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Stabilization of Gaze during Early *Xenopus* Development by Swimming-Related Utricular Signals.

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Swim style-dependent utricular activation ensures gaze-stabilization during early development --Manuscript Draft--

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Abstract:	<p>Locomotor maturation requires concurrent gaze stabilization improvement for maintaining visual acuity [1, 2]. The capacity to stabilize gaze, in particular in small aquatic vertebrates where coordinated locomotor activity appears very early, is determined by assembly and functional maturation of inner ear structures and associated sensory-motor circuitries [3-7]. Whereas utriculo-ocular reflexes become functional immediately after hatching [8, 9], semicircular canal-dependent vestibulo-ocular reflexes (VOR) appear later [10]. Thus, small semicircular canals are unable to detect swimming-related head oscillations, despite the fact that corresponding acceleration components are well-suited to trigger an angular VOR [11]. This leaves the utricle as sole vestibular origin for swimming-related compensatory eye movements [12, 13]. We report a remarkable ontogenetic plasticity of swimming-related head kinematics and vestibular endorgan recruitment in <i>Xenopus</i> tadpoles with beneficial consequences for gaze-stabilization. Swimming of older larvae generates sinusoidal head undulations with small, similar curvature angles on the left and right side that optimally activate horizontal semicircular canals. Young larvae swimming causes left-right head undulations with narrow curvatures and strong, bilaterally dissimilar centripetal acceleration components well-suited to activate utricular hair cells and to substitute the absent semicircular canal function at this stage. The capacity of utricular signals to supplant semicircular canal function was confirmed by recordings of eye movements and extraocular motoneurons during off-center rotations in control and semicircular canal-deficient tadpoles. Strong alternating curvature angles and thus linear acceleration profiles during swimming in young larvae therefore represents a technically elegant solution to compensate for the incapacity of small semicircular canals to detect angular acceleration components.</p>

Swim style-dependent utricular activation ensures gaze-stabilization during early development

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* H.S. and M.B. contributed equally to this work.

Key words: Swimming, kinematics, vestibular system, otolith organ, semicircular canal, vestibulo-ocular reflex

Running title: Head motion kinematics and eye movement during swimming

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SUMMARY

Locomotor maturation requires concurrent gaze stabilization improvement for maintaining visual acuity [1, 2]. The capacity to stabilize gaze, in particular in small aquatic vertebrates where coordinated locomotor activity appears very early, is determined by assembly and functional maturation of inner ear structures and associated sensory-motor circuitries [3-7]. Whereas utriculo-ocular reflexes become functional immediately after hatching [8, 9], semicircular canal-dependent vestibulo-ocular reflexes (VOR) appear later [10]. Thus, small semicircular canals are unable to detect swimming-related head oscillations, despite the fact that corresponding acceleration components are well-suited to trigger an angular VOR [11]. This leaves the utricle as sole vestibular origin for swimming-related compensatory eye movements [12, 13]. We report a remarkable ontogenetic plasticity of swimming-related head kinematics and vestibular endorgan recruitment in *Xenopus* tadpoles with beneficial consequences for gaze-stabilization. Swimming of older larvae generates sinusoidal head undulations with small, similar curvature angles on the left and right side that optimally activate horizontal semicircular canals. Young larvae swimming causes left-right head undulations with narrow curvatures and strong, bilaterally dissimilar centripetal acceleration components well-suited to activate utricular hair cells and to substitute the absent semicircular canal function at this stage. The capacity of utricular signals to supplant semicircular canal function was confirmed by recordings of eye movements and extraocular motoneurons during off-center rotations in control and semicircular canal-deficient tadpoles. Strong alternating curvature angles and thus linear acceleration profiles during swimming in young larvae therefore represents a technically elegant solution to compensate for the incapacity of small semicircular canals to detect angular acceleration components.

RESULTS

Eye motion dynamics during free-swimming

The ability of *Xenopus* tadpoles to stabilize gaze during free swimming was evaluated from high-frequency video recordings at two larval stages (stage 47, $n = 7$; stage 57, $n = 5$; Figure 1A1,2). Reconstruction of eye-in-space and head-in-space trajectories over several consecutive swim cycles (Figure 1B1,2) revealed

50 that animals at both developmental stages produce conjugate eye movements in phase-opposition to head
51 movements (Figure 1C1,2) with comparable ranges of ocular excursion angles (5-30°) and degrees of eye-head
52 correlation (Figure 1D). Eye motion magnitudes were maximal (eye-in-head ratio ~1) for small head oscillations
53 (<10°) and minimal (~0.3) for large head oscillations (>40°; Figure 1E), indicating that gaze stabilization is
54 equally effective at both stages and thus independent of larval size or morphometric characteristics. Because
55 tadpoles at the two stages differ in their capacity to encode angular head acceleration [10], potential ontogenetic
56 changes of head motion kinematics were evaluated.

57 *Swim speed and head oscillation kinematics*

58 Kinematic parameters were obtained from a total of 125 swimming episodes ($n = 65$ for stage 47; $n =$
59 60 for stage 57; 16 animals each). Even though the swim speed of individual animals was rather variable (Figure
60 1F), older larvae generally swam faster than younger larvae (Figure 1G; $p < 0.001$ Mann-Whitney U -test).
61 While the distribution of swim speeds overlapped in the low velocity range, stage 57 tadpoles reached
62 considerably higher velocities compared to stage 47 larvae (Figure 1H) with smaller variance as indicated after
63 normalization to the average speed (Figure 1I).

64 The capacity to effectively stabilize gaze was estimated by reconstructing head trajectories during
65 swimming (green and blue lines in Figure 2A,B) from the highly contrasted outline of the eyeball on each side.
66 While tadpoles at both stages produced left-right head movements during swimming, stage 47 larvae exhibited
67 strong, alternating excursions of the head to both sides (Figure 2A1-3). During each swim cycle, the eyeball on
68 the inner side of the head turn remained almost stationary in space (green inward marks in Figure 2A2-3). The
69 minimal displacement for ~60 ms (Figure 2C, black trace) corresponded to the low velocity on the side of the
70 inward curve (2.6 ± 1.6 cm/s; Figures 2D, S2E). Simultaneously, the outer side of the head turn (blue outward
71 marks in Figure 2A2-3) advanced considerably farther forward. During the second half cycle, this forward
72 progression profile was inverted (Figure S2E).

73 At stage 57, the head exhibited a more rectilinear motion pattern (Figure 2B1-3). During maximal head
74 excursion, the eyeball on the inner side of the head turn moved rather constantly (Figure 2C, red trace) and with
75 a considerably faster velocity (6.4 ± 2.9 cm/s; mean eye velocity $p < 0.001$ Mann-Whitney U -test; Figure 2D,
76 S2E) compared to young larvae. Velocities at normalized swimming speed (Figure 2E) confirmed that the inner
77 side of the head turn experienced a longer stationary phase at stage 47 than at stage 57 and thus requires
78 dynamically different compensatory eye movements, which might derive from different sets of vestibular
79 endorgans.

