum*. The environmental temperature varied from 34°C during the day to 22°C at night. An incandescent bulb provided the animals with a basking place at a higher temperature.

Video recordings

The lizards were filmed at 250 Hz in lateral view using a Redlake Motionscope digital high-speed camera while eating food types differing in their physical attributes [isopods (*Porcellus scaber*),

crickets (*Acheta domestica*), ants and small pieces of endive]. A quantitative assessment of food properties is represented in Table 1 (Schaerlaeken et al., 2007). A background grid of 10 mm squares was used as a scale. At least three sequences were recorded for each individual transporting each of the four food items before and after transection. From each sequence, five transport cycles were analysed. Only sequences where the animal was positioned lateral with respect to the camera were retained for analysis. A total of 190 cycles before and 135 cycles after transection were included in the analysis.

Nerve transections

To test whether lingual sensory information plays a role in coordinating jaw and tongue movements the lingual ramus of the mandibular branch of the trigeminal nerve was bilaterally transected in three individuals (Herrel et al., 2001; Meyers et al., 2002). Before transection, the animals were anaesthetised using ketamine (200 mg kg⁻¹ body mass; ketamine hydrochloride, 50 mg ml⁻¹, Parke-Davis, Brussels, Belgium). The animals were filmed eating all four food types (ants, crickets, isopods and endive) before and after bilateral transection. A full description of the procedure can be found in Schaerlaeken et al. (Schaerlaeken et al., 2007). All post-surgery recordings were completed within 2 weeks because re-innervation can occur within 4 weeks after transection (Meyers and Nishikawa, 2000). All procedures were approved by the animal ethics committee at the University of Antwerp.

Video analysis

Only transport sequences in which the animals remained lateral with respect to the camera and in which all phases of a prey transport event (slow opening, SO; fast opening, FO; fast closing, FC; slow closing/power stroke, SC/PS) were present, were analysed. Two externally visible landmarks were digitised on each frame using Didge (Image Digitizing Software version 2.2.0; Alistair Cullum, Creighton University, Omaha). These landmarks included the anterior tip of the upper jaw and the anterior tip of the lower jaw. From the *x* and *y* coordinates of these markers we calculated the distance between upper and lower jaw (gape distance). Based on the raw kinematic profiles of jaw movement, the total duration of a transport cycle was determined.

Next, the raw displacement profiles of the jaws were smoothed using a zero phase shift, fourth-order low pass Butterworth filter at 25 Hz. Velocities and accelerations were calculated from the filtered displacement data by taking the first and second derivatives. From these data the maximal jaw opening and jaw closing velocity were calculated. The different phases within a transport cycle were determined based on the jaw acceleration data as outlined in Schaerlaeken et al. (Schaerlaeken et al., 2007). In brief, the duration of the slow open phase (SO) was defined as the time between the beginning of the prey transport event and the first pronounced acceleration peak during jaw opening; the fast open phase (FO) was defined as the time between the first acceleration and the deceleration peak; the fast close phase (FC) was defined as the time between the

Table 1. Quantitative characterization of food types used in this study

Food type (N)	Mass (g)	Hardness* (N)	Length (mm)	Width (mm)	Mobility
Cricket (35)	0.18±0.14	1.66±0.91	14.23±4.04	3.90±0.47	Fast
Ant (10)	0.016±0.004	2.52±1.45	5.26±1.37	0.99±0.39	Intermediate
Isopod (39)	0.05±0.02	0.97±0.37	7.66±1.20	3.68±0.55	Slow
Endive (20)	0.11±0.03	4.02±0.78	17.60±1.50	18.05±2.33	Stationary

*For a description of the measurement of food hardness (see Herrel et al., 1999; Herrel et al., 2001).

peak deceleration and peak acceleration during jaw closing and the slow close phase (SC) was defined as the time from the peak acceleration during closing until the end of the transport cycle (see also McBrayer and Reilly, 2002).

In total, eight kinematic variables were calculated and used in the statistical analyses: gape distance, maximal jaw opening velocity, maximal jaw closing velocity, the total duration of a prey transport event and the duration of SO, FO, FC and SC/PS.

