RESEARCH ARTICLE

A gyroscopic advantage: phylogenetic patterns of compensatory movements in frogs

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ABSTRACT

Head and eye compensatory movements known as vestibulo-ocular and vestibulo-cervical reflexes are essential to stay orientated in space while moving. We have used a previously developed methodology focused on the detailed mathematical description of head compensatory movements in frogs without the need for any surgical procedures on the examined specimens. Our comparative study comprising 35 species of frogs from different phylogenetic backgrounds revealed species-specific head compensatory abilities ensuring gaze stabilization. Moreover, we found a strong phylogenetic signal highlighting the great ability of compensatory head movements in families of Pyxicephalidae and Rhacophoridae from the Natatanura group. By contrast, families of Dendrobatidae and Microhylidae exhibited only poor or no head compensatory movements. Contrary to our expectation, the results did not corroborate an ecomorphological hypothesis anticipating a close relationship between ecological parameters and the head compensatory movements. We did not find any positive association between more complex (3D structured, arboreal or aquatic) habitats or more saltatory behavior and elevated abilities of head compensatory movements. Moreover, we found compensatory movements in most basal Archeobatrachia, giving an indication of common ancestry of these abilities in frogs that are variously pronounced in particular families. We hypothesize that the uncovered proper gaze stabilization during locomotion provided by the higher head compensatory abilities can improve or even enable visual perception of the prey. We interpret this completely novel finding as a possible gyroscopic advantage in a foraging context. We discuss putative consequences of such advanced neuromotor skills for diversification and ecological success of the Natatanura group.

KEY WORDS: Anura, Ecomorphology, Compensatory movement, Locomotion

INTRODUCTION

Terrestrial vertebrates have to manage gaze stabilization during active or passive movement. The head and/or body movement is compensated by movements of the eyes and neck in order to prevent displacement of the retinal picture and visual degradation (Dieringer and Precht, 1982; Dieringer, 1995). Head compensatory movement is known to be the dominant mechanism of gaze stabilization (80%), with a limited contribution of movement of the eyes (Dieringer and Meier, 1994). Head and eye movements act together to achieve proper gaze stabilization, and both use the sensorial inner ear organs and anatomical substrate at the level of the vestibular nuclei in the brainstem. Vestibulo-ocular reflex (VOR) stabilizes the eye position in the head, so the gaze direction remains stable during head or body movements. The main efferent pathway of this reflex is fasciculus longitudinalis medialis, which connects the vestibular and oculomotor nuclei. Anatomy and physiology of this three-neuron reflex is alike in fish, frogs and cats, as revealed by experiments of Dieringer (1991), pointing to this system's great universality. Vestibulo-collic reflex (VCR; also known as the vestibulo-cervical reflex) adjusts the head position via the medial vestibulo-spinal tract (Goldberg and Cullen, 2011). VORs and VCRs are complementary and driven at low frequency (<0.1 Hz) by stimulation of otoliths and at higher frequencies by stimulation of semi-circular canals, disappearing following a canal destruction (Takemura and King, 2005). Deficits in prey capture due to VCR dysfunction following a labyrinth lesion in *Rana pipiens* were described by King and Straka (1998). For a detailed description of anatomical networks connecting vestibular sensors with oculomotor (VOR) and neck muscles (VCR) neurons, see the review by Uchino and Kushiro (2011). Gain of VCR is variable depending on a behavioral context and decreases with a predictable stimulation (Reynolds and Gdowski, 2008).

Increased complexity of surroundings requires an improvement in performance of both the VOR and VCR. Locomotor performance is linked to animal fitness such as foraging efficiency and escape from predators (Dickinson et al., 2000) and is expected to be under a strong selection. Hence, Dieringer (1991) suggested that locomotion is: "an important evolutionary driving force for the adaptation of the performance of these reflexes". We consider this idea as an ideal model for studies dealing with the ecomorphology of anurans.

The body plan of frogs, with their short tailless bodies, broad neckless heads and long muscular hindlimbs, is unique in tetrapods (Zug et al., 2001). The prevailing uniformity and morphological specializations are associated with, and likely evolved as, an adaptation for saltatory locomotion (Havelková et al., 2007; Přikryl et al., 2009; Jenkins and Shubin, 1998; Reilly and Jorgensen, 2011; but see Herrel et al., 2016). Despite this morphological specialization, numerous studies on anuran morphology, ecology and performance have corroborated the relationship between the habitat type, locomotion mode and morphology (Zug, 1978; Reilly and Jorgensen, 2011; Moen et al., 2013; Robovská-Havelková et al., 2014; Reilly et al., 2015, 2016; Manzano et al.,

2017). Such relationships are associated with ecological morphology (ecomorphology), which is a comparative discipline focused on the interaction of morphological and ecological diversity among organisms both in the present and over evolutionary time (Motta and Kotrschal, 1992). Some aspects of the inter-individual morphological variation may lead to functional and performance differences that result in differences in how these individuals use available resources. According to these assumptions, it can be causally linked to fitness (Garland and Losos, 1994). As ecomorphology becomes a framework for addressing adaptation, phylogenetic relationships among examined species should be considered (Harvey and Pagel, 1991). The whole discipline increased the conceptual advances after the incorporation of explicit phylogenetic hypotheses resolving the statistical dilemma of the nonindependence of characters for those taxa that share a trait due to common ancestry (Felsenstein, 1985; Losos and Miles, 1994; Revell, 2012).

Following the ecomorphological methodology comprising the morphological, functional, performance and comparative approach (Miles, 1994; Garland, 1994; Motta and Kotrschal, 1992; Birn-Jeffery and Higham, 2014), we presume that, in frogs, ecology and compensatory head movements are strongly related. The head compensatory movements were under various selective pressures in different habitats. Evolutionary history of such selection can be reconstructed from the current distribution of ecological, morphological and behavioral traits (Garamszegi, 2014; Herron and Freeman, 2014). We assume a positive association between a more complex (3D) habitat as well as more saltatory behavior and head compensatory movement. 3D habitats are those that force the animal to be oriented in all 3D spatial axes due to the complex structure of vegetation. Compared with plain habitats where only two directions of movements are essential (terrestrial habitats, like muds, semideserts, etc.), these more heterogenous and fine-grained 3D habitats possess more continuous variation between all three dimensions of habitats. In Anurans, arboreal and semi-aquatic species inhabit such types of 3D complex habitats.

