Kinematic analysis of tongue movements during chemosensory behaviour in the European green lizard, *Lacerta viridis* (Reptilia: Lacertidae)

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Received May 28, 1991
Accepted March 17, 1992

GOOSSE, V., and BELS, V. L. 1992. Kinematic analysis of tongue movements during chemosensory behaviour in the European green lizard, *Lacerta viridis* (Reptilia: Lacertidae). Can. J. Zool. **70**: 1886–1896.

High-speed cinematography (100 frames/s) was used to allow quantitative analysis of the kinematic profiles of tongue and jaw displacements during chemosensory activities in the scleroglossan lizard *Lacerta viridis*. The types of tongue flicking were simple downward extensions (SDE), single oscillations (SOC), and submultiple oscillations (SMOC) of the tongue out of the mouth. The SMOC type involves a downward or upward movement of the tongue performed before a typical oscillation and it is therefore suggested that this is an intermediate category of flick between the typical SOC and MOC of lizards. Closing and opening of the mouth in SDE, SOC, and SMOC cycles may or may not be separated by a stationary stage during which the jaws are held open at a constant gape. The duration of this stationary interval increases from SDE to SMOC. Gape cycles do not show any division into slow and fast stages. The gape is produced largely by depression of the lower jaw; the upper jaw is slightly elevated by protrusion of the tongue. Patterns of correlation of kinematic variables depicting jaw and tongue movements differed between SDE, SOC, and SMOC. A principal component analysis shows that the three flick types overlap in a multivariate space constructed from the kinematic variables depicting jaw and tongue displacements. Overlap between SOC and SMOC categories is greater than that between SOC, SMOC, and SDE categories. The kinematic patterns of tongue displacement during SMOC in *Lacerta viridis* show similarities with those of MOC in other lizards and in snakes. Kinematically, the pattern of jaw and tongue displacements of *Lacerta viridis* during chemosensory activities shows similarities with those that occur during drinking and prey capture.

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Les mouvements des mâchoires et de la langue au cours des comportements d'exploration ont été étudiés chez un lézard scléroglosse, *Lacerta viridis*, à partir de films cinématographiques à grande vitesse (100 images/s). Trois types de darders de la langue sont exécutés : des extensions simples (SDE), des oscillations simples (SOC) et des oscillations sous-multiples (SMOC). Ce dernier type de darders comprend toujours un déplacement de la langue vers le haut ou vers le bas avant une oscillation simple; ces caractéristiques semblent indiquer qu'il s'agit d'une catégorie intermédiaire entre une oscillation simple (SOC) et une oscillation multiple (MOC) typique. L'ouverture et la fermeture des mâchoires au cours des trois types de projection ne présentent pas de division en phases lente et rapide et sont parfois séparées par une pause dont la durée augmente de l'extension simple à l'oscillation sous-multiple. L'angle d'ouverture de la gueule dépend surtout de l'abaissement de la mandibule; la mâchoire superieure est légèrement soulevée par la poussée de la langue. Les corrélations entre les variables cinématiques reliées à la langue et aux mâchoires diffèrent selon qu'il s'agit d'extensions simples, d'oscillations simples ou d'oscillations sous-multiples. Une analyse en composantes principales a démontré que les trois types de projection de la langue se chevauchent dans une espace multivarié créé à partir des variables cinématiques décrivant les mouvements de la langue et des mâchoires. Le chevauchement des oscillations simples et des oscillations sous-multiples est plus important que le chevauchement de ces deux types de mouvements et des extensions simples. Les déplacements de la langue au cours des oscillations sous-multiples de ces lézards ont des similitudes avec ceux des oscillations multiples d'autres lézards et de serpents. Enfin les mouvements des mâchoires et de la langue qu'utilise *Lacerta viridis* au cours de ses activités d'exploration sont semblables à ceux qu'il utilise pour boire ou capturer des proies.

Introduction

Chemoreception is a widespread form of communication among vertebrates. But squamates are unusual among tetrapods in using simultaneous cyclic movements of the hyolingual system and jaws during chemosensory activities by means of which chemicals are carried to the vomeronasal organ. In snakes, the key role of the tongue is to collect molecules from the substratum or the air and transfer them to the buccal floor. After tongue retraction, the buccal floor may be elevated and the "vomodors" (Cooper and Burghardt 1990) enter into contact with the ducts of Jacobson's organ (Halpern and Frumin 1979; Halpern and Kubie 1980; Gillingham and Clark 1981; Young 1990). So far, however, there has not been a complete study of the functional mechanism of the connection between tongue, jaw, and buccal floor displacements and stimulation of the vomeronasal organ by the odours transmitted by the tongue. For instance, Graves and Halpern (1989) showed that the tongue is not required for transferring chemicals to Jacobson's organ when snout contact occurs.

By means of cinematographic analysis (24 frames/s) of the boa, *Constrictor constrictor*, Ulinski (1972) describes the temporal vertical displacement of the tongue as a "flick cluster," which is a protrusion of the tongue followed by a variable number of upward and downward movements (oscillation phase) completed by retraction. A flick cluster is composed of several flicks, each defined as a movement of the snakes's tongue that does not cross the horizontal plane (Ulinski 1972, p. 375). Based on tongue displacements filmed at the same rate, 24 frames/s, Gove (1979, p. 62) defines a tongue flick as "the movements of the tongue from its appearance outside the mouth until its complete withdrawal. This corresponds to the tongue-flick cluster of Ulinski (1972)," and describes three tongue-flick categories in lizards and snakes: simple downward extension (SDE), single oscillation (SOC), and multiple oscillation (MOC). SDE, the simplest tongue flick, does not include an oscillation phase between protraction and retraction of the tongue, and is performed by all squamates. During SOC and MOC, a complex oscillation phase occurs between pro-

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traction and retraction in which the tongue moves horizontally and vertically and thus crosses the horizontal plane a variable number of times (once for SOC and more for MOC). Oscillation is defined by Gove (1979) as "a component of a tongue-flick which consists of one upward and downward swing of the tongue as seen from the side. During oscillation, the tongue usually crosses the midline of the profile of the animal." The single oscillations (SOC) are performed by all snakes and scleroglossan lizards, multiple oscillations are common in snakes and rare in the lizards that Gove (1979) studied. Multiple oscillations (MOC) are common in "advanced" snakes and very rare in lizards. In lizards, this last tongue-flick type was observed only in some anguids and scincids. Gove (1979) hypothesizes that chemosensory behaviours in squamates evolved from the motor patterns involved in drinking behaviour, and speculates that the multiple oscillation category (MOC) arose independently in lizards and snakes.

Ignorance of detailed kinematic profiles seriously hinders understanding of the evolution of the chemosensory motor patterns of reptiles. Gove's paper (1979) is the only study of tongue-flicking behaviour patterns in lizards. To date, virtually no quantitative studies of the kinematics of tongue flicking have been conducted in reptiles. These data are, however, critical for comparing the process of collecting chemicals during the different types of tongue-flicking behaviour. Such data make it possible (*i*) to test the hypothesized transition from drinking movements to chemosensory movements of the tongue (Gove 1979), and (*ii*) to suggest an evolutionary relationship between the different types of tongue flick.

In this study, we used high-speed cinematography (100 and 200 frames/s) to analyse the motor-action pattern of tongue-flicking behaviours in a scleroglossan lizard (Estes et al. 1988), *Lacerta viridis*. The movements of the tongue and the jaw apparatus are used to suggest an evolutionary relationship between the different tongue-flick categories as well as possible transformations from drinking or feeding behaviours to these chemosensory activities.