Statistical analyses

All kinematic data were \log_{10} transformed prior to analyses to meet the assumption of homoscedascity and normality for regression analyses (Sokal and Rohlf, 1981; Kachigan, 1991). To reduce the complexity and dimensionality of the data set, we performed a factor analysis with Varimax rotation on the kinematic data set before transection. The Varimax rotation was used as it maximises the sum of the variances of the loadings on the factors. Next, a MANOVA was performed on the factor scores to test for potential individual, food type and interaction effects. Since the interaction effect was highly significant, food type effects were further analysed for each individual separately using univariate F -tests coupled to Bonferroni *post-hoc* tests on the significant factor scores. For all univariate F -tests performed, the significance level was corrected using a sequential Bonferroni correction (Rice, 1989).

Kinematic data from both before and after transection were used to test whether the transection of sensory afferents had an effect on the kinematics of prey transport. Again a factor analysis coupled to a Varimax rotation was performed on the full kinematic data set for individuals 6, 9 and 10. A MANOVA was performed on the factor scores to test for individual, food type, transection and interaction effects. As interaction effects between individual and transection, between food type and transection and between individual and food type were significant, transection effects were tested for each individual and each food type separately. All analyses were performed using SPSS 13.0.

RESULTS

Pogona vitticeps uses lingual transport, whereby cyclical movements of the tongue are used to transport the food item through the oral cavity and into the pharynx. As suggested by Bramble and Wake (Bramble and Wake, 1985) a typical transport cycle in these animals can be divided into four phases determined by changes in velocity of the jaws (SO, FO, FC and SC). Lingual transport starts with the tongue moving forward underneath the food item inducing close contact between food and tongue (SO). This phase is often thought to be important because during the SO sensory information about the position and characteristics of the food items can be gathered and used to modulate the next cycle (Bramble and Wake, 1985). As the jaws are parted during FO, the bolus is freed from contact with the palate and teeth. The tongue together with the attached food item is then rapidly moved caudally, and the jaws close rapidly onto the food item (FC). Finally, the jaws close upon contact with the food item and the prey reduction takes place. Depending on the cycle, the food item may have been moved backwards in the oral cavity, remained stationary and crushed, or switch from side to side in the mouth (Schwenk, 2000). In *P. vitticeps*

Table 2. Results of a factor analysis (varimax rotation) performed on the kinematic data before transection to explore modulation of prey transport kinematics in function of food type

	Component			
	1 (31.25%)	2 (27.29%)	3 (17.34%)	4 (15.55%)
Prey transport duration (s)	0.930	-0.068	-0.084	0.311
Duration of the slow open phase (s)	0.649	-0.146	-0.638	0.211
Duration of the fast open phase (s)	0.032	0.041	0.972	0.078
Duration of the fast close phase (s)	0.091	0.104	0.016	0.977
Duration of the slow close phase (s)	0.938	0.101	0.022	-0.158
Gape distance (mm)	0.560	0.705	0.158	0.326
Jaw opening velocity (mm s ⁻¹)	0.022	0.907	0.030	0.090
Jaw closing velocity (mm s ⁻¹)	-0.111	0.902	0.039	-0.044
Eigenvalues	2.50	2.18	1.16	0.99

Four factors were retained in the analysis that jointly explained 91.43% of the variation in prey transport kinematics.

Factor loadings greater than 0.7 are indicated in bold. The proportion of variation explained is given in parentheses and eigenvalues are listed below the respective factor scores.

most transport and repositioning cycles also involve extensive prey reduction as indicated by the pronounced slow close phases present in nearly all cycles.

Modulation of the feeding cycle – food type effects

A factor analysis performed on the kinematic data set revealed four factors that together explained 91.43% of the variation in prey transport kinematics (see Table 2). For factor 1, the total duration of a prey transport event and the duration of the SC phase showed the highest loadings. Gape distance, jaw opening velocity and jaw closing velocity loaded most strongly on factor 2. For factor 3, the duration of the FO phase showed the highest loading, and for factor 4 the duration of the FC phase (see Table 2).