80 *Stage-dependent swim motion-related acceleration components*

81 Effective head motion parameters during swimming, as relevant stimulus for vestibular endorgans,
82 were calculated from the triangulated trajectories of the inner ears (otic capsule, OC in Figures S1A,D,E; Figure
83 2A,B). The head of stage 47 larvae rotates around alternating eccentric vertical axes located only at a distance of
84 1-5 mm from the center of the eyeball. This causes the ear on the inner side to follow a narrow curve and on the
85 outer side to proceed along a wider path (Figure 2A3). Ears of stage 57 tadpoles follow trajectories around
86 rather distant rotation axes (>5 mm) with comparably wide curvature angles (Figure 2B3). During each head
87 turn, the maximum curvature of the ear on the inner and outer side is thus highly different on the left and right
88 side of the head for each half-cycle at stage 47, but bilaterally more similar at stage 57 (black and red traces in
89 Figure 2F,I). This was confirmed after cycle-by-cycle averaging and quantification of the motion trajectory of
90 both ears (Figure 2G,H,I; mean maximal curvature, $p < 0.001$ in H and $p < 0.0001$ in I, Mann-Whitney U -test).

91 The magnitudes of angular acceleration and forward, lateral and centripetal linear acceleration at peak
92 curvature were calculated separately during each swim cycle at the level of the vestibular endorgans (OC;
93 Figures S1E, S3). The more pronounced peak curvature at stage 47 causes considerably larger centripetal linear
94 accelerations (Figure 2J, S3A4) compared to stage 57, whereas forward, lateral and angular accelerations were
95 stage-independent (Figure S3B1-3). Thus, swimming in young tadpoles causes pronounced left/right dissimilar
96 translational acceleration components whereas older larvae experience only small, left-right similar centripetal
97 acceleration components.

98 *Otolith-ocular eye movements as substitute for deficient semicircular canal-ocular reflexes*

99 Eye movements were recorded in head-fixed semi-intact preparations (stage 47, $n = 7$) in the absence
100 of visual and proprioceptive sensory signals and spinal locomotor efference copies. In stage 47 tadpoles,
101 semicircular canal-evoked eye movements during sinusoidal head-center rotations (1 Hz and $\pm 120^\circ/s$) were
102 absent (Figure 3A1) as previously reported [10]. In contrast, robust conjugate utricle-derived eye oscillations
103 were recorded during cyclic lateral head translations, Figure 3A2). To evaluate a utricular contribution to gaze-
104 stabilization during swimming, stage 47 tadpole preparations were rotated around eccentric vertical rotation

105 axes, located 5 mm outside the head, respectively. Such off-center head rotations produced conjugate eye
106 movements with a gain of ~ 0.2 during both left-out (Figures 3A3) and right-out rotations (Figures S4B). Despite
107 relatively small gains, eye movements were robust, directionally appropriate and likely derived from an
108 asymmetric activation of bilateral utricular hair cells corroborating previous results in adult frogs [14].
109 Recordings of lateral rectus (LR) nerve activity during rotation around different axes (1 Hz; ± 30 - 240° /s) as more
110 precise functional output confirmed a differential horizontal semicircular canals and utricular activation (Figure
111 S4F). The larger discharge modulation during rotation around an eccentric *versus* centered axis (Figure S4F2,3)
112 likely derives from utricular signals, supporting the conclusions drawn from eye motion recordings.

113 A predominant if not exclusive utricular origin of swim-related compensatory eye movements was
114 substantiated by two further sets of experiments. First, bilateral injections of 0.5% MS-222 into the otic capsule,
115 known to block vestibular afferent spike discharge [15] reversibly abolished both translational and eccentric
116 rotational motion-evoked eye movements (Figures 3A2,3 red traces, S4C). Second, bilateral semicircular canal-
117 deficient stage 50 larvae were generated by hyaluronidase injections into both otic capsules at stage 44, as
118 previously described in *Xenopus* [16-18]. As confirmation for the absence of bilateral semicircular canals and in
119 compliance with prior studies [17, 18], these animals completely lacked cyclic eye movements during rotation
120 around a centered vertical axis (Figure 3B1,C1). However, lateral translation (Figure 3B2,C2) as well as rotation
121 around eccentric axes (Figures 3B3,C3, S4E) evoked robust, compensatory eye movement. In the absence of all
122 other motion-related sensory signals, these experiments therefore collectively confirm a utricular origin of these
123 eye movements and suggest that the swim style of young tadpoles is able to recruit otolith-ocular pathways for
124 gaze-stabilization.

125

126

DISCUSSION

127 Swimming of stage 47 in contrast to stage 57 larvae is accompanied by strongly curved head
128 trajectories that bilaterally alternate during each swim cycle (Figure 4). The pronounced curvature profile causes
129 considerable centripetal acceleration components and differentially activates utricular signals on both sides that
130 dominate reactive compensatory eye movements, supplanting the negligible angular VOR of young tadpoles.

131 *Developmental plasticity of swimming performance*

132 Tadpoles between stage 47 and 57 experience a 3-4 fold increase in body length, whereas the
133 morphometric ratio of several anatomical markers (Figure S1B) and normalized swim speed remain constant.
134 While this suggests similar swimming dynamics and scaling of forward thrust magnitude with increasing tail
135 propulsive capacity, forward motion is achieved by different propulsive dynamics, respectively (Figures 4A).
136 Parameters such as tail thickness and elastic capacity, relevant for tail bending, are non-linearly scaled with
137 body growth [11]. Thus, the relatively larger mass of the head/body with respect to the tail [19] and smaller
138 Reynolds numbers of small larvae [20] are obviously more relevant factors for stage-specific swim style
139 dynamics. Independent of head motion kinematics, however, gaze-stabilizing eye movements are generated
140 throughout development.

141 *Role of predictive signals for gaze-stabilizing eye movements*

142 The occurrence of predictable visual perturbations during rhythmic locomotor activity, allows gaze-
143 stabilizing eye movements to be evoked by intrinsic copies of the propulsive motor commands [21, 22]. Spinal
144 locomotor efference copies in larval *Xenopus* initiate compensatory eye movements during swimming [11, 23].
145 While initially demonstrated for mid-larval stages, spino-extraocular motor coupling could also play an
146 important role for gaze-stabilization in young larvae. Compensatory eye movements appear early in
147 development, along with free swimming [24] and the maturation of the underlying spinal network [25]. Despite
148 the peculiar motion trajectory, the stereotypic swim style of young larvae make locomotor efference copies
149 nonetheless suitable to elicit gaze-stabilizing eye movements. This feedforward connectivity is however
150 calibrated by vestibular sensory feedback [11,24], which during ontogeny shifts in correspondence with the
151 swim style-related head motion kinematics from utricular only- to utricular and semicircular canal-based
152 signals.