We tested the following questions: (1) Are there differences in compensatory head movements among frog species? (2) Is there any relationship between the habitat type and the ability and degree of compensatory head movements? (3) Is there any association between the locomotion type and ability and degree of compensatory head movements? (4) Are there privileged clades of frogs possessing advanced compensatory abilities as a result of their evolutionary history regardless of their current ecology? Finally, we discuss putative consequences of such compensatory mechanisms for diversification and ecological success of certain frog taxa.

MATERIALS AND METHODS
Specimens
We tested 35 species (113 adult individuals) of 12 families from phylogenetically different clades to cover the whole diversity of Anura. Frogs were housed individually in a temperature-controlled room and fed by crickets and earthworms supplemented with vitamins and minerals (Nutri Mix, Trouw Nutrition Biofaktory, Ltd) twice weekly. Animals were weighed by a digital balance to the nearest 0.01 g and measured by digital callipers to the nearest 0.01 mm. For each individual, we measured the snout–vent length (SVL) and the tibiofibular length. We calculated the body mass index (BMI) as a ratio of body mass to SVL with the scaling exponent set to 3 (Green, 2001). BMI is representing a parameter of body robustness/gracility. The length of the tibiofibula was related to SVL as relative tibiofibula (rTF). As the length of hindlimbs is

usually positively associated with jumping performance, rTF can be considered as an ideal proxy of jumping ability (Emerson, 1988; Rand, 1952; Zug, 1972, 1978; but see Jorgensen and Reilly, 2013). Experiments were performed in accordance with Czech law implementing all corresponding European Union regulations. This experiment was focused only on the natural behavior with no application of anesthesia, surgical procedures and immobilization.

Design of experimental testing
Compensatory head movements were measured on a dynamic platform prototype (Fig. 1A,B) constructed at the Faculty of Biomedical Engineering, Czech Technical University (Hýbl et al., 2016; Kutílek et al., 2015, 2017). A cyclic platform movement has been used in studies measuring vertebrate body movements, i.e. the body segment movement (Dieringer, 1987, 1991; Tempia et al., 1991). We focused on the application of methods for the assessment of periodical movement of body segments in the sagittal plane. Movement of the platform is based on the control of angular velocity. The angular velocity was set to 5 deg s^{-1}, the amplitude was 21.6 deg (the whole range of the platform movement was 43.2 deg). This gives an angular frequency of 0.12 deg s^{-1}, stimulating mainly saccular otolithic macula in the vertical plane (Uchino and Kushiro, 2011). Individual periods of motion are indicated by a sequence number (1–10). One period of the platform movement is composed of two parts – descending and ascending – corresponding to the head extension and head flexion (Fig. 2). The platform was fixed in the center and moved periodically with one end up and the second down and *vice versa* (the principle of double-acting lever). One experiment lasted 174.4 s and contained 10 periods. For each animal we recorded one trial. Nevertheless, it was not usually possible to record all the ten periods (mean=5.94; range=1–9) due to the motion of the whole frog's body (walking, hopping, burrowing) during the experiment. For the analysis, we used all available periods.

We put two markers (non-toxic color) on the temporal side of the head (between eye and ear; Fig. 1C) for measurement of compensatory head movements in the sagittal plane in relation to the platform. The body of the frog was unrestrained (in a plastic box, Fig. 1A) and placed on the platform in a way that the longitudinal axis corresponded to the longitudinal axis of the platform (Kutílek et al., 2015). The digital camera was a subsystem of the dynamic platform device. It recorded (with a frequency of 30–60 fps according to the light conditions) the experimental animals in the box while moving synchronically together with the platform. The digital camera was focused on the head markers. We tracked markers on the head after processing the video recording. Marker coordinates were detected on pictures automatically based on the contrast between their color and the skin color. The records contained the timestamps, which incorporated the information concerning when each frame was recorded. It allowed us to synchronize the head movement with that of the platform (for a detailed description see Kutílek et al., 2015, 2017). We analyzed only those parts of the recording where the markers on the temporal side of the head were perpendicular to the digital camera, and the frog was sitting motionlessly and did not lean against the wall of the plastic box. The line of the two markers (expressing the head movements) was related to the movements of the platform and the compensatory head movements were evaluated (Fig. 1D).