A MANOVA was performed on the factor scores that demonstrated significant food type (Wilks' lambda, $F=41.645$, $P<0.001$) and individual effects (Wilks' lambda, $F=12.762$, $P<0.001$) on the kinematics of prey transport. Thus, the kinematics of prey transport are different for different food types (Fig. 1), and

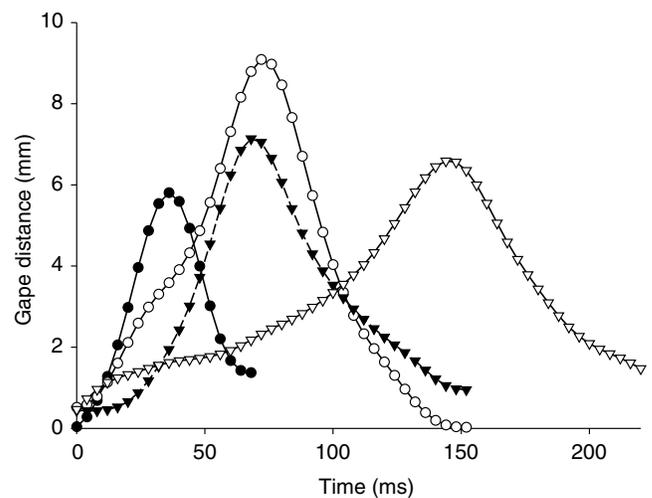


Fig. 1. Representative smoothed gape profile illustrating the effects of food type on prey transport kinematics in *P. vitticeps*. Significant differences in maximal gape distances between transport of ants (solid circles), crickets (open circles), isopods (solid triangles) and endive (open triangles) are apparent. Also note significant differences in the total duration of a transport cycle between ants and the other food items.

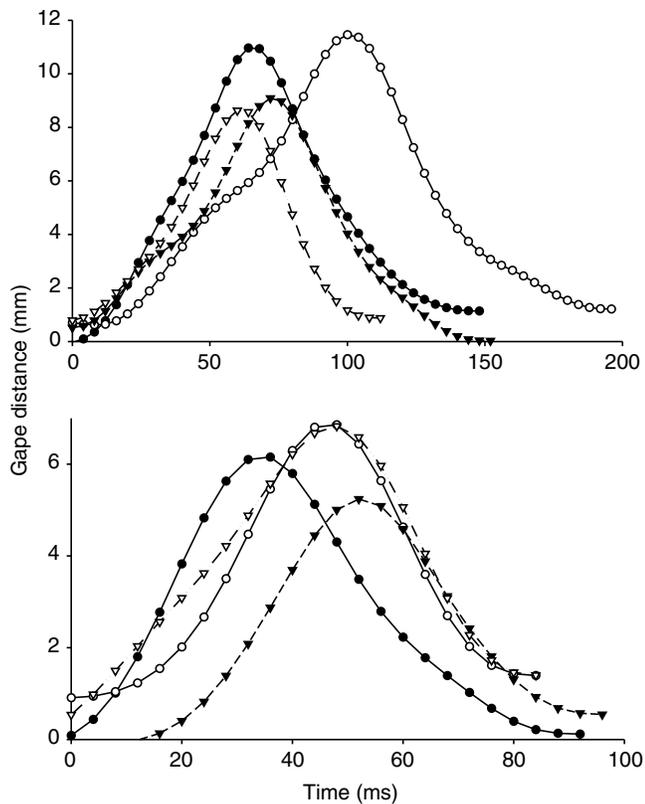


Fig. 2. Individual, and individual by food type interaction effects. (A) Smoothed gape profiles of the four different individuals transporting a cricket. Note how individuals 6 (solid circles) and 7 (open circles) have higher gape distances during transport than individuals 9 (solid triangles) and 10 (open triangles) and how the total transport cycle duration of individual 7 is significant longer than that of the other individuals. (B) Smoothed gape profiles of the same individuals transporting an ant. Note how individual 9 (solid triangles) has a smaller gape distance during transport than the other individuals.

individuals differ from each other in their prey transport kinematics. Interaction effects were also significant (Wilks' lambda, $F=1.848$, $P=0.003$) suggesting that individuals respond differently to different food types (Fig. 2).