153 *Role of vestibular signals for gaze-stabilizing eye movements*

154 Gaze-stabilizing eye movements derive from a co-joint activation of semicircular canal and otolith
155 organs [14]. Following vectorial decomposition of angular and linear head/body motion components by the
156 endorgans, signals with common spatial field sensitivity converge at the level of central vestibular neurons [26-
157 28]. In compliance with such a fusion, the lateral utricular epithelial sector activates lateral rectus and
158 synergistic medial rectus motoneurons in rats [29] and frogs [30] during left-right translational motion to
159 produce conjugate horizontal eye movements comparable to those during yaw-axis head rotation [14]. This

160 extraocular motor pattern is ideally suited to compensate the presumed horizontal image shifts during such head
161 movements and is likely present in all vertebrates [31]. This varies from the general notion that activation of the
162 lateral utricular sector should elicit vertical/oblique eye movements during roll motion [6, 8], and is potentially
163 related to the neuronal computation underlying a disambiguation of tilt and translational motion. The
164 pronounced central convergence of signals from the horizontal semicircular canal and a lateral utricular
165 epithelial sector [26] thus indicates that different VOR components are not transmitted separately but rather
166 share a common pathway. Within this circuitry, the respective acceleration components are transformed into a
167 single spatio-temporally specific extraocular motor output. Thus, compensatory eye movements during
168 head/body motion originate from sensory-motor processing of co-jointly activated angular and linear head
169 acceleration vectors [14].

170 During ontogeny, the angular and linear VOR become functional with different time courses that
171 depend on the establishment of the neuronal circuitry, computational capacity of individual cellular elements
172 and physical integrity of the sense organs [1, 3, 5, 7]. In compliance with the simpler structure of otolith organs
173 [33], graviceptive gaze-stabilizing and postural reflexes appear very early during ontogeny [1, 12, 13, 32]. In
174 contrast, the functionality of the angular VOR depends on sufficiently large semicircular canals to allow
175 endolymph flow during head rotation [34-37], which is particularly critical for small vertebrates such as fish or
176 amphibian larvae [9, 10]. This limitation causes the horizontal angular VOR in *Xenopus* tadpoles to become
177 functional only at stage 49 [10], precluding semicircular canal signals as the origin of gaze-stabilizing eye
178 movements prior to this stage.

179 The absence of a functional angular VOR in young *Xenopus* larvae could be however supplanted by a
180 functionally equivalent, otolith-derived VOR, provided that the head motion contains the relevant sensory (i.e.
181 linear acceleration) stimuli. This assumption is supported by the finding that angular acceleration in the
182 mammalian vestibular system can be encoded by a linear accelerometer [38,39]. This complies with our finding
183 that adequate compensatory eye movements are activated in semicircular canal-deficient tadpoles (Figure 3B,C).
184 In the absence of semicircular canals, the eye movement-eliciting sensory signals must derive from the
185 utricle(s). Accordingly, activation of utricular signals by bilaterally alternating centripetal, linear acceleration
186 components can evoke spatially specific compensatory eye movements that contribute to offsetting the visual
187 perturbations of swimming-related head motion. The generation of linear acceleration signals during swimming
188 in young *Xenopus* larvae therefore represents a technically elegant solution to overcome the incapacity of small
189 semicircular canals to detect angular acceleration components and to drive an angular VOR.

190

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200

201 **Author Contributions**

202 Conceptualization: FML; HS; MB;

203 Methodology: FML; JBC; ALS; JA; GC; MT; SE; HS; MB

204 Software: ALS; GC; MT; SE

205 Formal analysis: FML; JBC; ALS; JA; GC; SE; MB

206 Investigation: FML; JBC; ALS; JA; MB

207 Writing original manuscript: FML; SE; HS; MB

208 Writing – review and editing: FML; JBC; MT; HS; MB

209 Visualization: FML; JBC; JA; SE; HS; MB

210 Supervision: FML; HS; MB
211 Project administration: FML; MB
212 Funding acquisition: FML; HS; MB

213

214 Declaration of Interests

215 The authors declare no competing interests.

216

217

FIGURE LEGENDS

218 Figure 1. Compensatory eye movements during free swimming.

219 (A) Frame-by-frame motion trajectory of larval swimming at stage 47 (A1) and 57 (A2) obtained from high-
220 speed videos.

221 (B and C) Representative examples of multiple cycles (B) and average (\pm SD, shaded area) over a single cycle
222 (C) of swimming-related head and concurrent compensatory movements of the left (Le) and right (Ri) eye at
223 stage 47 (B1 and C1) and 57 (B2 and C2).

224 (D and E) Scatter plots of eye excursion angle (D) and eye in head ratio (excursion angles of eye/head, E) as
225 function of the head excursion angle.

226 (F and G) Mean swim speed as function of body length (F) at stage 47 ($n = 25$) and stage 57 ($n = 27$) and
227 distribution of mean swim speeds (G); *** $p < 0.001$ (Mann-Whitney U -test).

228 (H and I) Distribution of absolute (H) and normalized average swim speed (I; relative to average swim speed,
229 see G).

230

231 Figure 2. Comparison of head motion trajectories.

232 (A and B) Head trajectory (A1 and B1, see videos S1 and S2); magnified views of the head turn (A2 and B2)
233 over a period of 60 ms (dashed rectangular area marked with * in A1 and B1) during swimming of stage 47 (A)
234 and 57 (B) tadpoles; note that the displacement of the inner side of the head turn (green) causes the head
235 movements (interconnecting lines between the eyes in A2 and B2) to be more accentuated in younger animals;
236 frame-by-frame position of eyeballs and inner ears at the peak of the head turn (A3 and B3) indicate the
237 curvature and the direction (dashed lines) on the inner ear from the first to the last image of the 60 ms time
238 window;

239 (C) Trajectory (mean \pm SEM) of the inner side of the head turn, averaged over 60 ms at the peak of the rotation
240 (A2 and B2) during the swimming episode shown in A1 and B1.

241 (D) Mean velocity of the eye on the inner side of the head turn; note the overall smaller velocity in stage 47
242 animals; *** $p < 0.001$ (Mann-Whitney U -test).

243 (E) Scatter plot depicting the velocity of the inner side of the head turn as a function of normalized swimming
244 speed.

245 (F) Trajectory of the inner ear (otic capsule, OC) on the inner (dark red, black) and outer side (light red, gray) of
246 the head turn over several swim cycles; note the difference in curvature magnitudes at the two stages and the
247 complete overlap of the trajectories of the inner and outer side (red) at stage 57.

248 (G-I) Trajectory (mean \pm SEM) of the inner ear on the inner (dark) and outer side (light) of the head turn (G)
249 averaged from the cyclic swim-related head motion shown in A1 and B1 and F; mean \pm SD of the maximal (H)
250 and Delta curvature (left - right inner ear curvature, I) obtained from all sequences; note that the trajectories of
251 the inner and outer side overlap completely at stage 57 (G); *** $p < 0.001$, **** $p < 0.0001$ (Mann-Whitney U -
252 test).

253 (J) Distribution of centripetal linear acceleration at the level of the inner ears during swimming; corresponding
254 distributions of forward, lateral and angular accelerations are illustrated in Figure S3; **** $p < 0.0001$
255 (Kolmogorov-Smirnov test).

256

257 Figure 3. Influence of rotation axis position on eye movements in tadpoles with intact, pharmacologically 258 impaired or semicircular canal-deficient inner ears.