Data record should be normalized to make the data comparable across the groups of subjects and different species of animals (Stansfield et al., 2006). The normalization of measured variables (i.e. record is normalized for movement amplitude) is derived from
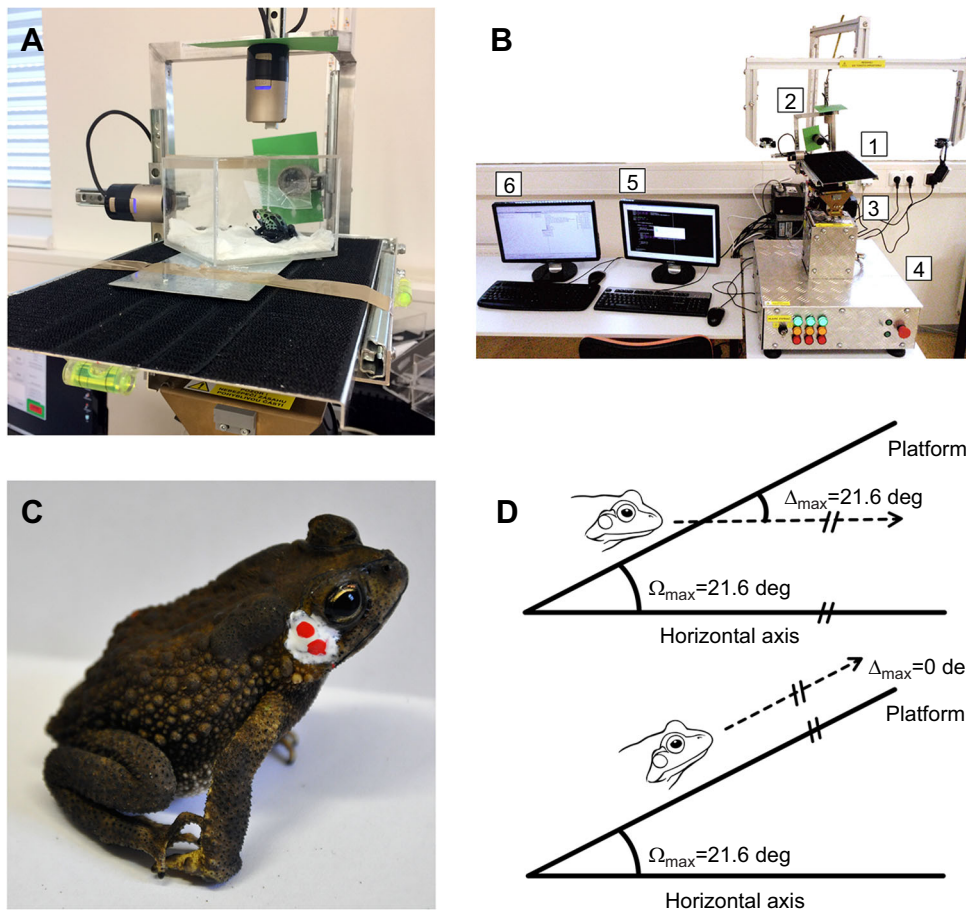
Fig. 1. Experimental design scheme. A frog in the experimental box (A); the laboratory system measuring animal body response on a dynamic platform (B); a frog's head with markers on the temporal side (C); and a schematic drawing describing the measurements of the platform and head angles in extreme cases (D). (B) 1, moving platform; 2, camera subsystem; 3, actuator unit; 4, control and data collection unit; 5, PC instructing platform movement; 6, PC for data processing and movement-angles determination. (D) The case of perfect head compensatory movements (the maximal tilt angle of the head, Δ_{max}, is the same as the maximal angle of the dynamic platform, Ω_{max}) above and the case of the absence of head compensatory movements (the maximal tilt angle of the head, Δ_{max}, is zero) below.

medical applications (Stansfield et al., 2006). Δ_i is tilt angle of movement of a body segment (in deg), Ω_i is tilt angle of the platform (in deg), and Ω_{min} and Ω_{max} are tilt angles of the platform when the platform reaches the extreme angles. The range of movement (ROM; in deg) of the platform is $ROM_P=2\times\Omega_{max}$. Then the normalized values of the tilt angle of movement of a body segment and the tilt angle of the platform are:

$$\%\Delta_i = 100 \times \frac{\Delta_i}{ROM}, \tag{1}$$

$$\%\Omega_i = 100 \times \frac{\Omega_i}{ROM_P}. \tag{2}$$

In accordance with preliminary research, periodical movements of the platform were used (Kutílek et al., 2015; Hýbl et al., 2016). The one period of platform movement is composed of two parts – descending and ascending – corresponding to the head extension and head flexion. Each half of period was divided into three unequal parts: I, II and III. Parts I and III cover a quarter of the duration (i.e. only initial and final parts of the platform movement) of a half of period when the platform performs non-uniform circular motion. Part II covers half of the duration (middle part) of a half of period when it is a uniform motion at a constant angular velocity.

To evaluate the head angular movement, we have proposed following quantitative parameters (Table 1, Fig. 2). The ROM describes the flexibility of head movements during the platform movement head extension (ROM_E; a range of the head movement during extension) and flexion (ROM_F; a range of the head movement during flexion). The parameter ROM, representing

head compensatory movements, describes the neck mobility as a response and correlative to the movements of the platform (for the calculation of ROM in percent see Eqns 3 and 4):

$$ROM_E = 100 \times \frac{\Delta_{1max} - \Delta_{1min}}{\Omega_{1max} - \Omega_{1min}}, \tag{3}$$

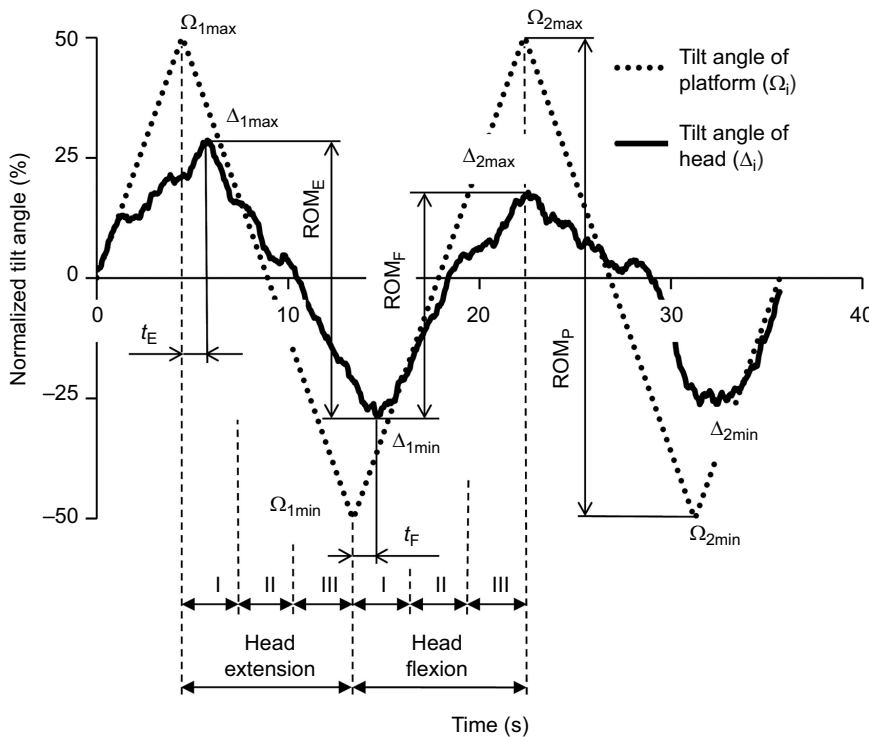$$ROM_F = 100 \times \frac{\Delta_{1min} - \Delta_{2max}}{\Omega_{1min} - \Omega_{2max}}. \tag{4}$$