Owing to the significance of the interactions effects, food type effects were analysed for each individual separately. Table 3 summarizes the results of the *post-hoc* tests on the significant factors. For individuals 6 and 7, food type effects were significant on factor 1 (Wilks' lambda, $F=56.179$, $P<0.001$ and Wilks' lambda, $F=23.950$, $P<0.001$), factor 2 (Wilks' lambda, $F=30.324$, $P<0.001$ and Wilks' lambda, $F=6.231$, $P=0.001$) and factor 4 (Wilks' lambda, $F=5.196$, $P=0.010$ and Wilks' lambda, $F=5.298$, $P=0.003$). For individuals 9 and 10, food type effects were significant on factor 1 (Wilks' lambda, $F=39.661$, $P<0.001$ and Wilks' lambda, $F=35.136$, $P<0.001$), factor 2 (Wilks' lambda, $F=3.173$, $P=0.032$ and Wilks' lambda, $F=9.498$, $P<0.001$) and factor 3 (Wilks' lambda, $F=2.851$, $P=0.046$ and Wilks' lambda, $F=3.533$, $P=0.020$). In general, differences between food types on factor 1 are mainly between ants and the other food types (crickets, endive and isopods) suggesting that transport of ants is associated with shorter total transport cycle durations and shorter SC phases (see Fig. 1). For factor 2, differences between isopods and the other food types, between endive and crickets, and also between crickets and ants, were significant. Thus, transport of crickets

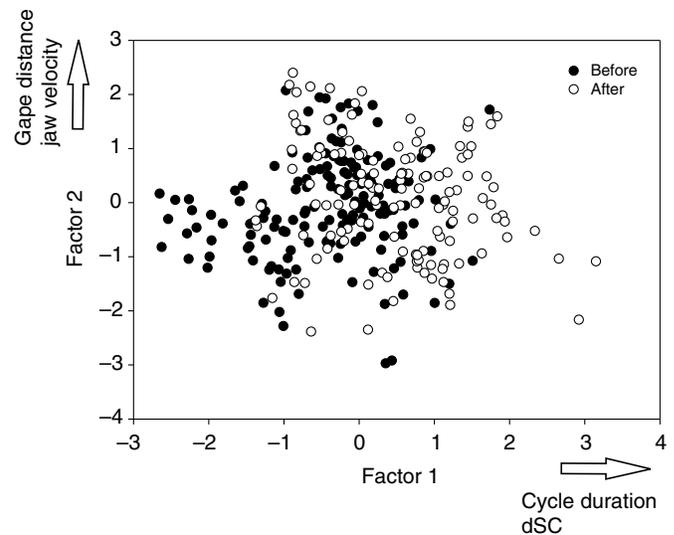


Fig. 3. Results of a factor analysis performed on the kinematic data set before (solid circles) and after (open circles) transection. The first factor, along which the transection effect is most prominent, is mostly affected by duration of slow closing phase (dSC) and total transport cycle duration.

is associated with high gape distances compared to the other food items and transport of isopods is associated with higher gape distances than ants and endive (see Fig. 1). Differences between isopods on the one hand and crickets and endive on the other hand were significant on factor 3, and suggest that transport of isopods is associated with longer FO phases compared with the transport of crickets and endive. Finally, for factor 4, differences between isopods and ants and also between crickets on the one hand and isopods and ants on the other hand, were significant. Thus, transport of ants is associated with shorter FC phases than that of isopods and crickets, and the transport of isopods is associated with shorter FC phases than that of crickets (see Table 6 for averages of raw data).

Effects of nerve transection and role of lingual sensory feedback

A factor analysis performed on the kinematic data before and after bilateral transection of the trigeminal lingual afferent, revealed three factors, which explained 79.16% of the variation in prey transport kinematics (see Table 4). For regression factor 1, the total duration of a prey transport event and the duration of the SC phase showed the highest loadings. Gape distance, jaw opening velocity and jaw closing velocity loaded most strongly on regression factor 2 (see Fig. 3). For regression factor 3, duration of the FO phase showed the highest loading (see Table 4).