259 (A) Movement of the left (dark traces) and right (light traces) eye at stage 47 during horizontal rotation with the
260 vertical axis in the center (A1, blue), left-right linear translation (A2, pink; see videos S3) and during off-center
261 (A3; Le-out, purple; see videos S4) under control condition (blue traces) and after injection of 0.5% MS-222
262 into both inner ears (red traces); note that the robust conjugate compensatory eye movements during translation
263 (A2) and off-center rotation (A3) were completely abolished by the local anesthetic.

264 (B and C) Four successive motion cycles (B) and average over a single cycle (mean \pm SEM, C) of the left (dark
265 traces) and right eye (light traces) during horizontal rotation with the vertical axis in the center (B1 and C1,
266 blue), left-right linear translation (B2 and C2, pink) and during off-center (B3 and C3; Le-out, purple) in a
267 semicircular canal-deficient stage 50 tadpole ($n = 5$); note the absence of eye movements during centered
268 vertical-axis rotations and their persistence during off-center rotations and translations.

269

270 **Figure 4. Developmental plasticity of locomotor dynamics and corresponding inner ear organ**
271 **recruitment.**

272 (A) Presumed differential activation of the utricle (utr.), semicircular canals (can.) VOR and spinal feedforward
273 efference copies (Sp. fwd) during swimming at stage 47 and 57 (upper row) in correspondence with changes of
274 head centripetal acceleration and curvature profiles (lower rows).

275 (B) Swim pattern and spatial displacement of the bilateral utricle during the different swimming-related head
276 rotations at stage 47 (left) and stage 57 (right) between time point t_{n-1} (gray) and time point t_n (black); linear,
277 utricular (blue solid arrows) and angular, semicircular canal acceleration components (red solid arrow) are
278 indicated; magenta dashed arrows represent the resulting centripetal linear component during out-axis rotation.
279 α , θ , angular displacement between t_{n-1} and t_n .

280

281

282 **STAR★Methods**

283 **KEY RESOURCES TABLE**

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Chemicals, Peptides, and Recombinant Proteins		
MS-222	Sigma-Aldrich, France	886-86-2
Hyaluronidase	Sigma-Aldrich, France	H1136-1AMP
Deposited Data		
Raw data and videos	This paper, Mendeley data	Mendeley dataset CURRENT-BIOLOGY-D-19-01330 http://dx.doi.org/10.17632/gn6pnsnkv.1
Experimental Models: Organisms/Strains		
<i>Xenopus laevis</i> larva	Centre de Ressources Biologiques Xénopes, UMS 3387, CNRS, Rennes France	N/A
Software and Algorithms		
Software	This paper, mendeley data	Mendeley dataset CURRENT-BIOLOGY-D-19-01330 http://dx.doi.org/10.17632/gn6pnsnkv.1
MATLAB2014b, 2018a MathWorks https://www.mathworks.com/products/matlab.html	MATLAB2014b, 2018a MathWorks https://www.mathworks.com/products/matlab.html	MATLAB2014b, 2018a MathWorks https://www.mathworks.com/products/matlab.html
CED 1401, Signal, Spike 2; Cambridge Electronic Design	Cambridge Electronic Design	http://ced.co.uk/products/spkovin
Dataview	St-Andrew University	https://www.st-andrews.ac.uk/~wjh/dataview/
Custom-build software with Python 3.5	IMAGYS core facility INCLIA CNRS UMR 5287	http://www.incia.u-bordeaux1.fr/spip.php?article629
Other		
Digital camera MemView	MemView, Southern Vision Systems Inc., USA	N/A
60mm lens 1:2.8D, and 50mm lens 1:1.8D lens AF NIKKOR,	Nikon, Japan	https://www.nikon.com/
Digital camera Basler ac1920	Basler AG An der Strusbek 60 – 62 22926 Ahrensburg Germany	https://www.baslerweb.com/en/
Optem MVZL macro video zoom lens, QIOPTIQ	QIOPTIQ	http://www.qioptiq.com/

284

285 **LEAD CONTACT AND MATERIALS AVAILABILITY**

286 Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact,
287 François Lambert (François.Lambert@u-bordeaux.fr). This study did not generate unique reagents.

288 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

289 Animals were obtained from an authorized supplier (Centre de Ressources Biologiques *Xénopes*, UMS 3387,
290 CNRS, Rennes France) and kept in the laboratory in filtered water at 18°C until use for experimentation.
291 Experiments were conducted on *Xenopus laevis* tadpoles of either sex ($n = 72$) at developmental stages 47, 50,
292 52 and 57 [40] and complied with the "Principles of Animal Care", publication No. 86-23, revised 1985 by the
293 National Institute of Health. Experimental protocols were approved by the local ethical committee for animal
294 research at the Université Paris Descartes (#3301100012-A) and the University of Bordeaux
295 (#2016011518042273 APAFIS #3612).

296 **METHOD DETAILS**297 **Anatomical landmarks for motion tracking**

298 To faithfully track head and concurrent eye movements during free swimming in *Xenopus* tadpoles (see
 299 Figure 1), animals were subjected to a topographic mapping of selected anatomical markers prior to the
 300 conduction of behavioral experiments. The position of both eyes and otic capsules (OC, inner ears) in the head
 301 as well as the heart as a reference for the center of the body was determined in each animal (Figure S1A). These
 302 parameters allowed triangulation of the anatomical distances between the eyes and the center of the OCs and
 303 their positions relative to each other and to the heart. To obtain these reference markers, tadpoles were
 304 anesthetized in 0.03% 3-aminobenzoic acid ethyl ester (MS-222; Pharmaq Ltd., Fordingbridge, Hampshire, UK)
 305 in water. Animals were secured to the bottom of a small petri dish and images were taken from the dorsal and
 306 ventral side (MemView Camera, Southern Vision Systems Inc., USA; 60 mm lens 1:2.8D, AF NIKKOR, Nikon,
 307 Japan; Resolution: 1024 x 1024 pixels; Figure S1A). Images were processed off-line using analysis software
 308 (ImageJ) to determine the distances between the different anatomical markers in stage 47 ($n = 24$) and stage 57
 309 tadpoles ($n = 20$; table 1). To compensate for potential inter-individual variations in body size, data were
 310 normalized to the inter-ocular distance. This procedure showed that the relative distance between the otic
 311 capsules and the heart or the eyes and the otic capsules is very similar at both developmental stages (Table 1;
 312 Figure S1B). Based on the better view of the eyes from the ventral side, swimming episodes were video-tracked
 313 with the camera positioned underneath the tank (Figure S1C). The reconstruction of head and eye movements
 314 and the position of both OCs by automated off-line analyses (see below) were performed on the basis of the pre-
 315 determined distances of the respective anatomical structures prior to the video tracking (Figure S1A).