Ω_{max} and Ω_{min} are the maximal and minimal tilt angle of the dynamic platform, respectively (1 and 2 refer to the sequence number of the period of platform movement). Δ_{max} and Δ_{min} are the maximal and minimal tilt angle of the head, respectively (1 and 2 refer to the sequence number of the period of platform movement; for details, see Fig. 2).

The more complex parameter P is variance angle of the head movement during head extension (P_E) and flexion (P_F). This parameter is reflecting smoothness of the head movement. For further analysis, we selected a middle part (part II) of the movement to avoid transitions between extremes of the cyclic platform movement. Variance of the angle of head movement during the platform movement is obtained from the data samples as follows:

$$P_\Delta^2 = \frac{1}{N} \sum_{i=1}^{N} \left(\Delta_i - \frac{1}{N} \sum_{i=1}^{N} \Delta_i \right)^2. \tag{5}$$

N is the number of measured sample points, i.e. states during half (or I, II and III part) of the period of head extension or head flexion. There are two factors affecting the number of points: the time of each measurement interval and the sample frequency (determined

Fig. 2. Diagram of head and platform movement. Example of data recorded during the platform movement and animal head movement in sagittal plane. Ω_{max} and Ω_{min} are the maximal and minimal tilt angle of the dynamic platform, respectively (1 and 2 refer to the sequence number of the period of platform movement); Δ_{max} and Δ_{min} are the maximal and minimal tilt angle of the head, respectively (1 and 2 refer to the sequence number of the period of platform movement); ROMs describes the range of movement during the movement of the platform up (ROM$_E$; head extension) and down (ROM$_F$; head flexion); ROM$_P$ is the range of movement of the platform (ROM$_P$=2·Ω_{max}); t is the time delay in the animal's reaction to the movement of the platform up (t_E) and down (t_F). I, II and II refer to the initial, middle and final parts of the period of platform movement.

by the recording frequency of the camera); for details, see Kutílek et al. (2015) and Hýbl et al. (2016).

Parameter T describes the time delays in the animal's reaction to the platform movement in the case of head extension (t_E) and flexion (t_F). This parameter (for the calculation see Eqns 6 and 7) can reflect habituation and/or anticipation of the cyclic movement by the tested animal. The values of time delay of head movement during extension and flexion are calculated as:

$$t_E = t_{\Delta 1max} - t_{\Omega 1max}, \qquad (6)$$

$$t_F = t_{\Delta 1min} - t_{\Omega 1min}. \qquad (7)$$

Unfortunately, it was not possible to finish the experiment and/or evaluate the measured variables in some individuals/species (*Xenopus laevis*, *Pelobates fuscus*, *Hyla cinerea*, *Hyla arborea*,

Hyperolius mitchelli, 13 individuals altogether). This was caused by various factors, e.g. removing marks from the body surface through increased mucous gland secretion or constant attempts to burrow in the experimental box.

Statistical analysis

Species were classified into three broad ecological groups based on the literature. We considered species as terrestrial if they spend most of their time away from water (Table 2). These species cannot be found in the immediate vicinity of water outside the breeding season. We considered as aquatic those species that spend most of their life in water. Finally, we classified as arboreal those frogs that spend most of their life on trees. Moreover, we classified four groups of a locomotion type based on the literature (Zug, 1978; Emerson, 1979, 1982; Reilly and Jorgensen, 2011), web resources (AmphibiaWeb) or personal communications with frog keepers. We adopted the categories of hoppers and jumpers based on Emerson's definition (greater than or less than nine body lengths per jump, respectively). Hoppers were divided into two subcategories; walkers/hoppers (WH) and those known to be fossorial and burrow (BWH). Jumpers were categorized as terrestrial (JT) and arboreal (JA). In addition, we classified a tongue-protraction mechanism (mechanical pulling, inertial elongation and hydrostatic elongation according to Nishikawa, 1999) of each frog species, as it represents another ecological parameter that can be associated with performance.

Since species cannot be considered as independent data points (Felsenstein, 1985), we included the effect of phylogeny in most of the analyses. We adopted a large-scale phylogeny of Amphibia (Pyron and Wiens, 2011) completed with the most recent phylogeny of frogs (Feng et al., 2017). The sample size was defined according to the requirement to cover the huge diversity of frog species/main phylogenetic clades comprising the most basal Archeobatrachia as well as those from modern Neobatrachia. Moreover, the phylogenetic comparative methods are highly sensitive to the phylogenetic sample distribution rather than to the sample sizes of

Table 1. Summary of the proposed parameters determined using methods of evaluation of time domain data for quantitative evaluation of angular movement response of animals to changes in their body orientation on a rotating platform

Parameter	Abbreviation	Unit
Normalized range of head angular movement relative to the platform during the extension	ROM$_E$	%
Normalized range of head angular movement relative to the platform during the flexion	ROM$_F$	%
The time delay between the achieved maximum angle of head movement and maximum angle of platform movement	t_E	s
The time delay between the achieved minimum angle of head movement and minimum angle of platform movement	t_F	s
Variance of the angle of head movement during the platform movement and extension until reaching the maximum angle of head movement	P_E	%²
Variance of the angle of head movement during the platform movement and head flexion until reaching the minimum angle of head movement	P_F	%²