A MANOVA performed on the factor scores demonstrated significant individual (Wilks' lambda, $F=7.284$, $P<0.001$), food type (Wilks' lambda, $F=41.856$, $P<0.001$) and transection (Wilks' lambda, $F=49.975$, $P<0.001$) effects. Additionally, the interaction between individual and food type (Wilks' lambda, $F=1.80$, $P=0.02$), between individual and transection (Wilks' lambda, $F=3.93$, $P=0.001$) and between food type and transection (Wilks' lambda, $F=6.80$, $P<0.001$) were significant but the three-way interaction was not significant (Wilks' lambda, $F=1.26$, $P=0.241$). As suggested by the significant interaction effects, the effect of transection was not identical for all the individuals and all food types.

As interaction effects were significant, further analyses of transection effects were performed for each individual and each food

type separately (see Table 5). Differences on factor 1 (correlating strongly with the total duration of a prey transport event and the duration of the SC phase) remained significant in most cases while transporting crickets, ants and endive. The total duration of a prey transport event and of the slow closing phase was thus longer after transection than before transection (see Fig. 4). In individuals 6 and 9, differences on factor 2 were significant for transport of crickets and isopods. Maximal gape distance (correlating highly with factor 2) during transport of crickets after transection was lower in individual 6, whereas transport of isopods in individual 9 had higher maximal gape distances after transection. Finally, in individual 10, transport of crickets and endive had shorter FO phases after transection than before transection (see Table 6 for averages of raw data).

DISCUSSION

Intraoral transport cycles have been described for other acrodont lizards including *Uromastix aegyptius* (Throckmorton, 1976), *Uromastix acanthinurus* (Herrel and De Vree, 1999), *Phrynocephalus helioscopus* (Schwenk and Throckmorton, 1989), *Agama agama* (Kraclau, 1991) and *Agama stellio* (Herrel et al., 1996). Qualitatively, the kinematics of prey transport in the agamid lizard *Pogona vitticeps* are similar to those observed for other agamids. The variety of food items presented to the lizards in our study, allow us to test if *P. vitticeps* is capable of modulating prey transport kinematics in response to this different food types. Despite the striking overall similarity in prey transport behaviour across acrodont lizards, different food types elicited marked variation in prey transport kinematics in *P. vitticeps*. Although intuitively obvious, this has only been demonstrated for a few species: *Agama*

Table 3. Summary table showing on which factors significant food type effects could be demonstrated for the different individuals and the results of Bonferroni *post-hoc* tests to determine which food types differed from one another

Lizard	Factor	F	P	Bonferroni <i>post-hoc</i> tests		P
Individual 6	Factor 1	56.18	<0.001	Ant	Cricket	<0.001
				Ant	Isopod	<0.001
	Factor 2	30.32	<0.001	Ant	Cricket	<0.001
				Ant	Isopod	0.001
	Factor 4	5.20	0.010	Cricket	Isopod	0.001
				Cricket	Isopod	0.008
Individual 7	Factor 1	23.95	<0.001	Ant	Cricket	<0.001
				Ant	Isopod	<0.001
				Ant	Endive	<0.001
	Factor 2	6.23	0.001	Cricket	Endive	0.030
				Cricket	Isopod	0.026
	Factor 4	5.30	0.003	Cricket	Endive	0.001
Ant				Cricket	0.039	
Individual 9	Factor 1	39.66	<0.001	Ant	Cricket	<0.001
				Ant	Isopod	<0.001
				Ant	Endive	<0.001
	Factor 2	3.17	0.032	Cricket	Isopod	0.049
				Cricket	Isopod	0.049
	Factor 3	2.85	0.046	Cricket	Isopod	0.049
Cricket				Isopod	0.049	
Individual 10	Factor 1	35.14	<0.001	Ant	Cricket	<0.001
				Ant	Isopod	<0.001
				Ant	Endive	<0.001
	Factor 2	9.50	<0.001	Ant	Cricket	0.005
				Cricket	Endive	<0.001
	Factor 3	3.53	0.020	Isopod	Endive	0.002
Isopod				Endive	0.015	

Only results for those factors that remained significant after sequential Bonferroni correction are shown.

stellio (Herrel et al., 1996), *Uromastix aegypticus* (Throckmorton, 1980) and *Uromastix acanthinurus* (Herrel and De Vree, 1999). Moreover, distinct inter-individual differences in prey transport kinematics were observed (see also Herrel et al., 1996).