Methods

Study animals and their maintenance

Kinematic data were obtained from six adult (snout–vent length 110.5 ± 6.5 mm; this and subsequent values are given as the mean ± standard deviation) European green lizards, *L. viridis*, from France (the area near Montpellier and the Vendée). Each specimen was housed and filmed in a 100 × 40 × 40 cm cage, at room temperature fluctuating between 18°C (night) and 22°C (day). Photoflood lights (100 W) provided a warmer area in each cage (temperature range 28–30°C). Food (living crickets and mealworms dusted with vitamins) and water were provided ad libitum.

Experiments

Thirty-three flicking sequences were filmed from three views: lateral (N = 27), ventral (N = 5), and front (N = 1). Tongue flicks were cinematically recorded on Kodak 16-mm colour film at a rate of 100 (N = 28) and 200 (N = 5) frames/s, using a Photosonic 1 PL camera fitted with an Angénieux zoom lens, under two 1000-W tungsten photoflood lights. The filmed tongue flicks occurred during exploratory and foraging (searching for crickets) activities.

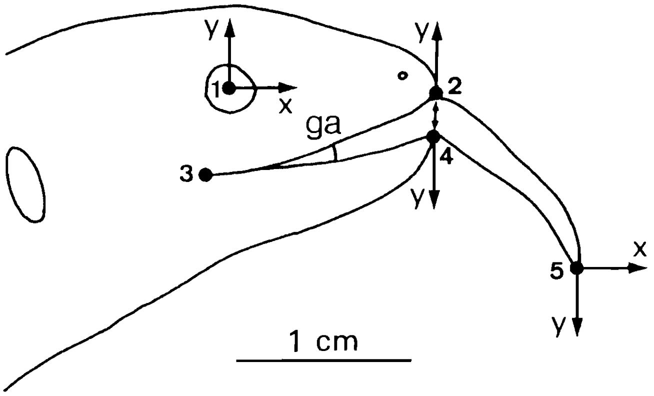

FIG. 1. Positions of the five points digitized to obtain the kinematic variables measured from film frames of chemoreception in *Lacerta viridis*. Point 3, corresponding to the commissure, was very difficult to digitize accurately. *ga*, gape distance; *x*, horizontal coordinates; *y*, vertical coordinates.

All recorded sequences were studied using an Old Delft or Eiki cine projector; only the lateral views were selected for constructing quantitative kinematic profiles. These sequences were studied by digitizing selected points on the skull, mandible, and tongue by means of a graphic table (Agmee, Ulg) and a Copam AT or IBM microcomputer. For each sequence, frame 1 was defined as the frame preceding the first frame in which the mouth begins to open. To standardize the analysis and facilitate comparison with previous results obtained on feeding behaviours in *L. viridis* (Bels and Goosse 1990), the following method was used. For each frame, the horizontal (X) and vertical (Y) components of five points were digitized (Fig. 1). The digitized data were stored as a series of bipolar coordinates in a data file corresponding to each sequence analysed. A set of computer programs developed in the Laboratory of Functional Morphology, University of Liège (V. Bels, P. Theate, M. Rinné), was used to analyse the permanently stored raw data. The programs allowed us to simultaneously compute the coordinates of selected points with a resolution of 0.14 mm on the magnified frame (scale: 4–5 times the size of the original specimen), the length of the segments between two successive points, and the angles between two successive segments. For kinematic comparison, seven variables were analysed for each frame: movements (X and Y) of the eye, vertical movement (Y) of the upper jaw, vertical movement (Y) of the lower jaw, horizontal displacement (X) of the tongue tips, vertical displacement (Y) of the tongue tips, horizontal distance between the two tongue tips, and gape angle. The gape angle (in degrees) was measured in 23 lateral sequences when the position of the commissure (point 3 in Fig. 1) was digitized precisely. Displacement of the head may affect the measurements of the kinematic variables. Because distances X and Y between the eye and a reference point on the grid change slightly with time, X and Y displacements of the points on the upper jaw were used for describing the rotation of the neurocranium. X and Y displacements of the other digitized points were used directly for constructing kinematic profiles. All the variables are given in millimetres and plotted against time. Data are presented as means ± 1 SD of the mean (N = 20).

For comparing amplitude and duration of the kinematic variables of the tongue-flick types, 12 variables were measured: maximum gape angle, maximum elevation of the upper jaw, maximum depression of the lower jaw, maximum protrusion of the tongue, maximum vertical upward and downward movements of the tongue, total duration of the gape cycle, duration of jaw opening, duration of the stationary stage between jaw opening and closing, duration of jaw closing, maximum duration of tongue protrusion, and maximum duration of vertical upward and downward movements of the tongue.

Statistical analysis

In a first comparison of jaw movements during the different flick types, statistical analysis (Kruskal–Wallis one-way ANOVA) was conducted according to the procedure for a single-factor group (tongue-flick types) with a repeated measures design and was used to compare the durations (ms) and maximal gape angles (deg.) of all the categories of tongue flicks. Mann–Whitney U-tests of significance were used for comparisons between paired tongue-flick categories. The probability level for rejection of the null hypothesis was set at