Table 2. Experimental animals and ecological parameters

Species	Family	N	Life code	Movement	Tongue-protraction mechanism
Bombina bombina (Linnaeus 1761)	Bombinatoridae	2	Aquatic	Walkers/hoppers	Mechanical pulling
Bombina variegata (Linnaeus 1758)	Bombinatoridae	3	Aquatic	Walkers/hoppers	Mechanical pulling
Bufo bufo (Linnaeus 1758)	Bufonidae	39	Terrestrial	Walkers/hoppers	Inertial elongation
Bufotes viridis Laurenti 1768	Bufonidae	2	Terrestrial	Walkers/hoppers	Inertial elongation
Dendrobates leucomelas Steindachner 1864	Dendrobatidae	2	Terrestrial	Walkers/hoppers	Inertial elongation
Dendrobates tinctorius (Cuvier 1797)	Dendrobatidae	2	Terrestrial	Jumping terrestrial	Inertial elongation
Dendropsophus microps (Peters 1872)	Hylidae	2	Arboreal	Walkers/hoppers	Mechanical pulling
Duttaphrynus melanostictus (Schneider 1799)	Bufonidae	2	Terrestrial	Walkers/hoppers	Inertial elongation
Dyscophus guineti (Grandidier 1875)	Microhylidae	2	Terrestrial	Burrowing	Hydrostatic elongation
Epidalea calamita (Laurenti 1768)	Bufonidae	1	Terrestrial	Burrowing	Inertial elongation
Epipedobates anthonyi (Noble 1921)	Dendrobatidae	2	Terrestrial	Jumping terrestrial	Inertial elongation
Hylarana erythraea (Schlegel 1837)	Ranidae	2	Terrestrial	Jumping terrestrial	Inertial elongation
Kaloula pulchra Gray 1831	Microhylidae	2	Terrestrial	Burrowing	Hydrostatic elongation
Leptopelis vermiculatus (Boulenger 1909)	Arthroleptidae	2	Arboreal	Jumping arboreal	Inertial elongation
Osteopilus septentrionalis (Duméril & Bibron 1841)	Hylidae	3	Arboreal	Jumping arboreal	Mechanical pulling
Pelophylax esculentus (Linnaeus 1758)	Ranidae	1	Aquatic	Jumping terrestrial	Inertial elongation
Phlyctimantis maculatus (Duméril 1853)	Hyperoliidae	2	Arboreal	Jumping arboreal	Inertial elongation
Phrynomantis bifasciatus (Smith 1847)	Microhylidae	2	Terrestrial	Walkers/hoppers	Hydrostatic elongation
Phyllobates terribilis Myers, Daly & Malkin, 1978	Dendrobatidae	2	Terrestrial	Jumping terrestrial	Inertial elongation
Phyllobates vittatus (Cope 1893)	Dendrobatidae	2	Terrestrial	Jumping terrestrial	Inertial elongation
Polypedates leucomystax (Gravenhorst 1829)	Rhacophoridae	3	Arboreal	Jumping arboreal	Inertial elongation
Pyxicephalus edulis Peters 1854	Pyxicephalidae	2	Terrestrial	Jumping terrestrial	Inertial elongation
Rana dalmatina Fitzinger 1839	Ranidae	4	Terrestrial	Jumping terrestrial	Inertial elongation
Rana temporaria Linnaeus 1758	Ranidae	3	Terrestrial	Jumping terrestrial	Inertial elongation
Rentapia hosii (Boulenger 1892)	Bufonidae	1	Arboreal	Jumping arboreal	Inertial elongation
Sclerophrys regularis (Reuss 1833)	Bufonidae	4	Terrestrial	Walkers/hoppers	Inertial elongation
Rhinella marina (Linnaeus 1758)	Bufonidae	2	Terrestrial	Jumping terrestrial	Inertial elongation
Theloderma corticale (Boulenger 1903)	Rhacophoridae	2	Terrestrial	Jumping arboreal	Inertial elongation
Trachycephalus resinifictrix (Goeldi 1907)	Hylidae	2	Arboreal	Jumping arboreal	Mechanical pulling

A table of experimental animals, family membership, number of studied frog species and ecological factors depicting the habitat use, typical mode of movement and the mechanism of tongue protraction.

individuals (Herron and Freeman, 2014). We validated the method on the common toad (*Bufo bufo*, N=39 individuals). The repeatability of examined parameters was evaluated (see below). We analyzed untransformed data using the gls function of the 'nlme' package in R (https://cran.r-project.org/web/packages/nlme/citation.html) with the individual and species as nested random factor. The random factor of species was implemented based on the prediction of high correlation between species-specific and family-specific variations. The aim of the study was to investigate the relationship between head compensatory movements and higher taxonomic levels (family); therefore, we treated the effects of the individual and the effect of the species as confounding factors. We employed Akaike information criterion (AIC) to compare a model with and without the species as a random factor (AIC with 3072.655; AIC without 3070.655 for ROM_E). To avoid the above-mentioned relationship between the family and species taxon level, we employed the model with the species as a random factor, although the AIC was slightly higher. The data followed a normal distribution (according to the Shapiro–Wilk W-test). The outliers of ROMs were excluded (ROM>60 and ROM<−60) because we found that it was the error of measurement due to the movement of the whole body of the frog during the experiment and not the movement of the head itself. We included the family, ecology, locomotion type, body mass, SVL, BMI, rTF, tongue-protraction mechanism and period of platform movement as fixed effects into the models. Repeatability was calculated according to the methods described in Nakagawa and Schielzeth (2010) to assess the proportion of total variance explained by inter-individual differences. The analyses were conducted using the 'rptR' package in R, command rptGaussian (Stoffel et al., 2017). This function uses mixed-effects

models fitted by the lmer function implemented in the 'LME4' package (https://cran.r-project.org/web/packages/lme4/index.html). We explored the effect of phylogeny under 'phytools' package in R (Revell, 2012) using Pagel's Lambda (Pagel, 1999) and Blomberg's K (Blomberg et al., 2003) employing the Brownian motion model. As phylogeny had a robust effect on several factors, we conducted the same statistical testing under the 'ape' package in R (Paradis et al., 2004) to eliminate the effect of common ancestry. The branch lengths were computed by the method of Grafen (1989) under the 'ape' package in R by command 'compute.brlen'. For visualization, we employed Mesquite, version 3.31 (https://www.mesquiteproject.org/). Basic tests and descriptive statistics were done in Statistica, version 6 (http://www.statsoft.com/Products/STATISTICA-Features). Calculations of reduced major axis regression parameters and their confidence intervals (computed by linear and bootstrapping methods) were computed using RMA version 1.14b (http://www.bio.sdsu.edu/pub/andy/RMA.html).