316

Anatomical feature	Stage 47 (in mm)	Stage 47 (normalized)	Stage 57 (in mm)	Stage 57 (normalized)
Eye-Eye	4.1 +/-0.4	1	9.4 +/-0.4	1
Otic capsule-Heart	1.3 +/-0.2	0.4	3.4 +/-0.4	0.38
Eye-otic capsule	2.1 +/-0.3	0.53	4.6 +/-0.6	0.52
Eye-Heart	2.8 +/-0.3	0.68	5.3 +/-0.02	0.57

317

318 **Anatomical feature table:** Anatomical features were studied in stage 47 ($n = 24$) and stage 57 tadpoles ($n =$
 319 20). Distances between the different anatomical markers shown in Figure S1B are reported in mm for stage 47
 320 (first column) and stage 57 (third column), and normalized to the individual inter-ocular distance (second and
 321 fourth column for stage 47 and 57, respectively). Note that the relative distance between the otic capsules and
 322 the heart or the eyes and the otic capsules is constant despite the body growth.

323

324 **High-speed video tracking of swimming episodes**

325 Tracking of swimming episodes and eye movements was performed in two complementary recording
 326 sessions: a first set of experiments aimed at high spatial and temporal resolution of swimming sequences in
 327 order to track eye movements during free swimming. A second set of experiments aimed at tracking the motion
 328 kinematics during longer swimming episodes. Accordingly, the motion kinematics of the head, eye and heart in
 329 space during free swimming was studied in animals (stage 47, $n = 24$; stage 57, $n = 20$) that were placed in a
 330 Plexiglas tank (5 x 25 cm) with a water depth of 5 cm. Video sequences were recorded with a digital camera
 331 (MemView, Southern Vision Systems Inc., USA), positioned underneath the tank (Figure S1C). Eye movements
 332 were tracked by placing the camera as close as possible to the ventral surface of the tank to restrain the field of
 333 view and to increase the spatial resolution. A 60 mm lens (1:2.8D, AF NIKKOR, Nikon, Japan) was used to
 334 monitor magnified views of the animals. A wide-angle lens (50 mm 1:1.8D lens AF NIKKOR, Nikon, Japan)
 335 was used to capture longer swimming episodes and to extract the kinematics of swimming-related head
 336 movements. Light sources (Barefly 200, KINOFLO Lighting system; Figure S1A) were placed underneath the

337 tank and oriented such that variations in light reflections were minimal. A second light source (LED LitePad HO
338 (15 x 30 cm, Rosco, USA) was placed above the pool to provide a homogeneous white illuminated background
339 (Figure S1C). To account for size differences between animals at stage 47 and 57 [19], the distance between
340 camera and tank was adjusted to maintain a similar relative image size of the animal (determined by the inter-
341 ocular distance). Eye and head movements were recorded during separate swimming episodes at an image
342 acquisition rate of 750 and 250 frames per seconds (fps), respectively. Swimming episodes lasted for up to 20
343 tail oscillations (Figure S1D). Only uninterrupted episodes of free swimming that consisted of at least 5
344 consecutive cycles of tail undulations were further analyzed. The analysis was restricted to swimming episodes
345 that occurred in the horizontal plane, i.e. without concurrent roll motion. Head/body roll movements during
346 swimming were detected in the video recordings by calculating the distance between the two eyes. Episodes in
347 which the individual, pre-determined inter-ocular distance cyclically varied by more than 1% (corresponding to
348 ~8° vertical oscillations of the head) due to roll movements were excluded from the analysis. See videos S1 and
349 S2 (also deposited at <http://dx.doi.org/10.17632/gn6pnsnkvm.1>)

350

351 **Video recordings and analysis of eye movements in mechanically secured semi-intact head preparations**

352 Experiments on semi-intact head preparations served to isolate otolith-related eye movements during
353 specific motion stimulation paradigms. All procedures were performed according to the protocol by Bacqué-
354 Cazenave et al. [11]. In brief, *Xenopus* larvae at stage 47 ($n = 5$) were anesthetized in a 0.05% MS-222 solution
355 and placed in oxygenated (95% O₂, 5% CO₂) Ringer solution. The temperature of the bath solution was
356 maintained at 18°C. Viscera and forebrain were removed, the brainstem was exposed to give access to the
357 Ringer solution and the tail was removed at the level of the upper spinal cord. To abolish visual sensory inputs,
358 both optic nerves were transected and the semi-intact preparation was firmly secured onto the Sylgard floor of a
359 chamber with insect pins.

360 The chamber with the preparation was mounted onto a computer-controlled, motorized motion
361 stimulation device that allowed placement of the recording chamber either in the center or at off-center positions
362 with respect to the vertical axis of the stimulator (turntable and sled, Technoshop COH@BIT, IUT de Bordeaux,
363 University of Bordeaux). Motion stimuli consisted of sinusoidal translations at 1 Hz ± 25 mm along the
364 transverse axis, or of sinusoidal rotations at a frequency of 1 Hz and peak stimulus velocities that ranged from
365 $\pm 30^\circ/s$ to $\pm 240^\circ/s$ with the rotation axis either centered between the two OCs or located laterally outside the
366 head (5 mm).

367 Left- and rightward directed eye movements were video-recorded from top at 200 fps with a high-
368 speed digital camera (Basler, ac1920) equipped with a micro-inspection lens system (Optem MVZL macro
369 video zoom lens, QIOPTIQ). Automatic tracking of eye motion segments was performed using a custom-built
370 software written in Python 3.5 environment (IMAGYS core facility, INCIA UMR CNRS 5287). For eye
371 movement measurements, a ROI was drawn around each eye and a binary threshold was applied before tracking
372 the angle between the minor axis of the eye ellipse and the head axis. See videos S3 and S4 (also deposited at
373 <http://dx.doi.org/10.17632/gn6pnsnkvm.1>)

374 Raw data from video recordings were processed off-line and analyzed with Dataview (by W.J. Heitler,
375 University of St Andrews, Scotland). For video image processing, traces of angular movements of the eyes were
376 first filtered with a 25 Hz low-pass filter. Thereafter, maximal angular excursions of the eyes (peak sinewave)
377 were detected for each individual motion cycle and used to calculate the amplitude of eye movements.

378 **Injection of MS-222 or hyaluronidase in the bilateral otic capsule**

379 After video recordings of eye movements in stage 47 semi-intact head preparation under control conditions ($n =$
380 6; see Figure 3A), a calibrated 10 nl volume of a 0.5% MS-222 solution dissolved in artificial endolymph
381 Ringer solution [10,41] was injected into both otic capsules, respectively. The injection was performed by
382 inserting a beveled microelectrode (30°, 10-15 μm tip diameter; GB150F-8P, Science Products GmbH,
383 Germany) inserted into the center of the transparent otic capsule with a micromanipulator under visual control.
384 The calibrated volume of 10 nl was pressure-injected (0.5 bar, 5 s) with a PICOSPRITZER III pressure injector
385 (Intracel, UK). To prevent the developmental formation of semicircular canals on both sides, a previous
386 established method was employed [16-18]. Accordingly, a calibrated volume (10 nl) of a hyaluronidase enzyme
387 solution (0.5 mg/ml, Sigma-Aldrich, France), dissolved in artificial endolymph Ringer solution was injected into
388 bilateral otic capsules of tadpoles at stage 44 ($n = 5$). Subsequently, animals were allowed to develop into older
389 stages.