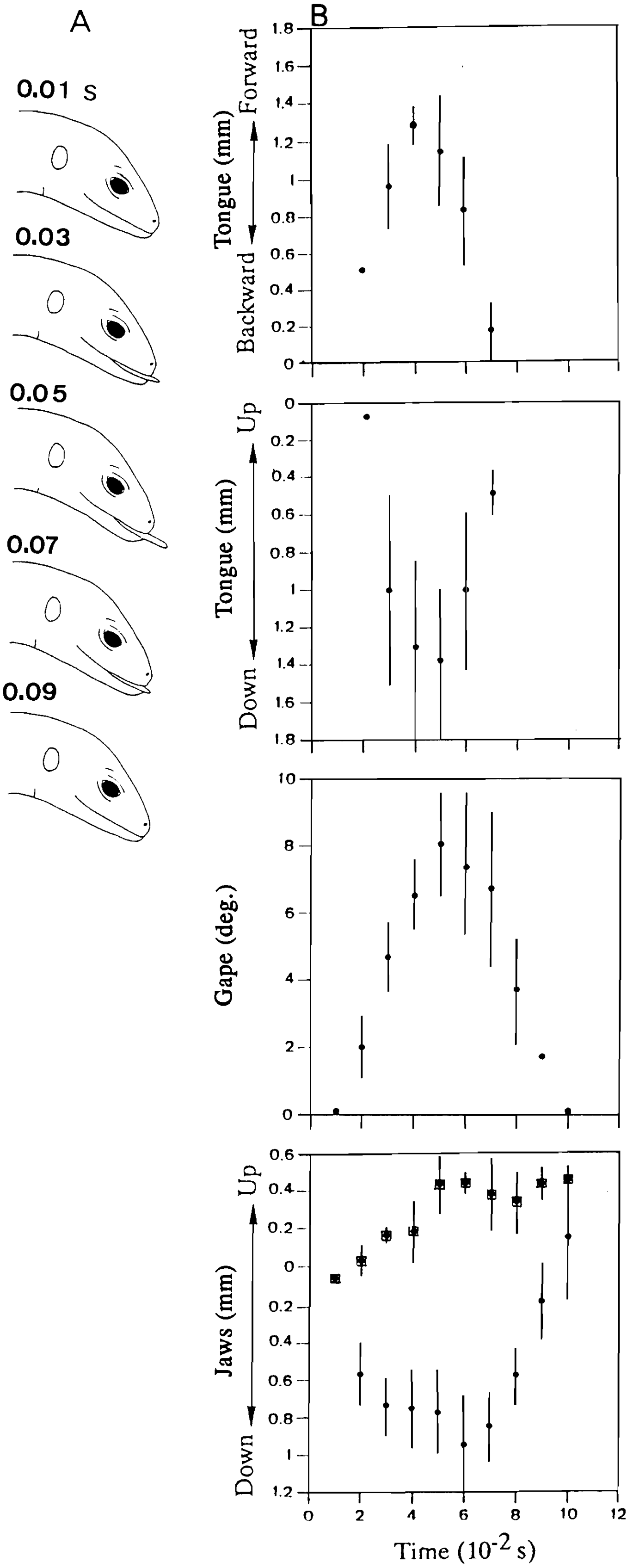

FIG. 2. (A) Five successive frames of a simple downward extension in a young *Lacerta viridis*. Each diagram corresponds to a frame; the time between two frames is 0.01 s. (B) Quantitative profiles for five variables describing the kinematics of simple downward extensions (SDE) in *Lacerta viridis*. Mean profiles (± standard deviation) are plotted against time for each variable. ▣, upper jaw; ●, lower jaw.

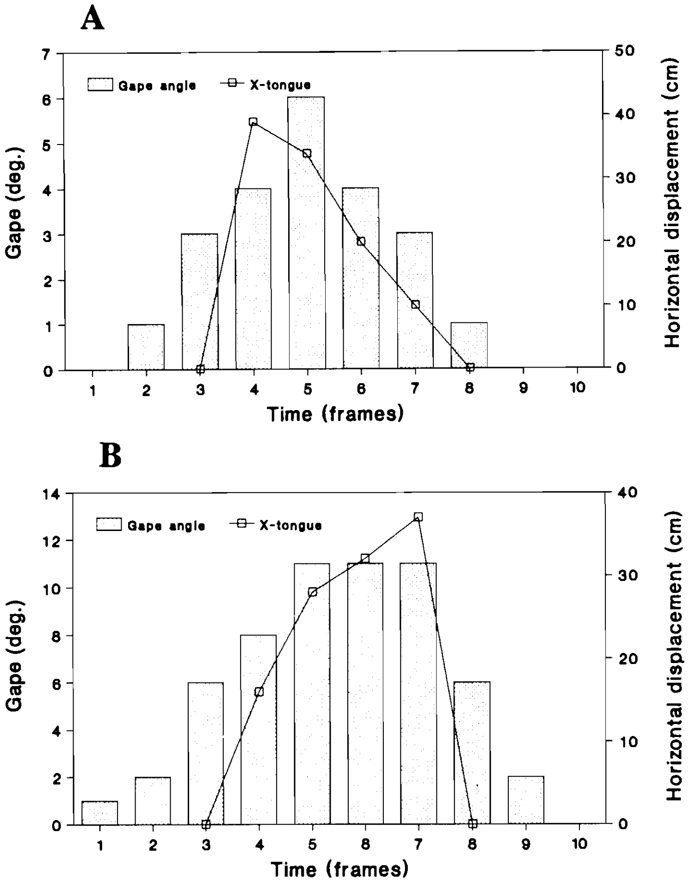

FIG. 3. Kinematic profiles of two simple extensions in *Lacerta viridis*. (A) The gape cycle does not include a stationary stage between opening and closing of the jaws. (B) The gape cycle includes a stationary stage. "X-tongue" denotes displacement of the tongue.

TABLE 1. Kinematic variables depicting jaw and tongue displacement during simple extensions (SDE), simple oscillations (SOC), and submultiple oscillations (SMOC) in *Lacerta viridis*

	SDE	SOC	SMOC
GA (deg.)	8.2±1.8	8.4±3.4	10.5±1.9
TD (s)	0.12±0.03	0.27±0.08	0.21±0.05
UJE (mm)	0.33±0.2	0.44±0.42	0.54±0.38
LJD (mm)	1.1±0.5	1.8±1.3	1.6±0.5
TLJD (s)	0.05±0.02	0.12±0.07	0.10±0.04
JLJE (s)	0.05±0.01	0.10±0.04	0.08±0.02
TP (mm)	7.8±5.4	20.9±8.5	24.3±11.9
TTP (s)	0.07±0.02	0.08±0.03	0.09±0.04
TVD (mm)			
Upward	—	2.3±1.4	2.1±0.1
Downward	2.0±1.2	7.1±3.2	6.55±2.8
TTVD (s)			
Upward	—	0.11±0.05	0.09±0.03
Downward	0.07±0.02	0.15±0.04	0.13±0.03
TSS (s)	0.02±0.01	0.07±0.03	0.06±0.03

NOTE: Values are given as the mean ± SD. GA, gape angle; LJD, maximum lower jaw depression; TD, total duration of the gape cycle; TLJD, time to maximum lower jaw depression; TLJE, time to maximum lower jaw elevation; TP, maximum tongue protrusion; TSS, time of stationary stage; TTP, time to maximum tongue protrusion; TTVD, time to maximum vertical displacement of tongue, TVD, maximum vertical displacement of tongue; UJE, maximum upper jaw elevation. During SOC and SMOC, maximum vertical displacements of the tongue are either downward or upward.

TABLE 2. Correlation matrix for the 11 kinematic variables measured from the chemosensory behaviours SDE, SOC, and SMOC in *Lacerta viridis*

Variable	GA	TD	TLJD	TSS	TLJE	UJE	LJD	TP	TTP	TVD*	TTVD
GA	—	0	0.59	0.12	−0.14	−0.18	0.38	−0.10	0.44	0.20	0.44
TD	0.75	—	−0.25	0.89	−0.18	−0.58	0.37	0.99	0.86	0.91	0.86
TLJD	0.61	−0.97	—	−0.48	0.70	−0.39	0.73	−0.36	0.21	0	0.21
TSS	−0.12	−0.72	−0.85	—	−0.59	−0.27	0.17	0.91	0.74	0.76	0.74
TLJE	0.64	−0.99	0.98	−0.79	—	−0.41	0.65	−0.23	0	−0.06	0
UJE	0.87	0.92	0.80	−0.42	0.88	—	−0.90	−0.46	−0.64	−0.82	−0.64
LJD	0.71	0.87	0.90	−0.70	0.82	0.70	—	0.24	0.62	0.62	0.62
TP	0.83	0.64	0.62	−0.28	0.53	0.58	0.88	—	0.80	0.84	0.80
TTP	0.10	−0.58	−0.71	0.92	−0.69	−0.31	0.42	0.04	—	0.87	1.00
TVM*	0.17	0.60	0.76	−0.85	0.63	0.26	0.78	0.52	−0.72	—	0.87
TTVM	0.38	0.84	0.92	−0.93	0.88	0.63	0.81	0.46	−0.77	0.73	—
GA...	—	−0.50	−0.37	−0.20	−0.42	−0.30	−0.38	0.66	−0.39	−0.31	−0.32
TD		—	0.88	0.20	0.75	0.08	0.21	0.56	0.64	0.07	0.79
TLJD			—	−0.16	0.59	0.11	0.13	0.34	0.49	0.19	0.78
TPA				—	−0.14	0	0.12	0.31	0.26	−0.04	0.21
TLJE					—	0.10	0.15	0.52	0.63	0.03	0.49
UJE						—	−0.65	0.64	0.08	0.79	−0.15
LJD							—	−0.08	0.42	0.37	0.27
TPP								—	0.54	0.36	0.25
TTP									—	0.18	0.69
TVD*										—	0
TTVD											—

NOTE: Correlations above the diagonal are for the SDE sequences only. Correlations below the diagonal are for SOC sequences only. The last set of data is for SMOC sequences only. For the entire data set, correlations above 0.60 are significant at $P < 0.05$. See Table 2 for variable codes.