RESULTS

We found a high level of repeatability in parameter ROM_E (R=0.615, CI=0.507–0.706, P<0.001) and ROM_F (R=0.643, CI=0.537–0.723, P<0.001); parameters concerning the delay of compensation movement (t_E and t_F) had smaller (R=0.175 and 0.166, respectively) but still significant (CI=0.064–0.289, P≤0.001 and CI=0.032–0.289, P<0.001, respectively) repeatability. Nevertheless, parameters P_E and P_F were not repeatable due to the high intra-individual variability, which we further considered in our models.

We found a strong phylogenetic signal in parameter ROM_E (Pagel's lambda=0.831, P=0.037, Blomberg's K=0.272, P=0.006)

and ROM_F (Pagel's lambda=0.894, $P<0.001$, Blomberg's $K=0.353$, $P=0.001$). Similar results were revealed by the GLM model, supporting a strong effect of family (for visualization see Fig. 3) in ROM_E ($F_{9,18}=7.489$, $P<0.001$) and ROM_F ($F_{9,19}=5.958$, $P<0.001$). We found that the families Pyxicephalidae ($t=3.404$, $P=0.003$) and Rhacophoridae ($t=4.898$, $P<0.001$) exhibited higher, while Dendrobatidae ($t=-4.006$, $P<0.001$) and Microhylidae ($t=-3.229$, $P=0.005$) exhibited lower values of ROMs (Fig. 4) compared with corresponding overall means (t- and P-values were provided for ROM_E). We found no effect of the habitat, locomotion, repetition, tongue-protraction mechanism, BMI and rTF.

We found no phylogenetic signal in parameter P_E (Pagel's lambda<0.001, $P=1$, Blomberg's $K=0.154$, $P=0.216$) and P_F (Pagel's lambda<0.001, $P=1$, Blomberg's $K=0.126$, $P=0.448$). The GLM model revealed no effect of the family, habitat, locomotion, repetition and body size.
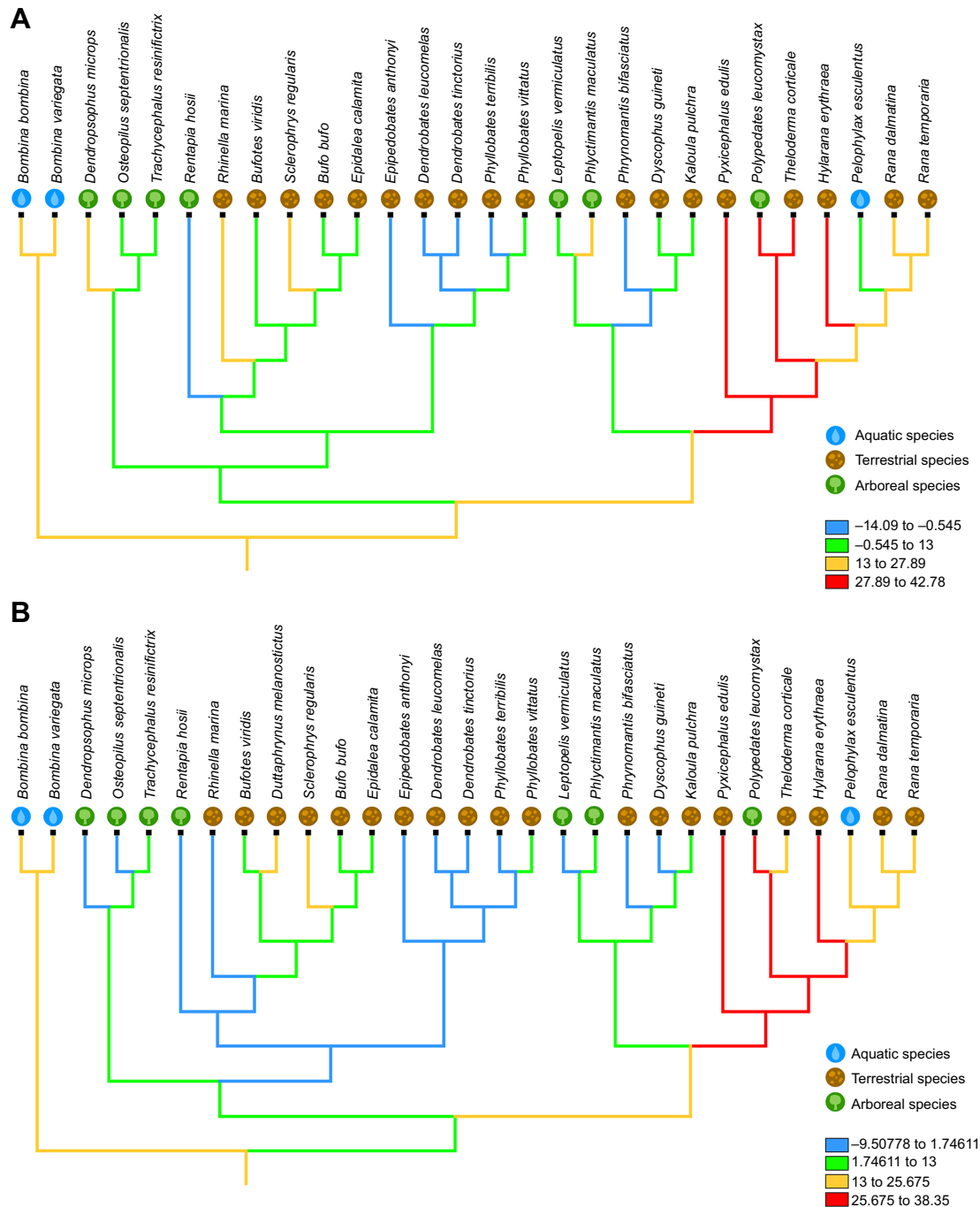
Fig. 3. Visualization of the range of movement (ROM) of the tested frogs on a phylogenetic tree. (A) The head extension during the movement of the platform up (ROM_E). (B) The head flexion during the movement of the platform down (ROM_F). The color of the lines indicate the median values of ROM_E and ROM_F for species in categories increasing from the lowest values of blue, through green and yellow to the highest values of red. The ecology of studied species is depicted. For the number of studied species see Table 2. Reconstruction of ancestral states by parsimony method implemented in Mesquite (https://www.mesquiteproject.org/) is provided for illustration only.
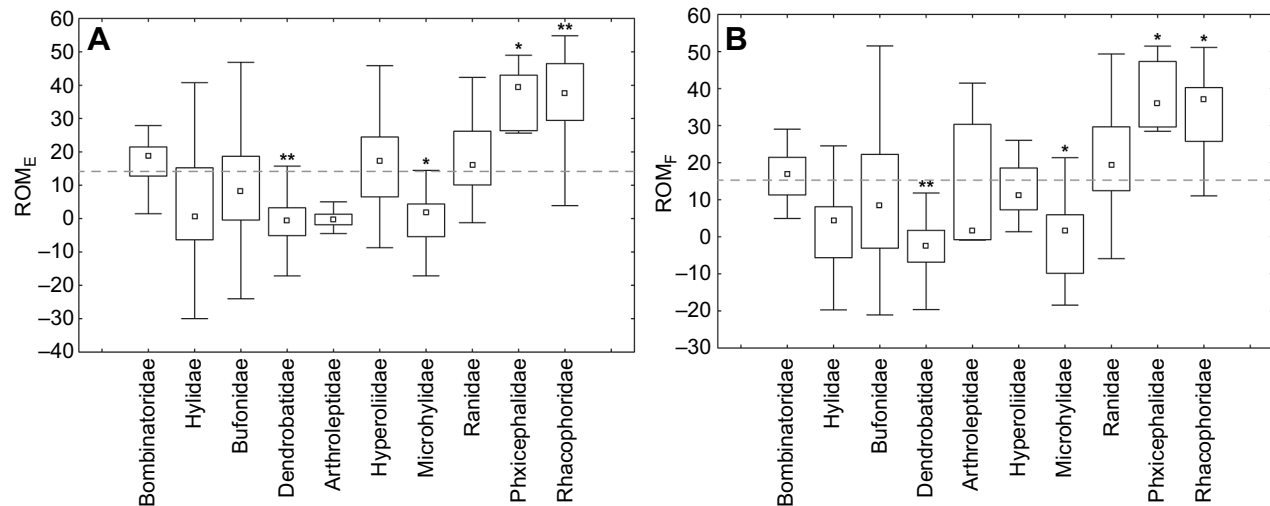
Fig. 4. Box plots of ROMs categorized for each family. Original untransformed values of the ROM during (A) head extension (ROM_E) and (B) head flexion (ROM_F) visualized in a form of box plots in categories of consecutive families. Medians, 25th and 75th percentiles, minimal/maximal non-outlier values and significance (ANOVA P-values: *$P<0.01$; **$P<0.001$) results of ROMs compared to corresponding overall means (hashed gray line) are depicted. For the summary of studied species in each family, see Table 2.