Food items offered to the lizards were chosen specifically for their differences in physical attributes including size and mass (e.g. ant vs cricket), mobility (arthropods vs endive) and mechanical resistance (i.e. hardness; arthropods vs endive). Based on *a priori* mechanical reasoning we expected that prey transport cycles of hard and tough food items would be associated with longer cycle

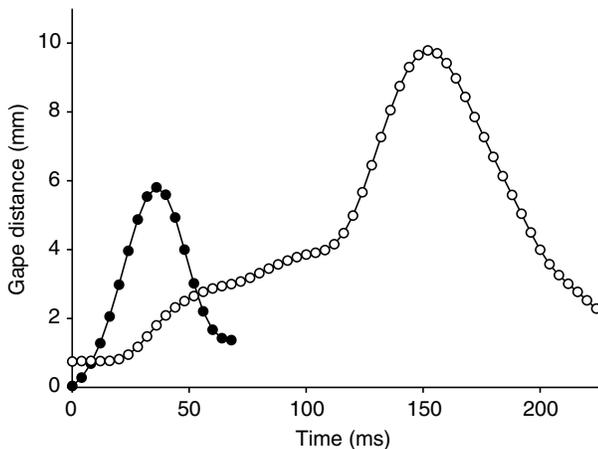


Fig. 4. Representative smoothed gape profiles illustrating the effects of elimination of lingual trigeminal feedback on prey transport kinematics in *P. vitticeps*. Note the differences in gape distance and cycle duration during the transport of ants before (solid circles) and after (open circles) transection.

Table 4. Results of a factor analysis performed on the kinematic data before and after transection

	Component		
	1 (34.13%)	2 (28%)	3 (17.03%)
Prey transport duration (s)	0.972	-0.082	-0.067
Duration of the slow open phase (s)	0.677	-0.125	-0.625
Duration of the fast open phase (s)	0.117	-0.021	0.943
Duration of the fast close phase (s)	0.629	0.053	0.237
Duration of the slow close phase (s)	0.751	0.078	-0.057
Gape distance (mm)	0.555	0.763	0.133
Jaw opening velocity (mm s ⁻¹)	0.041	0.911	0.009
Jaw closing velocity (mm s ⁻¹)	-0.205	0.893	-0.035
Eigenvalues	2.730	2.240	1.362

Three factors that together explained 79.16% of the variation in prey transport kinematics were retained.

Factor loadings greater than 0.7 are indicated in bold. The proportion of variation explained is noted in parentheses, and eigenvalues are listed below each respective factor.

Table 5. Summary table showing on which factors significant transection effects could be demonstrated for the different individuals and different food types

Lizard	Food	Factor	F	P
Individual 6	Ant	Factor 1	71.61	<0.001
	Cricket	Factor 1	13.00	0.002
		Factor 2	6.01	0.025
Individual 9	Ant	Factor 1	18.41	<0.001
	Cricket	Factor 1	9.19	0.007
	Isopod	Factor 2	9.46	0.005
	Endive	Factor 1	10.14	0.038
Individual 10	Cricket	Factor 1	29.52	<0.001
		Factor 3	25.23	<0.001
	Endive	Factor 1	17.60	<0.001
		Factor 2	18.44	<0.001
		Factor 3	18.44	<0.001

Only results for those factors that remained significant after sequential Bonferroni correction are shown.

durations due to an increase in the slow closing (SC) phase, where the teeth engage the food. Interestingly, our data indicate that the intraoral transport cycles of ants are associated with shorter total transport cycle durations and shorter SC phases in all individuals. Although, ants are hard food items, they are minimally or not reduced after capture in most lizards (Meyers and Herrel, 2005). Consequently, a pronounced SC phase is not observed. Crickets and especially endive are associated with longer SC phases as predicted, suggesting the need for a more extensive reduction of these relatively tough food items.