*The peak vertical movements of the tongue selected for this analysis were those with the highest values.

$P \leq 0.05$ for both tests. To examine the relationships between the 13 variables depicting the amplitude and duration of jaw and tongue movements obtained from the kinematics of the tongue-flick types, a correlation matrix was performed. A principal component analysis was performed on the correlation matrix for the data set of each tongue-flick type to test the *a priori* expectation that the flick categories are not kinematically separated. Eight of the 13 variables, accounting for 30% of the five principal axes for each flick type, were then selected to explore the relationship between tongue-flicking behavioural motor patterns in a multivariate kinematic space.

Results

Contrary to Gove's evidence (1979) for lacertids, more than two tongue-flick categories were found in *L. viridis*. In fact, three types of tongue flicks were observed: simple downward extensions (SDE), single oscillations (SOC), and submultiple oscillations (SMOC).

Simple downward extensions

This type of tongue flick consisted of protrusion of the tongue, which remained straight, followed by rapid retraction (Fig. 2A). The tongue did not touch the substratum every time. The head was always oriented to the substratum and did not move during the tongue movements (Fig. 2A). The SDE jaw cycle was composed of two phases, opening and closing (Fig. 2B), separated by a short, variable pause in 60% of the cases (Fig. 3; stationary phase), highly correlated with the duration of the cyclic movement (Table 2). Gape opening was thus not divided into slow opening (SO) and fast opening (FO). Opening (TLJD) and closing (TLJE) phases of the lower jaw cycles were not correlated with the total duration (TD) of the cycle (Table 2). Depression of the lower jaw (LJD) was the dominant component of the gape cycle, elevation of the upper jaw (UJE) being less pronounced (Fig. 2B). The maximum vertical displacement of the upper jaw was 30−50% of the maximum vertical depression of the lower jaw (Table 1). The jaws opened 0.02 ± 0.01 s before tongue protrusion (Fig. 2B). There was no oscillation phase for the tongue, as shown by the high correlation between the time to maximum tongue protrusion (TTP) and vertical movement (TTVD) (Table 2). Maximum horizontal protrusion of the tongue (TP) was also highly correlated with its maximum vertical downward movement (TVD) and with maximum gape angle (GA).

Single oscillations

This type of tongue flick consisted of protrusion followed by oscillation of the tongue, corresponding to the oscillation phase described by Ulinski (1972) and oscillation as described by Gove (1979), and terminated by its retraction. Unlike SDE, the opening (TLJD) and closing (TLJE) phases of the lower jaw were highly correlated with the duration of the cycles (TD) and movements of the tongue, but less correlated with the duration of the stationary phase (TSS) than SDE (Table 2). During the tongue-protrusion phase of SOC, the tongue curved upward and then swung downward, touching or not touching the substratum. The tongue tips flexed downward during their retraction stage (Fig. 4). The gape was mainly produced by depression of the lower jaw (LJD), as in SDE (Fig. 5), which was correlated with the tongue movements (Table 2). The downward vertical movement of the tongue influenced the elevation of the upper jaw ($r = 86$), but in general the maximum vertical movements of the tongue were not highly correlated with upper jaw elevation (Table 2). The maximum vertical downward flexion of the tongue occurred simultaneously with maximum lower jaw depression ($r = 78$), and after the maximum horizontal movement of the tongue (Fig. 5). The tongue was maximally protruded during its farthest point of its downward movement (Table 2).

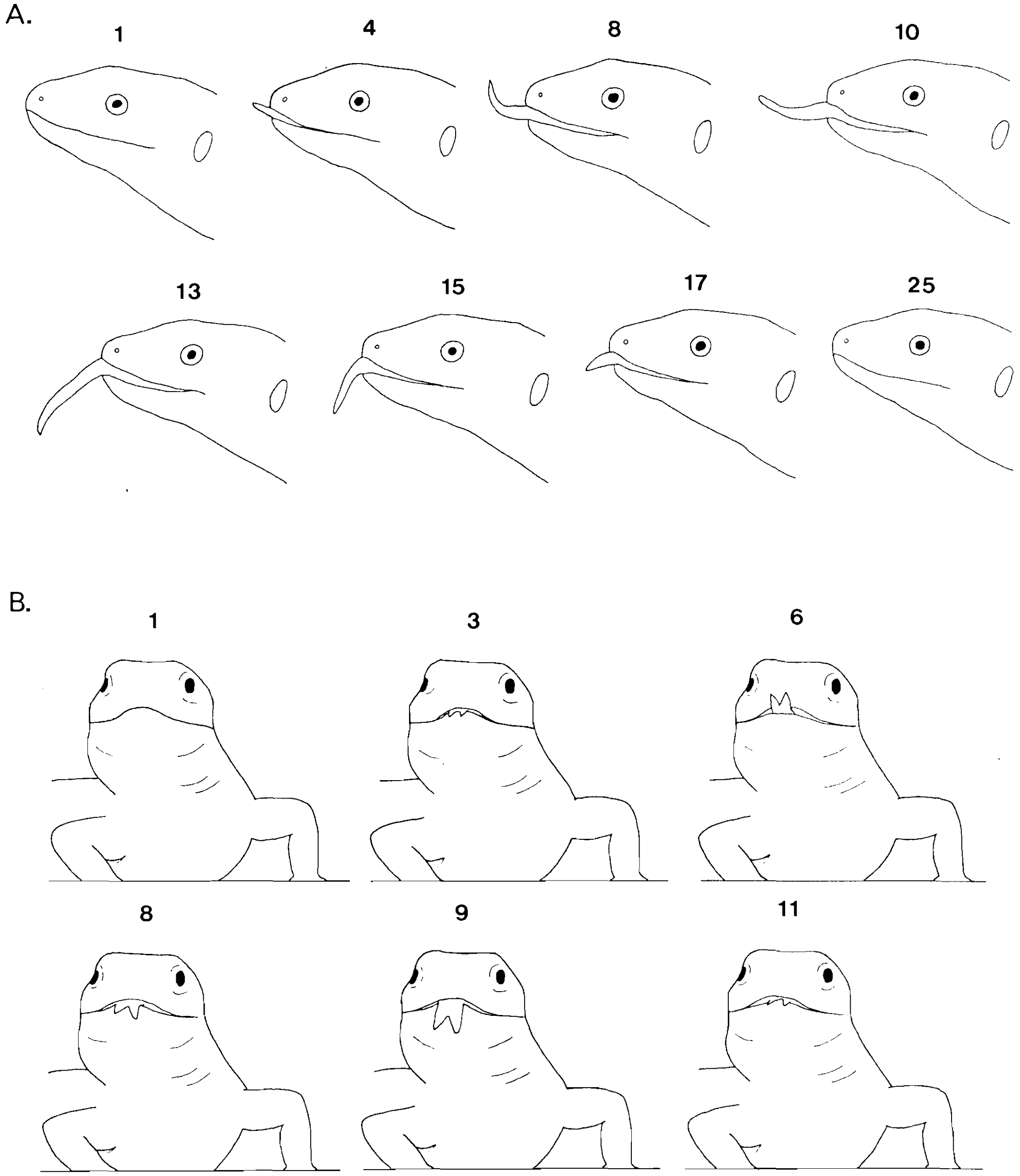

FIG. 4. (A) Eight successive lateral frames of a single oscillation in adult *Lacerta viridis*. (B) Six successive front frames of a single oscillation in adult *Lacerta viridis*. The horizontal mobility of the tongue tips is clear from frame 3 to frame 11. The numbers correspond to those of the frames. The time between two frames is 0.01 s.