We found no phylogenetic signal in parameter t_E (Pagel's lambda<0.001, P=1, Blomberg's K=0.102, P=0.787) and t_F (Pagel's lambda<0.001, P=1, Blomberg's K=0.192, P=0.13). The GLM model revealed no effect of family, habitat, locomotion, repetition and body size.

Range of movement during flexion (ROM_F) corresponded well with that measured during extension (ROM_E). This was confirmed by slopes and intercepts of the relationship between these parameters, which are not statistically different from 1 and 0, respectively (slope=0.992, s.e.=0.037, 95% CIbootstrap=0.933–1.056; intercept=0.769, s.e.=0.037, 95% CI_bootstrap=−1.518–1.297).

DISCUSSION

In this paper, we tested frogs' neuromotor reaction to cyclic movement, which is known as compensatory movement. Relevant studies (Dieringer and Precht, 1982; Darlington et al., 2002; Straka and Dieringer, 2004) usually apply rather a neurological approach (i.e. the anatomy of vestibular apparatus, unilateral labyrinthectomy, a description of compensatory movements) and a phylogenetic comparative study monitoring compensatory movements in the ecomorphological context across Anura is completely missing.

We were able to quantify the head compensatory movement (ROM_E and ROM_F), which is known to be the dominant way for gaze stabilization in frogs, compared to a limited contribution of eye movement (Dieringer and Meier, 1994). This parameter was highly repeatable and thus suitable for evaluation of the head compensatory movements in comparative studies. We presumed a close relationship between head compensatory movements and the type of habitat and/or locomotion. A large body of empirical work shows that the habitat and locomotion type is closely linked to morphology and/or performance (Jorgensen and Reilly, 2013; Gomes et al., 2009; Manzano et al., 2017; Moen et al., 2013; Robovská-Havelková et al., 2014; Knight, 2018; Hill et al., 2018). However, our results did not support this hypothesis. We found no relationship between the habitat type, reflecting the basic ecology of the studied species and their head compensatory movements. Similar results were found for the locomotion type, contradicting the idea of higher requirements of head compensatory movements according to a more complex 3D habitat and/or locomotion. The absence of a link

between ecology and performance indicates the possible explanation of head compensatory movement as an innate reflex and universal neuromotor reaction (i.e. part of VORs and VCRs).