Another prediction was that large food items would be associated with larger gape distances to allow the passage of the tongue with adhering food. This has already been observed for *Agama stellio* (Herrel et al., 1996). Differences in maximal gape distance during prey transport were observed here for the transport of crickets vs ants, isopods and endive, as well as for the transport of isopods vs ants and endive. As crickets are larger than any of the other food types offered, the jaws do indeed have to be opened more widely to allow the transport of the food through the oral cavity. The same explanation can be given for the higher maximal gape distances during transport of isopods vs ants and endive.

We also suggested that the transport of heavier food items would be associated with an increased slow opening (SO) phase and total cycle duration due to the required pronounced fitting of the tongue to the food item. This was, however, not observed in our study. Although, we found that transport of crickets and endive was associated with longer total transport durations compared with the other food items (see above), the duration of the SO phase was not longer. Thus it appears that size and hardness are more important during prey transport than mass *per se*.

The last hypothesis, that transport of elusive food items would be associated with a decrease in the duration of the fast opening (FO) and/or closing (FC) phases and an increase in the jaw velocity was not confirmed by our data. We expected that the transport of crickets, which are more elusive than other food items, would be associated with shorter fast opening and/or closing phases and would result in an increase jaw velocity during transport. However, in individual 6 the transport of isopods was associated with shorter FC phases than crickets. In individual 7, significant differences in the duration of FC phase of ant transport compared to crickets and isopods were observed. In individuals 9 and 10, finally, significant differences in the duration of the fast opening phase between crickets and isopods (ind. 9) and between endive and isopods (ind. 10) were

Table 6. Summary table showing means ± standard deviations of raw data before and after transection for the different individuals and different food types

Ind.	Food	Tot. transp. cycle (ms)		dSO (ms)		dFO (ms)		dFC (ms)		dSC (ms)		gd (mm)	
		Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
6	Ant	100.27±19.62	182.13±45.90	21.07±21.41	40.53±27.21	33.33±9.99	40.00±12.92	29.33±6.70	35.73±10.42	16.53±11.20	65.87±33.70	6.90±0.64	8.28±1.72
	Cricket	167.20±40.57	242.40±27.66	52.27±27.98	93.60±11.52	33.33±12.62	32.00±2.83	38.93±16.10	48.80±10.73	42.67±20.49	68.00±10.95	12.05±0.74	11.80±0.68
	Isopod	159.73±18.30	182.40±48.63	42.40±27.62	41.87±29.23	38.13±16.20	34.40±14.80	27.20±4.33	36.53±12.55	52.00±8.14	69.60±30.34	10.35±1.16	10.51±1.49
	Endive		315.71±96.15		131.71±69.22		36.00±15.92		54.86±22.92		93.14±30.28		11.66±1.46
7	Ant	110.93±17.60		25.07±15.45		31.73±8.21		27.47±3.34		26.67±9.76		7.94±0.59	
	Cricket	179.73±34.69		62.67±32.59		34.93±8.07		37.33±10.55		44.80±15.36		12.40±0.84	
	Isopod	218.13±76.95		83.20±56.69		35.47±7.07		41.60±13.16		57.87±26.27		11.60±0.88	
	Endive	227.20±27.31		87.20±22.22		34.40±6.02		35.60±11.69		70.00±9.66		10.86±1.05	
9	Ant	104.53±19.12	151.20±40.94	26.40±18.69	40.00±32.04	31.47±8.80	36.00±9.56	26.40±5.41	30.93±9.85	20.27±10.74	44.27±12.14	6.40±0.44	7.44±1.18
	Cricket	180.53±38.95	237.60±41.24	58.93±19.56	101.60±25.39	29.87±7.54	34.40±6.07	30.13±5.63	40.00±5.66	61.60±18.50	61.60±16.15	9.52±1.01	11.86±1.41
	Isopod	177.60±40.73	180.31±48.98	44.80±33.81	63.38±47.01	43.20±20.35	32.62±8.30	30.13±7.98	39.08±15.42	59.47±19.82	45.23±26.95	9.41±1.39	11.16±2.10
	Endive	204.40±27.68	237.20±26.13	70.00±30.48	90.00±24.09	31.20±9.58	34.80±4.64	27.60±5.15	34.00±6.60	75.60±28.06	78.40±21.43	9.49±2.58	9.59±1.15
10	Ant	101.33±18.18		30.67±13.32		26.40±5.41		28.27±4.65		16.00±10.25		7.48±0.52	
	Cricket	150.93±28.34	202.40±47.47	52.80±23.38	52.53±36.19	28.53±6.74	39.20±8.84	28.27±4.13	40.53±8.40	41.33±8.23	70.13±31.27	9.54±0.90	12.55±1.33
	Isopod	165.60±34.34	136.00±30.31	50.40±27.41	34.40±19.99	31.73±11.56	31.47±9.18	30.67±9.76	31.47±9.78	52.80±20.52	38.67±15.83	10.12±1.21	10.59±1.00
	Endive	200.80±33.54	254.57±61.80	97.33±27.28	98.29±69.95	24.53±2.56	34.00±9.38	27.73±5.55	37.71±14.01	51.20±19.78	84.57±21.10	8.24±1.41	9.17±2.07