Submultiple oscillations

The type of tongue flick consisted of protrusion followed by upward or downward vertical tongue displacement preceding a single oscillation and terminated by retraction. As in SDE and SOC, the gape profiles were typical opening and closing curves lacking SO and FO stages, separated by a stationary phase in 60% of cases (Fig. 6). Depression of the mandible (LJD) was the dominant component of gape increase (GA), and maximum upper jaw elevation (UJE) and depression of the lower jaw (LJD) were correlated with maximum tongue protraction (TP) (Table 2). As in SOC, the opening (TLJD) and closing (TLJE) phases were correlated with the duration of the cyclic movements (Table 2), but both jaws participated variably at each stage, as shown by the low correlation between jaw vertical displacement (LJD) and the duration of the phases (TLJD, TLJE) (Table 2). The maximum forward extension of the tongue occurred just before maximum opening of the jaws. Vertically, each tongue cycle started with a slight movement oriented upward (type 1) or downward (type 2). This semicyclic movement was always performed before maximum horizontal protraction of the tongue. In most sequences of type 1 (33% of SMOC sequences) the tongue did not cross the horizontal plane between the two successive upward movements, whereas it crossed this plane twice in type 2 (Fig. 6). In type 1, downward movement of the tongue closely followed maximum gape opening. At the end of retraction, the tongue tips curled posteriorly around the mandible. Therefore, the tongue movement involved one forward and one rearward horizontal maximum before complete retraction. In type 2, the horizontal movement of the tongue was monotonous. In both types the maximum downward movement of the tongue was correlated with its maximum protrusion (r = 0.66).

The tongue-flick categories were significantly different in duration (Kruskal–Wallis one-way ANOVA, F = 14.33, $P \leq$

0.05). The duration of the gape cycles increased significantly from SDE to SMOC (Table 3). The presence of an oscillation phase thus significantly increased the duration of tongue flicks (Table 2). The duration of tongue-flick cycles involving an oscillation phase is rather similar to that of drinking-movement cycles, which also involve oscillatory displacement of the tongue. In contrast, SDE is shorter and its duration is close to that of prey capture, which does not involve use of the tongue (Fig. 7). The gape angles were not significantly different among all the tongue-flick categories (Kruskal–Wallis one-way ANOVA, $F = 5.05$; $P = 0.17$), and the amplitude of the gape during the three chemosensory behaviours was less than during prey capture (Bels and Goosse 1990).

In the principal component analysis, the five principal axes accounted for 56.3, 19.8, 9.8, 6.4, and 4.1% of the total variance (Table 4). The first principal component was positively correlated ($P \leq 0.05$) with variables depicting the durations of the jaw-movement cycles (TDE, TLJD, TLJE) and the amplitudes of the movement (Table 4). A plot of the factor scores of the SDE, SOC, and SMOC movements on the first two principal components reveals a large overlap between the behaviours in the multivariate kinematic space, particularly for SOC and SMOC (Fig. 8).

Discussion

Previous studies of tongue movements during chemoreception in squamates, based on standard filming techniques (24 frames/s), provided behavioural data such as flick duration, relative areas scanned by the tongue, and frequencies (Ulinski 1972; Gove 1979). By means of high-speed (200 and 100 frames/s) kinematic analysis, we documented more variability in the flicking movements of lacertids than was described by Gove (1979), who observed only two categories of flicks (SDE and SOC) in *Lacerta pityusensis*. *Lacerta viridis* performs not only SDE and SOC but also a third category, here called SMOC (Figs. 2, 5, and 6). According to the definition of Gove (1979), a tongue flick involving one oscillation (SOC) is characterized by two maxima (one upward and one downward), and a flick involving several oscillations (MOC) by an even number of maxima. Gove (1979) states: "During an oscillation, the tongue usually crosses the midline of the profile of the animal." SMOC type 1 may be viewed as an MOC involving two oscillations, but SMOC type 2 does not fall easily into Gove's definition. Furthermore, Gove (1979) states: "However, the lizards exhibit a different pattern than snakes. There is no successive increase in relative area during tongue-flick and no significant difference between the relative area means of succeeding oscillations. The relative area of the second oscillation is smaller than that of the first in all three lizards observed. This can be explained by the observation that in tongue-flicks with only two oscillations, the second had a much smaller relative area than the first; it was almost a lip-licking action and did not touch the substrate." For snakes, Gove also includes very different flicking behaviours (circle tongue flick, rigid extension of the tongue, and slow-motion tongue flick) in the multiple-oscillation category. For lizards, at least, we suggest restricting the mulitple-oscillation category to successive repetitions of complete oscillations, with the tongue passing through the horizontal plane, as in Ulinski's (1972) definition of a flick, or the midline of the profile of the animal, as utilized by Gove (1979). All other flick patterns should be classified in a more variable category, submultiple oscillation called (SMOC).

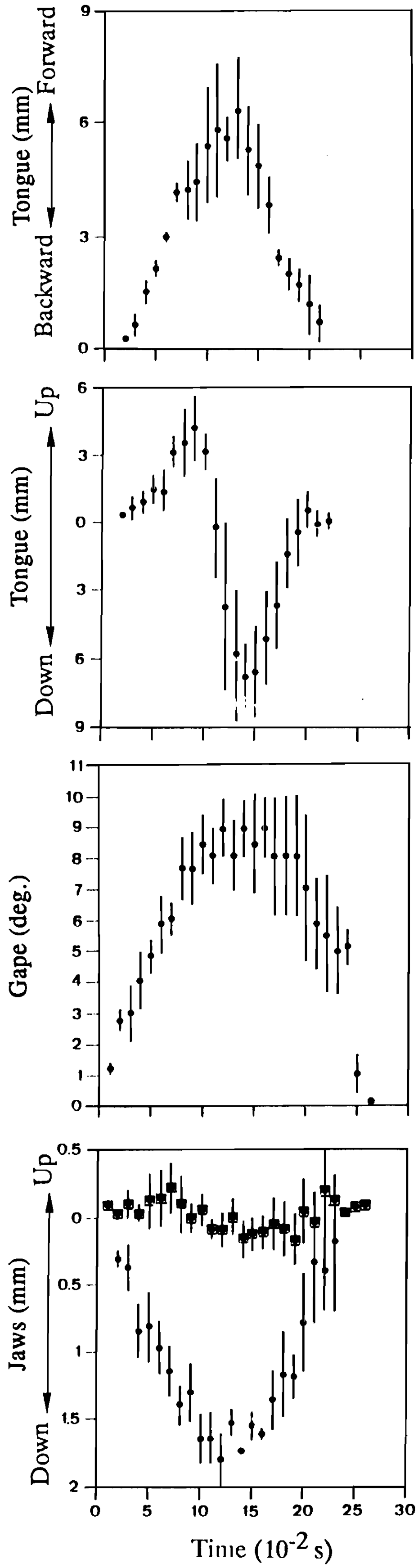

FIG. 5. Quantitative profiles for five variables describing the kinematics of five single oscillations in *Lacerta viridis*. Mean profiles (± standard deviation) are plotted against time for each variable. ■, upper jaw; ●, lower jaw.