390

391 **Electrophysiological recording of extraocular motor nerve spike discharge**

392 Recording of extraocular motor nerve activity was performed *in vitro* in semi-intact preparations of
393 stage 50 ($n = 4$) *Xenopus* tadpoles as described previously [10, 23]. In brief, animals were deeply anesthetized in
394 a cold (4-6°C) solution of 0.05% MS-222 in frog Ringer (75 mM NaCl, 25 mM NaHCO₃, 2 mM CaCl₂, 2 mM
395 KCl, 0.5 mM MgCl₂, and 11 mM glucose, pH 7.4) and decapitated at the level of the upper spinal cord. The skin
396 covering the dorsal region of the head was removed, the soft skull tissue opened and the forebrain disconnected.
397 This surgical procedure anatomically preserved the remaining central nervous system, bilateral inner ear
398 endorgans in the OCs including the VIIIth nerves as well as the extraocular motor nerves and eye muscle
399 innervations [10]. After selective disconnection of the abducens nerve from the lateral rectus (LR) target muscle,
400 preparations were transferred to a Sylgard-lined Petri dish (volume 5 ml), and continuously superfused with
401 oxygenated Ringer solution at a rate of 1.5 - 2.1 ml/min and a temperature of 17°C ± 0.1°C.

402 Multi-unit spike discharge of the LR nerve was recorded with glass suction microelectrodes, produced
403 with a horizontal puller (P-87 Brown/Flaming, Sutter Instruments Company, Novato, CA, USA). Electrode tips
404 were broken and individually adjusted to fit the LR nerve diameter. Natural activation of vestibular endorgans
405 was performed with a computer-controlled, motorized two-axis turntable (ACT-1002, Acutronic USA Inc.,
406 Switzerland) as described previously [10, 23]. The recording chamber with the preparation was mounted onto a
407 custom-built plate that allowed placement of the recording chamber either in the center or at off-center positions
408 with respect to the vertical axis of the turntable. Accordingly, the rotational axis was either centered between the
409 two OCs or located laterally outside the head. This configuration allowed recordings of LR nerve spike
410 discharge during centered or off-center vertical-axis head rotations. Motion stimuli consisted of sinusoidal
411 oscillations at a frequency of 1 Hz and a peak stimulus velocity that ranged from ±30°/s to ±240°/s. Spontaneous
412 and evoked multi-unit LR nerve spike discharges were recorded (Ext 10-2F; npi Electronics, Tamm, Germany),
413 digitized (10 kHz), stored on a computer and analyzed off-line (CED 1401, Signal, Spike 2; Cambridge
414 Electronic Design). The magnitude of the discharge modulation was determined by calculating the difference
415 between minimum and maximum firing rates of the averaged discharge over a single turntable motion cycle
416 [10].

417 **QUANTIFICATION AND STATISTICAL ANALYSIS**

418 **Analysis of head and otic capsule (inner ear) kinematics**

419 Custom image processing and analysis software was developed in Matlab to track head and eye
420 movements in video recordings and to determine 2-D spatial positions (X-Y coordinates) of the left and right
421 eye based on a frame-by-frame analysis with the Video Spot Tracker 5.3 (credit: CISMM at UNC-CH; see
422 acknowledgments). Predetermined anatomical landmarks (see above; Supplemental table 1) were used to
423 calculate the 2-D position of the heart as well as the position of the left and right OCs with respect to the X-Y
424 coordinates of the heart and eyes (Figure S1D).

425 The trajectories of four anatomical markers (head, heart, left and right OC) were further analyzed in
426 Matlab to provide relevant kinematic variables (curvature of head trajectories; acceleration magnitudes of heart,
427 eyes and OCs) that represent the animals' motion trajectory and swimming performance. A non-uniform circular
428 mobile point kinematic model was used to describe the curved trajectories of the landmarks (Figure S1D). In
429 this model, the trajectory of a moving point was decomposed into series of local circular trajectories (Figure
430 S1E), defined by a particular center and radius calculated for each video frame. This kinematic model allowed
431 distinguishing forward, lateral, centripetal and angular components of the acceleration profile for both OCs
432 during off-center head movements produced by undulatory tail-based swimming.

433 **High-speed video recordings and analysis of eye movements during episodes of free swimming**

434 Sequences of individual images were analyzed off-line using a custom Matlab script. Tracking of the
435 eyes and calculation of head-in-space and eye-in-space angular positions were performed using a semi-
436 automatic frame-by-frame analysis as described previously [42]. Briefly, a region of interest (ROI) was drawn
437 around each eye and processed using binary thresholding. This made the eyeball and lens to appear as two
438 distinct black/white morphological structures. The position of each eye in space was computed as the orientation
439 of the major axis of an ellipse, which approximates the outline of the eye [42]. The position of the head-in-space
440 was obtained from the angle of the inter-ocular connection line between the two eyes. These values served to
441 estimate the efficiency of compensatory eye movements during concurrent swimming-related head movements.
442 Accordingly, the magnitude of the eye motion with respect to the head motion was determined as the ratio
443 between the eye-in-space angle and the head-in-space angle.

444 **Statistics**

445 Free swimming kinematic values generated in CSV files obtained from Matlab were analyzed using
446 OriginPro 8 (OriginLab Corporation, USA). Data are presented as mean ± standard error of the mean (SEM)

447 unless stated otherwise. For whisker box plots shown in Figure 1G and Figure 2H,I, black circles represent 1%
448 and 99%, respectively; black bowls represent the mean, error bars are \pm SEM. Non-parametric unpaired Mann-
449 Whitney *U*-test was used to determine significant differences between mean values (detailed statistical
450 descriptions are provided in the respective result section and corresponding figure legends). Non-parametric
451 Kolmogorov-Smirnov test was used to determine significant differences between data distribution (detailed
452 statistical descriptions are provided in the respective result section and corresponding figure legends). Statistical
453 tests were performed with Prism 7.0 (GraphPad). Eye/head motion phase relationships were calculated with
454 Oriana 4.02 (Kovach computing services, UK).

455

456 DATA AND CODE AVAILABILITY

457 The accession number for the original videos and datasheets and experimental software generated through this
458 study have been deposited to Mendeley dataset CURRENT-BIOLOGY-D-19-01330
459 (<http://dx.doi.org/10.17632/gn6pnsnkvm.1>)

460

461 SUPPLEMENTAL VIDEOS

462 **Video S1. Video sequence of free swimming stage 47 larva. Related to Figure 2**

463 **Video S2. Video sequence of free swimming stage 57 larva. Related to Figure 2**

464 **Video S3. Video sequence of stage 47semi-intact head preparation during lateral translation. Related to**
465 **Figure 3**

466 **Video S4. Video sequence of stage 47semi-intact head preparation during out-axis rotation. Related to**
467 **Figure 3**

468 High resolution versions of supplemental videos are available at <http://dx.doi.org/10.17632/gn6pnsnkvm.1>

469

470

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- 567

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Please upload the completed table as a separate document. **Please do not add subheadings to the Key Resources Table.** If you wish to make an entry that does not fall into one of the subheadings below, please contact your handling editor. (NOTE: For authors publishing in *Current Biology*, please note that references within the KRT should be in numbered style, rather than Harvard.)