Nevertheless, we found a strong phylogenetic signal in our data. Some families exhibited a higher ROM, which is linked to greater head compensatory movement. It was most apparent in the group of Natatanura, comprising Pyxicephalidae and Rhacophoridae families (but not so apparent in Ranidae). By contrast, other groups (Dendrobatidae, Microhylidae) exhibited only poor head compensatory movements. We did not find any unique anatomical interpretation distinguishing Natatanura from other frog groups to explain the better ability to compensate the cyclic movement of the platform. Several anatomical (diplasiocoelous vertebrae, organization of pectoral and pelvic girdle) and behavioral (tongue-protraction mechanism) characteristics were examined but are shared with other groups of frogs. A previous study on the brain morphology of frogs revealed the relationship between locomotion/ecology and size of the cerebellum and diencephalon (Manzano et al., 2017). Thus, a comparative neuroanatomical survey examining the endorgans and associated innervation of the inner ear responsible for compensatory movements can be promising for rationale of the uncovered pattern.

The higher head compensatory ability can be interpreted as a gyroscopic advantage in foraging and/or antipredator contexts. Visual cues are the dominant sensory modality that most frogs use to detect prey (Lettvin et al., 1959; Kaess and Kaess, 1960; Ewert, 1985; Satou and Shiraishi, 1991). A multidisciplinary neurobiological approach to the neural basis of visually guided prey-catching behavior revealed the concept of the key stimulus and releasing mechanism in toads (Ewert, 1985). Later, studies dealing with the neuromuscular control of prey capture in frogs uncovered a variation in kinematic and behavioral characteristics (liner correction, feedback control, hypoglossal afferents, aiming) in three non-exclusive mechanisms to protract the tongue during foraging (Nishikawa, 1999). Detailed neuroanatomical surveys revealed a link between vision and proprioception (Anderson and Nishikawa, 1993). The head compensatory movement is essential during passive (e.g. drifting in water flow in aquatic species, hanging on moving twigs in arboreal species) as well as active

(locomotion, jumping) movements, which are both involved in foraging. Generally, we believe that gaze stabilization during locomotion can improve or even enable visual perception and catching of the prey. Thus, the uncovered higher ability of gaze stabilization in the families Pyxicephalidae and Rhacophoridae may enhance the evolutionary success of these groups belonging to Natatanura. The clade of Natatanura is evolutionarily a very successful group of modern frogs belonging to Neobatrachia. It was recently revealed that Neobatrachia, which comprises three species-rich clades (Hyloidea, Microhylidae and Natatanura) that together consist of 88% of extant frogs, simultaneously underwent rapid diversification at the Cretaceous–Paleogene boundary (Feng et al., 2017). Apart from a highly diversified and species-rich group of Hyloidea, the clade of Natatanura is more successful (according to the number of species) than the closely related group of Microhylidae. This is quite intriguing, as species belonging to Microhylidae exhibit a more plastic and innovative morphology. They express a higher ability to occupy new morphospace (Roelants et al., 2011) due to their plastic morphological responses to environmental changes (Liem, 1969). These attributes are not common in frogs, as most frog radiations are not connected with new morphological characteristics. Instead, homoplasy associated with convergent evolution and changes in the number/size of existing structures are frequent in anuran radiations (Bossuyt and Milinkovitch, 2000; Roelants et al., 2011; Moen et al., 2013).

From the distribution of ROMs over the phylogenetic tree, it can be inferred that the anuran ancestor was able to make the head compensatory movements. It was unfortunately not possible to evaluate exactly the ROMs of the basal frogs in this study due to the experimental problems. Nevertheless, from the simple view of tilting in frogs, we observed that the most basal species (*Alytes obstetricans*, *Pelobates fuscus*, *Xenopus laevis*) are capable of head compensatory movements. In the following anuran evolution, the decrease as well as increase of these abilities occurred.

Our results also revealed a uniform reaction to the platform movement across the families with respect to the timing and smoothness of the compensatory movements. We did not identify any habituation or anticipation of the platform movement during the experiment. This result is congruent with previous findings of the absence of a brainstem network that stores neural activity related to gaze stability (Dieringer et al., 1983). The speed and smoothness of reaction to the platform movement demonstrated as compensatory movements did not vary across the species and families. However, the lower level of repeatability of these parameters indicates a large amount of intra-individual variability. It may be related to personality, which is widespread even in cold-blooded vertebrates (Wilson and Krause, 2012; Brodin et al., 2013; Šimková et al., 2017).

In conclusion, we managed to quantify the head compensatory movements in different species of frogs. This is the first study using a platform prototype built for measuring fine movements of small-bodied vertebrates. To our best knowledge, this is the first comparative study focused on the VCR in anurans. Our results did not corroborate the ecomorphological hypothesis anticipating the relationship between ecology/locomotion type and the range of head compensatory movements. Nevertheless, we found a strong phylogenetic signal indicating great compensatory ability movements in families from the Natatanura group. Our results indicate a possible link between the higher neuromotor skills and evolutionary success of this group, and we interpret it as a possible gyroscopic advantage in the foraging and anti-predatory context. More efforts should be devoted to studying neuroanatomical characteristics to understand the underlying mechanism.

Author contributions
Conceptualization: P.K., E.L., R.C., D.F.; Methodology: B.Z., J.H., D.S., P.K., R.C.; Software: J.H., D.S., P.K.; Formal analysis: P.F., B.Z., D.F.; Investigation: P.F., K.S., B.Z., A.K., J.H., D.S., R.C.; Resources: K.S., P.K., D.F.; Data curation: P.F., K.S., J.H., D.S., P.K.; Writing - original draft: P.F., P.K., R.C.; Writing - review & editing: K.S., B.Z., A.K., P.K., E.L., R.C., D.F.; Visualization: P.F., P.K.; Supervision: P.K., E.L., R.C., D.F.; Project administration: P.K., E.L., R.C., D.F.; Funding acquisition: P.K., D.F.

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