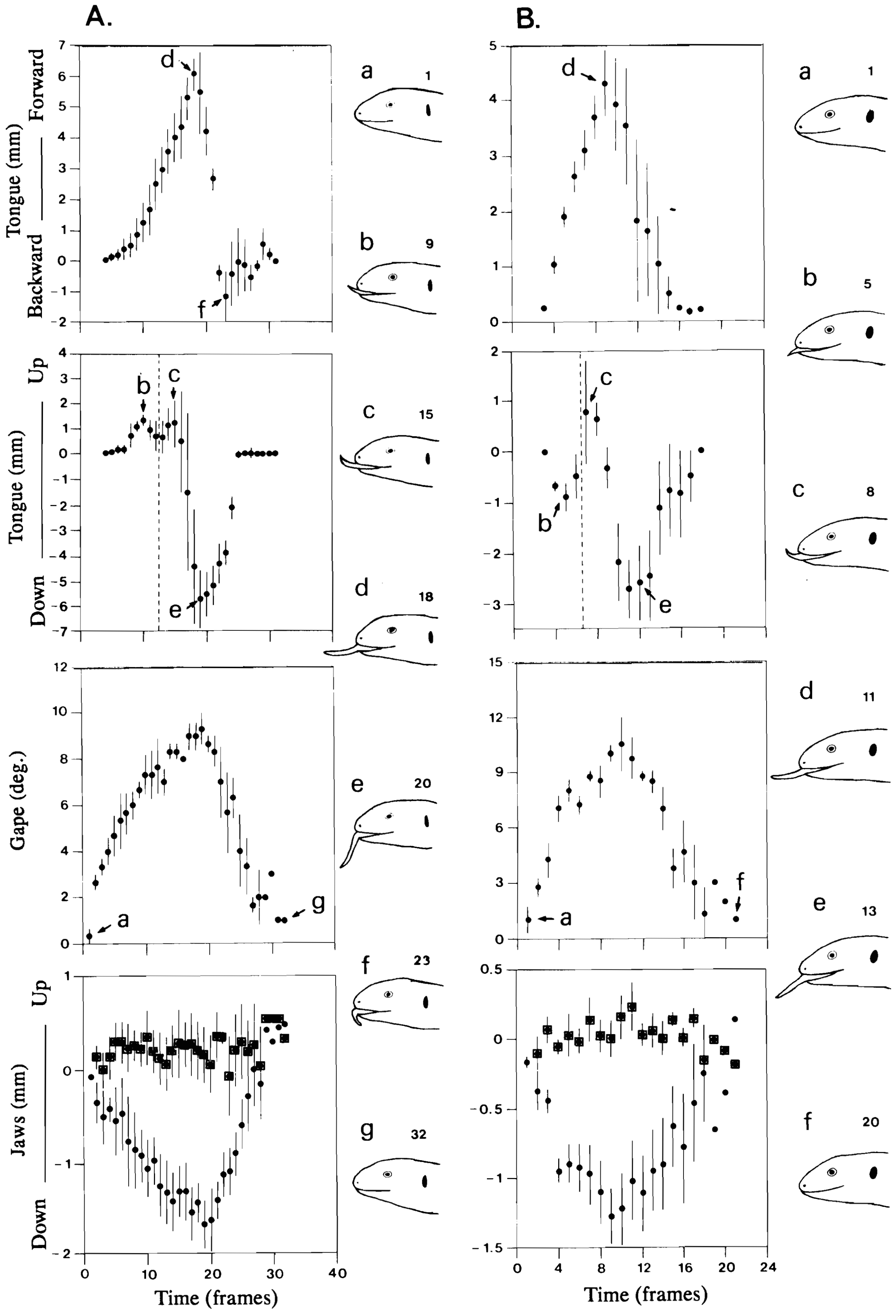

FIG. 6. Mean kinematic profiles for five variables of submultiple oscillation in *Lacerta viridis*. (A) Type 1. (B) Type 2. The successive drawings (*a*–*g*) of the lizard head illustrate the movements of the tongue. Numbers above the drawings are frame numbers. ▣, upper jaw; ●, lower jaw.

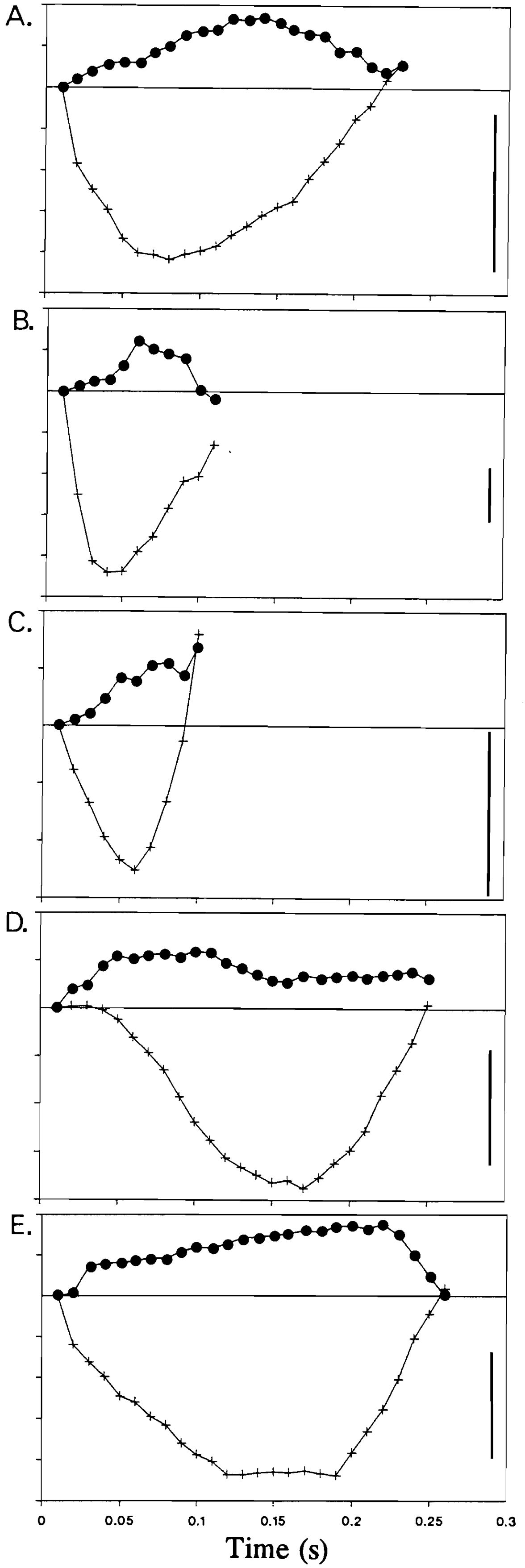

FIG. 7. Comparative kinematics of the generalized cyclic movements of the jaw in drinking (A), feeding (B), SDE (C), and SMOC (E) behaviours. ●, upper jaw, +, lower jaw.