KEY RESOURCES TABLE CURRENT-BIOLOGY-D-19-01330

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Antibodies		
<i>none</i>		
Bacterial and Virus Strains		
<i>none</i>		
Biological Samples		
<i>none</i>		
Chemicals, Peptides, and Recombinant Proteins		
MS-222	Sigma-Aldrich, France	886-86-2
Hyaluronidase	Sigma-Aldrich, France	H1136-1AMP
Critical Commercial Assays		
<i>none</i>		
Deposited Data		
Raw data and videos	This paper, Mendeley data	Mendeley dataset CURRENT-BIOLOGY-D-19-01330 http://dx.doi.org/10.17632/gn6pnsnkvm.1

Experimental Models: Cell Lines		
none		
Experimental Models: Organisms/Strains		
<i>Xenopus laevis</i> larva	Centre de Ressources Biologiques Xénopes, UMS 3387, CNRS, Rennes France	N/A
Oligonucleotides		
none		
Recombinant DNA		
none		
Software and Algorithms		
Software	This paper, mendeley data	Mendeley dataset CURRENT-BIOLOGY-D-19-01330 http://dx.doi.org/10.17632/gn6pnsnkvm.1
MATLAB2014b, 2018a MathWorks https://www.mathworks.com/products/matlab.html	MATLAB2014b, 2018a MathWorks https://www.mathworks.com/products/matlab.html	MATLAB2014b, 2018a MathWorks https://www.mathworks.com/products/matlab.html
CED 1401, Signal, Spike 2; Cambridge Electronic Design	Cambridge Electronic Design	http://ced.co.uk/products/spkovin
Dataview	St-Andrew University	https://www.st-andrews.ac.uk/~wjh/dataview/
Custom-build software with Python 3.5	IMAGYS core facility INCIA CNRS UMR 5287	http://www.incia.u-bordeaux1.fr/spip.php?article629
Other		
Digital camera MemView	MemView, Southern Vision Systems Inc., USA	N/A

60mm lens 1:2.8D, and 50mm lens 1:1.8D lens AF NIKKOR,	Nikon, Japan	https://www.nikon.com/
Digital camera Basler ac1920	Basler AG An der Strusbek 60 – 62 22926 Ahrensburg Germany	https://www.baslerweb.com/en/
Optem MVZL macro video zoom lens, QIOPTIQ	QIOPTIQ	http://www.qioptiq.com/