Tot. transp. cycle, total duration of a transport cycle; dSO, duration slow open phase; dFO, duration of fast open phase; dFC, duration of fast close phase; dSC, duration of slow close phase; gd, gape distance.

observed, with the duration of the FO phase being longer for the transport of isopods than for crickets and endive. As food items covary in multiple characteristics, this result cannot be readily explained. A more detailed study where physical properties (e.g. size, hardness, mobility, etc.) are controlled one by one would be needed to tease apart the differential effects of size, hardness and evasiveness.

Besides the specific modulation of prey transport kinematics in all individuals, a remarkable feature of the results of our analyses is the significant food type by individual effect, suggesting that each individual responds differently to different food types. This may suggest that different feedback pathways or sensory modalities are used for the modulation of the prey transport event. Our data from the nerve transection experiments appear to corroborate this.

The role of lingual sensory feedback

Our data suggest that elimination of lingual sensory feedback in *P. vitticeps* affects prey transport kinematics. Remarkably, each individual responded differently to the transection of the trigeminal nerve, indeed suggesting that different feedback pathways or sensory modalities may be more important during prey transport in certain individuals than in others. In agamid lizards two potential lingual feedback pathways exist, one by means of the lingual ramus of the mandibular branch of the trigeminal nerve and one by means of the glossopharyngeal nerve. We decided to focus on the sensory branch of the mandibular ramus of the trigeminal nerve as this branch innervates the anterior half of the tongue that comes into close contact with the food item during prey capture and transport.

The most striking differences we found after transection were an increase of total transport cycle duration, an increase of the duration of the slow closing phase, differences in maximal gape distance during transport of crickets and isopods and a decrease of the durations of fast opening phases during transport of crickets and endive. Changes in durations of total transport cycles, durations of the different phases and gape distances were predicted as the animals are apparently lacking the necessary information about their food item to appropriately control the movements of jaws and tongue. Moreover, significant food type by transection effects strongly suggest that in addition to sensory information about the food item fed back by the trigeminal nerve, other cues (e.g. glossopharyngeal nerve) play an important role in modulating prey transport kinematics. In most amphibians and reptiles investigated to date, this seems to be the case (e.g. Anderson, 1993; Anderson and Nishikawa, 1993; Anderson and Nishikawa, 1996; Deban, 1997; Valdez and Nishikawa, 1997; Deban and Dicke, 1999; Deban and Dicke, 2004; Schaerlaeken et al., 2007) (but see O'Reilly, 2000).

In summary, our data suggest that agamid lizards are capable of modulating their prey transport kinematics in response to different food types with different food type characteristics. This allows the animals to utilize a broad variety in food resources. Remarkably, the specifics of modulation were different for each individual, suggesting that different individuals may rely on different sensory modalities to a different degree. Additionally, lingual sensory feedback by means of the trigeminal nerve is probably important during prey transport but this sensory afferent is clearly not the only source of information used to modulate prey transport, as animals still responded differently to different food items after transection. Further experiments controlling single food item properties at a time and including dual transection of the trigeminal and glossopharyngeal nerve are needed to better understand the modulation of feeding kinematics in lizards.

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