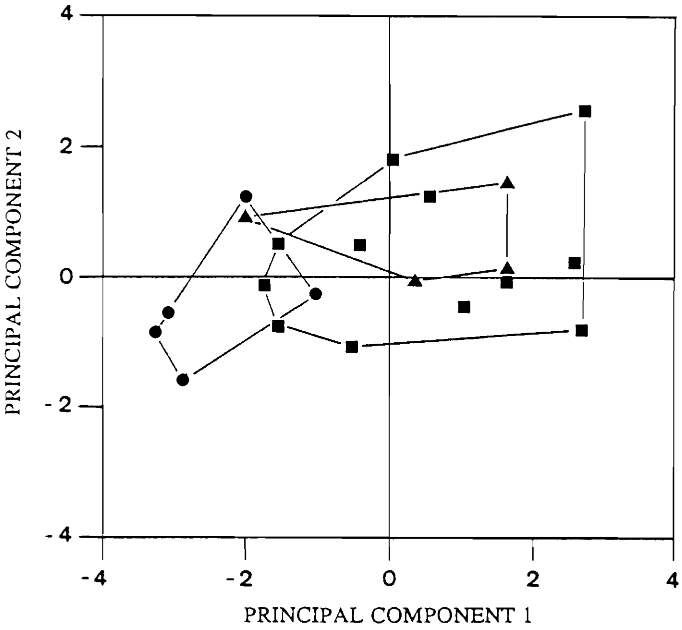

FIG. 8. Plot of the positions of SDE (●), SOC (▲) and SMOC (■) along the first two principal components in the analysis performed on the correlation matrix of eight kinematic variables.

By definition (Ulinski 1972; Gove 1979), flick types 1 and 2 of SMOC in *L. viridis* may be viewed as follows. Compared with a single oscillation, the additional maximum in type 1 of SMOC is a separated flick or an upward semicyclic movement of the tongue preceding a complete oscillation. In type 2 the tongue twice crosses the horizontal plane and complete tongue displacement thus comprises three successive flicks. Based on the kinematic profiles, the SMOC tongue displacements may be seen as intermediate (but not mutually exclusive) between the typical single-oscillation (SOC) and multiple-oscillation (MOC) tongue displacements described for some lizards (e.g., Scincidae and Anguidae) and Serpentes (Gove 1979). Only detailed electromyographic and kinematic analyses of flicking behaviours in squamates would allow us to hypothesize that (*i*) the MOC pattern sensu stricto is derived from the variable SMOC patterns in lizards and snakes, and (*ii*) that the SMOC patterns in *L. viridis* are species specific, or (*iii*) such SMOC patterns are not restricted to *L. viridis* and may be used by other lacertids or scleroglossans (Fig. 9).

Gove (1979) hypothesized that multiple oscillations (MOC) arose independently in snakes and lizards because these flick categories are kinematically different in lizards "which are not closely related to snakes" (Gove 1979, p. 72). The kinematic differences are that (*i*) the amplitude of successive flicks increases in snakes and decreases in lizards, (*ii*) the tongue slightly retracts between two successive oscillations in lizards, and (*iii*) an upward swing always precedes the downward swing in lizards and primitive snakes, whereas the first swing is more variable in advanced snakes. The tongue movements of the submultiple category (SMOC) seem to vary considerably in *L. viridis*. Compared with MOC in other squamates, the amplitude of the successive vertical maxima of the tongue displacements in SMOC of *L. viridis* increases as in snakes, or the first maximum is greater than the second as in scincids and anguids (Fig. 6). Furthermore, the tongue never appears to retract between successive flicks in SMOC, and the first flick may be either upwardly or downwardly oriented (Fig. 6).

TABLE 3. Mean duration and maximum gape angle of tongue flicks by *Lacerta viridis*

		Duration (s)				Gape angle (deg.)			
	N	Mean	SD	*U*	*P*	Mean	SD	*U*	*P*
SDE	5	12.0	2.8			8.2	1.7		
SOC	5	25.8	7.6			8.4	3.3		
SMOC									
Type 1 (1)	5	25.6	5.5			10.0	0.7		
Tye 2 (2)	5	17.6	2.3			11.2	1.8		
SDE–SOC				2.54	<0.05			0.10	0.91
SDE–SMOC (1)				2.54	<0.05			1.55	0.11
SDE–SMOC (2)				2.23	<0.05			1.91	0.05
SOC–SMOC (1)				−0.94	0.34			0.42	0.67
SOC–SMOC (2)				2.01	<0.05			1.26	0.20
SMOC (1)–SMOC (2)				2.12	<0.05			−0.97	0.38

NOTE: The Mann–Whitney *U*-test was used for comparisons between tongue-flick types; the level of significance was $P < 0.05$. *N* is the number of flicks examined.

TABLE 4. Component loadings from a principal component analysis run on the correlation matrix shown in Table 2; entries are correlations of each variable with the first four principal components

Variable	PC1 (56.3)	PC2 (19.8)	PC3 (9.8)	PC4 (6.4)
Total duration (TD)	0.44	−0.08	−0.22	−0.20
Time to peak (TLJD) lower jaw depression	0.40	−0.35	−0.03	0.02
Time to peak lower jaw elevation (TLJE)	0.40	−0.31	−0.10	0.13
Time of stationary stage (TSS)	0.12	0.67	−0.25	−0.55
Peak lower jaw depression (LJD)	0.28	−0.04	0.81	−0.42
Time to peak tongue protrusion (TTP)	0.23	0.50	0.38	0.58
Peak tongue protrusion (TP)	0.37	0.27	−0.19	0.33
Peak tongue vertical movement (TVM)	0.44	0.02	−0.15	−0.10

NOTE: Numbers in parentheses show the percentage of total variance explained by each principal component.

*The peak vertical movements of the tongue selected for this analysis were those with the highest values.

The vertical orientation of the tongue during the first flick is therefore more variable for lizards than was described by Gove (1979), and some SMOC tongue flicks are similar to MOC in advanced snakes. Actually, the kinematic pattern of SMOC in *L. viridis* may be related to those of MOC in other lizards as well as in snakes. Kinematically, the patterns of SMOC may merge into the pattern of MOC through slight modifications in the vertical displacements of the tongue. For instance, adding or increasing a downward displacement of the tongue between the two upward maxima in SMOC type 1 will produce MOC involving two successive SOC.

Gove (1979) hypothesized that chemosensory behaviours evolved from SDE used in drinking, through SOC, to the MOC pattern involved solely in chemoreception. The comparative kinematic patterns of chemoreception and feeding or drinking movements allow us to support Gove's (1979) suggestions concerning (*i*) the possible origin of tongue flicks and (*ii*) the possible derivation of kinematic patterns of some tongue-flick categories from others.

During all the chemosensory activities, the gape profiles in *L. viridis* have a shape without SO and FO stages. Because the opening and closing stages are separated merely by a stationary stage, the duration of the gape cycle lengthens from SDE to SOC and SMOC. The kinematic profiles of the upper and lower jaws in the three types of tongue flicking are very similar to those of drinking (V. L. Bels et al. 1992) and prey capture (Bels and Goosse 1989). Furthermore, the chemosensory kinematic pattern of the opening–closing cycle of the jaws lacks an SO stage, like those episodes of prey capture that do not involve the tongue (Bels and Goosse 1990) and those of drinking that do involve the tongue (V. L. Bels et al. 1992). It differs completely from the kinematic profiles of prey-capture cycles in iguanian lizards, which involves the tongue (Schwenk and Throckmorton 1989; Bels 1990). Kinematically, at least, the movements associated with the transfer of chemicals in modern lizards may have evolved from an ancestral pattern associated with drinking, because prey capture does not involve use of the tongue. In *L. viridis*, the gape profiles of all flick types (SDE, SOC, and SMOC) are strongly dependent on lower jaw depression (Figs. 2, 5, and 6) just as in drinking, and tongue displacements during drinking may be similar to those involved in the three chemosensory behaviours (V. Goosse and V. L. Bels, in preparation). The gape amplitude in tongue flicking with an oscillation phase (Table 2) was modulated by tongue protrusion and the gape distance never exceeded the thickness of the tongue. The amplitude of the gape cycles during prey capture (Bels and Goosse 1989) is considerably larger than that of tongue flicks. On the other hand, the maximum length of the protruded tongue does not influence the amplitude of the SDE gape cycle (Table 2). SDE may be thus considered to be a flicking pattern permitting a very rapid scanning of a small area of the air by the tongue, as suggested by Gove (1979). In contrast, the presence of an oscillation phase, producing a larger movement and thus a greater scanning area, may have an important controlling feedback effect on jaw movements during SOC and SMOC behaviours, and the addition of flicks in SMOC increases the variability of certain jaw variables such as the duration of opening and closing (Table 3).

The tongue of the Iguania and Scleroglossa plays an important role in bringing environmental information (e.g., conspecific and congeneric recognition, exploratory activities) to the vomeronasal organ. Prey location and recognition involves some combination of cues, either exclusively or, in some cases, principally visual (Burghardt 1973, 1980; Flandes 1985; Harkness 1977; Nicoletto 1985*a*, 1985*b*; Simon et al. 1981). For instance, some scleroglossans (Scincidae) tongue flick in order to track prey when visual contact is lost or in the

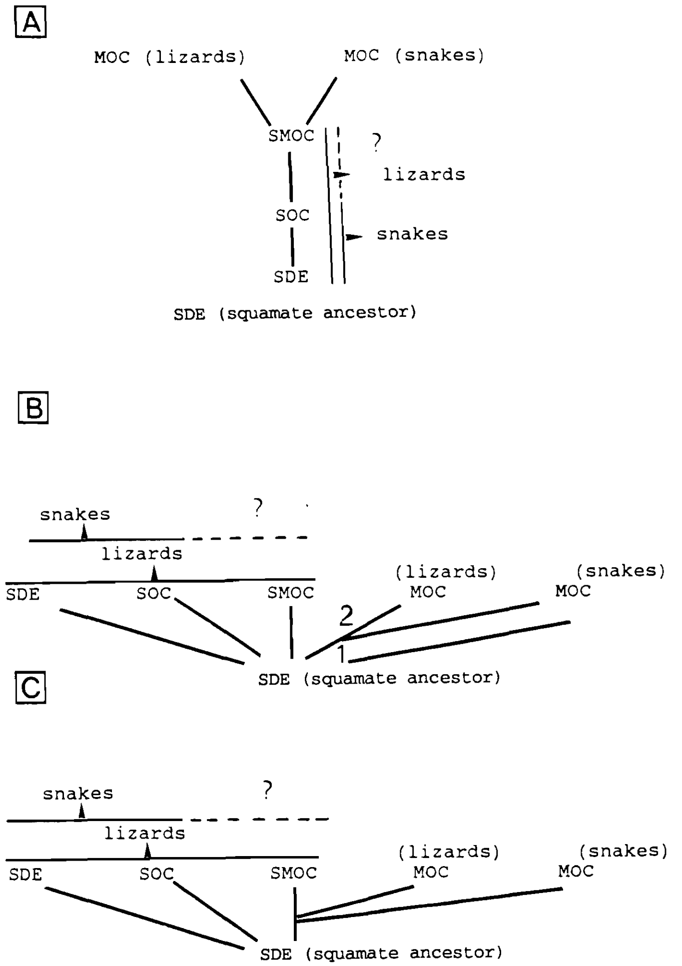

FIG. 9. Three possible (but not mutually exclusive) evolutionary relationships between tongue-flicking behaviours in Squamata. (A) The simple extension category (SDE) evolves through the single-oscillation (SOC) and submultiple-oscillation (SMOC) categories to the multiple-oscillation category (MOC), which arises independently in lizards and snakes. (B) The simple extension category (SDE) is the tongue-flicking behaviour considered to be the origin of all other categories. The multiple-oscillation category (MOC) arises independently (1) or not (2) in lizards and snakes. (C) The MOC category in lizards and snakes originates independently (or not) from the submultiple category (SMOC), involving highly variable tongue displacements in the ancestors of the lizards and snakes. The question marks indicate that, as in *Lacerta viridis*, SMOC has not so far been reported in snakes.

presence of a highly concentrated (''supernormal'') prey-chemical stimulus (Nicoletto 1985*b*). In addition, Cooper (1989) has recently shown that tongue flicks are an important means of locating and recognizing prey for varanoid lizards, as was previously suggested by Auffenberg (1981, 1988). The ancestors of both lizard sister-groups (Iguania and Scleroglossa) probably used all types of sensory cue to track prey, but visual and chemical cues may have played a dominant role. A diphyletic behavioural specialization in tongue use may have occurred during lizard evolution (Schwenk and Throckmorton 1989): the ancestors of the Iguania used the tongue mostly for prey capture and for drinking, and the ancestors of the Scleroglossa captured prey mainly with the jaws and used the tongue chiefly for drinking and chemoreception. Such behavioural evolution in tongue use may be associated with (*i*) the evolution of foraging activities (for a discussion see Cooper 1989), (*ii*) differences in the cues used for prey location and recognition, and (*iii*) modification of the jaws and tongue (for discussion see McDowell 1972). This proposed evolutionary modification in tongue use primarily affects the kinematic characteristics of the jaw apparatus as measured in modern species. In scleroglossans, the gape cycle during chemosensory behaviour does not include an SO stage.

In iguanians, the *preparatory phase* associated with an SO stage in the gape cycle would allow the lizard to ''aim one's tongue'' for optimizing prey capture with a protrusible tongue, as suggested by Schwenk and Bell (1988). Elongation of a free two-tipped tongue as described for scleroglossans should also improve the potential for detecting chemicals by scanning a larger area. Elongation and modification of the anterior region of the tongue may be viewed as a major morphological innovation related to chemoreception in scleroglossan lizards. An increase in the chemosensory function of the tongue is clearly demonstrated not only from iguanians to scleroglossans but also within scleroglossans: iguanians such as iguanids perform only chemosensory behaviour (SDE) (Goves 1979), whereas scleroglossans perform at least four types of tongue flicks (SDE, SOC, SMOC, and MOC). Among the scleroglossans, the frequency of tongue extrusions appears to be positively correlated with a greater bifurcation of the tongue tips (Bissinger and Simon 1979).

Finally, we note that the three flick types are interrelated in the multivariate space constructed from the kinematic variables for *L. viridis* (Fig. 8). The presence of an oscillation phase in SOC and SMOC could explain the separation between these flick types and SDE. The SOC polygon is included in the SMOC polygon, which is more extended along the two principal component axes because the kinematic variables of SMOC are more variable than those of SOC. From the correlation matrix, the interdependence between the jaw and tongue variables is different in SDE and SOC–SMOC movements (Table 2). An evolutionary transformation series may be hypothesized in which a fixed motor pattern, uninfluenced by tongue movement, is first modified into the tongue-dependent SDE cycle and finally into the much more variable motor pattern associated with SMOC.

Acknowledgments

We are extremely grateful to K. Kardong and G. Lauder for their critical reading of the manuscript and thank S. Renous for her interesting advice. We thank three anonymous reviewers for their helpful comments on an earlier draft of this paper. Part of the computer programs during this study was performed by P. Theate and M. Rinné. We thank J. P. Baron, J. Bons, C. Guillaume, P. Geneiz (licence N° 89-126) and G. Naulleau, who helped us to obtain the lizards. This project was partly supported by the grant Fonds de la Recherche Fondamentale Collective (Belgique, Communauté française) N° 2.9005.90.

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