Figure 1

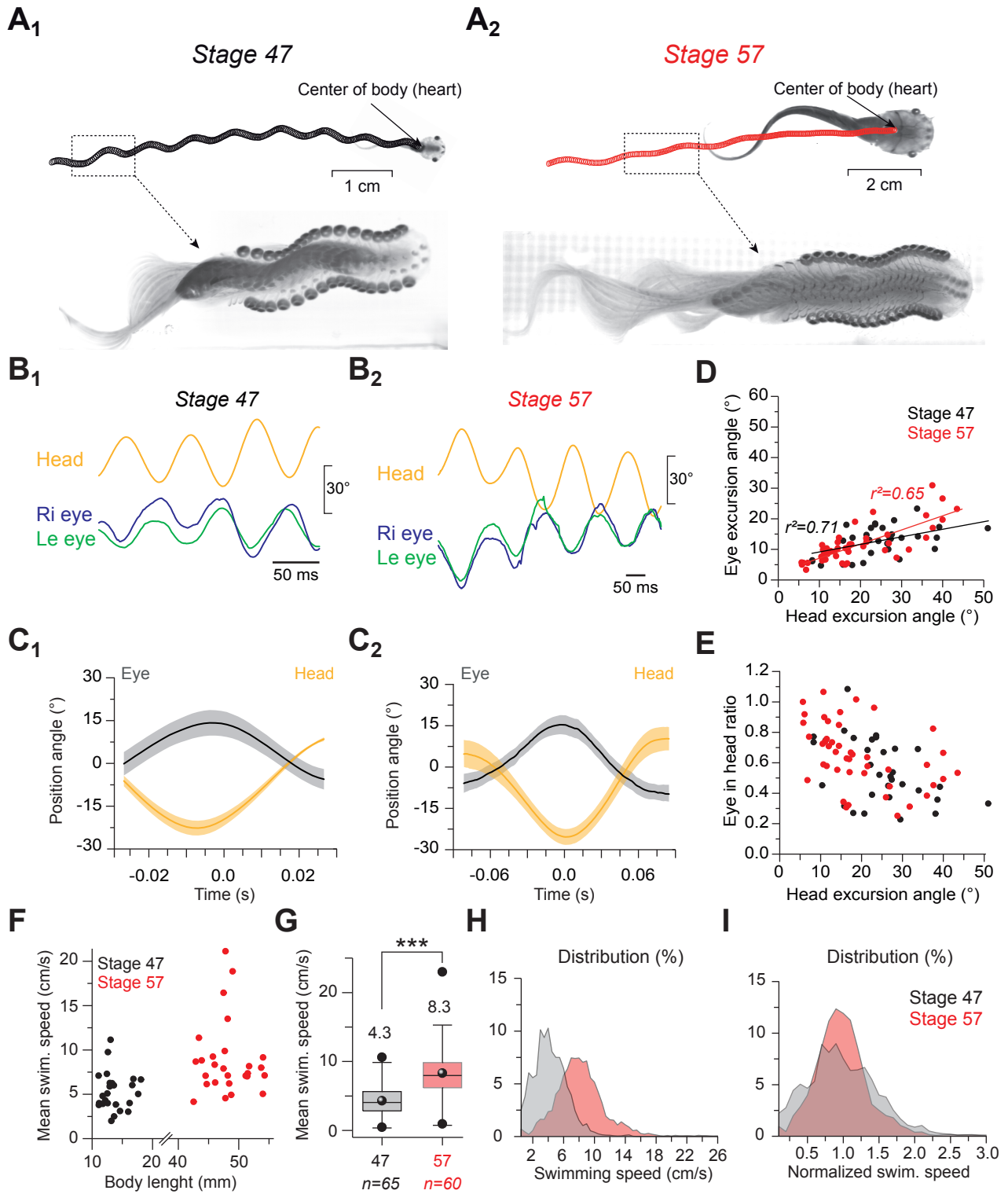


Figure 2

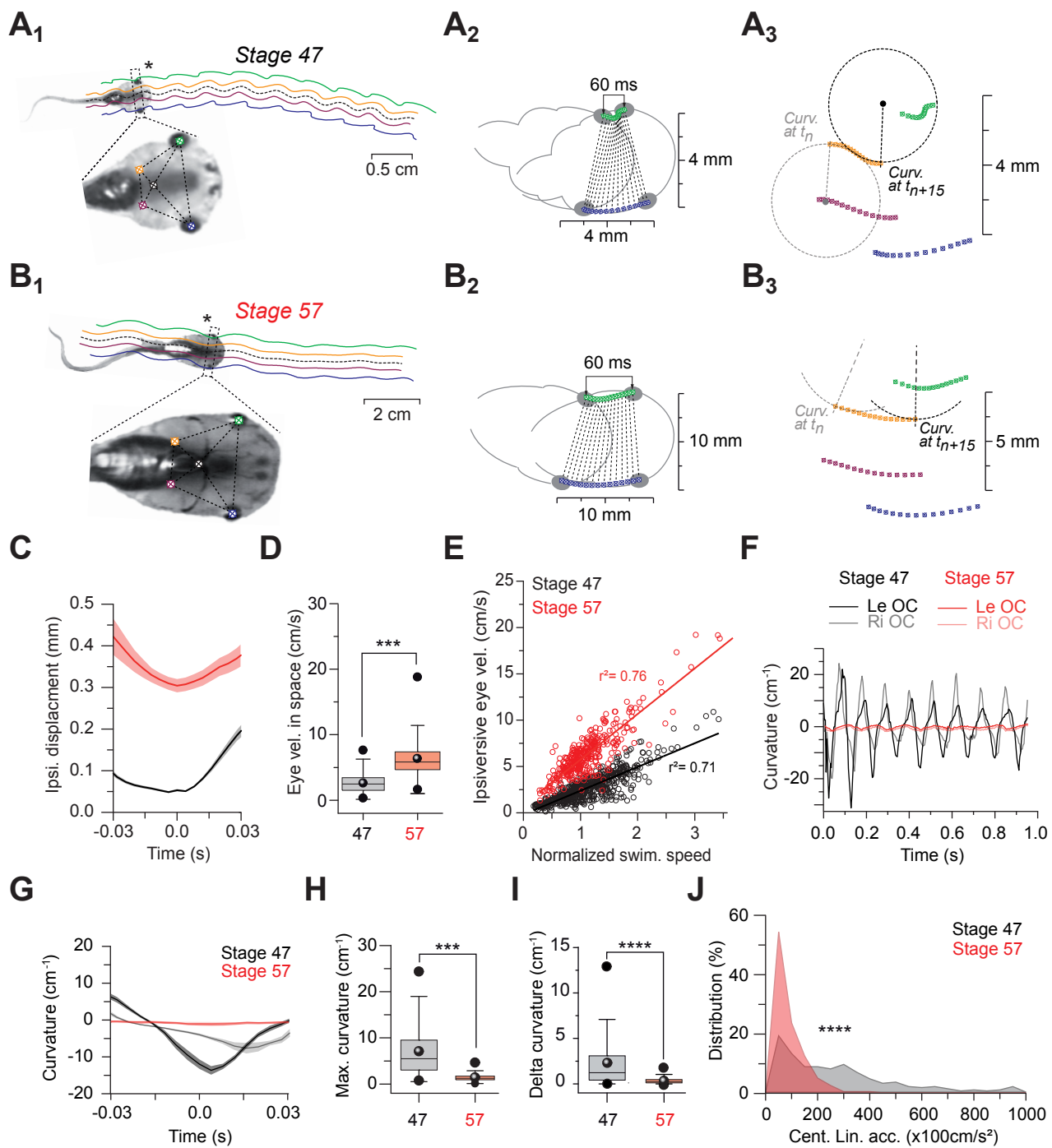


Figure 3

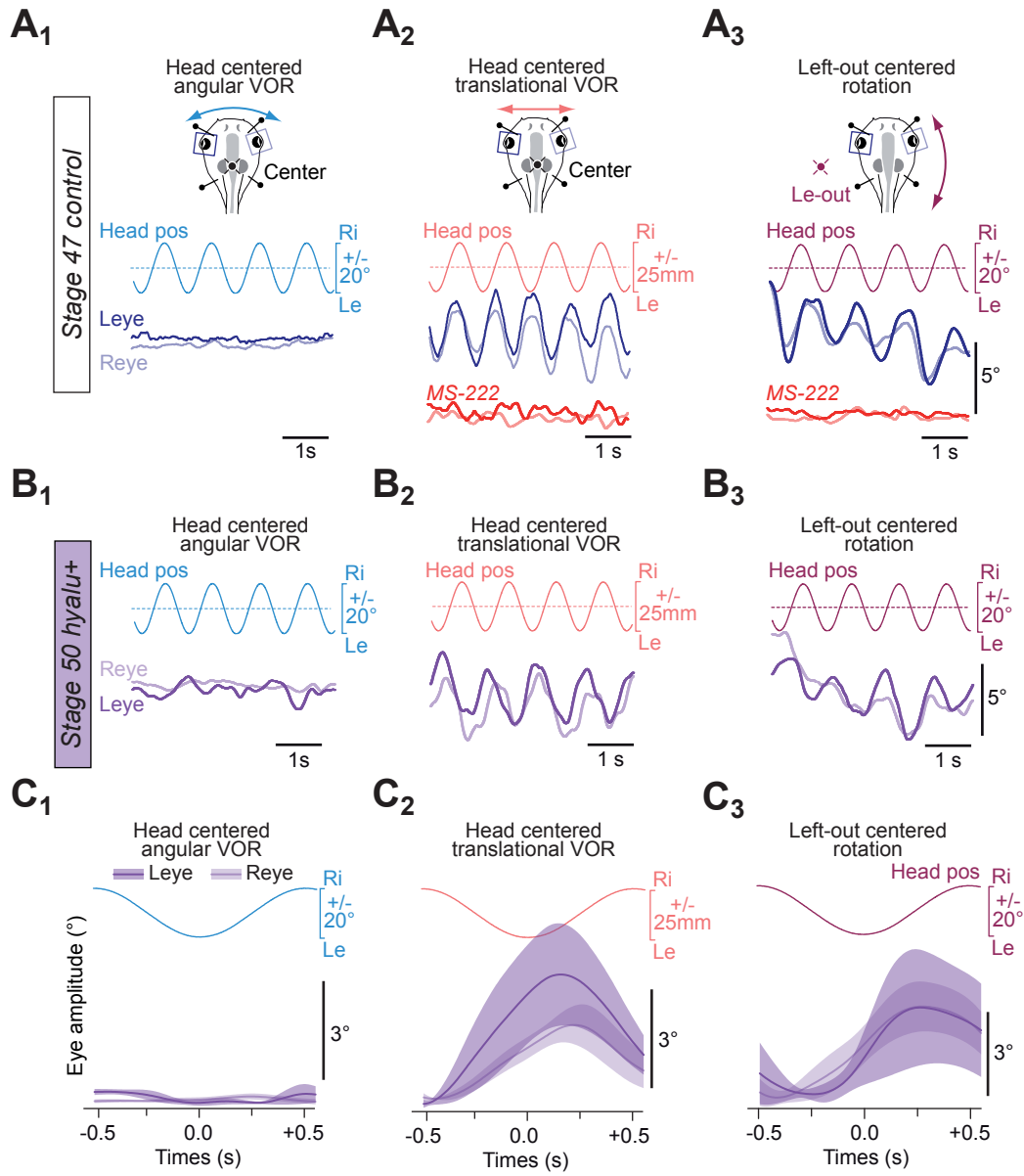
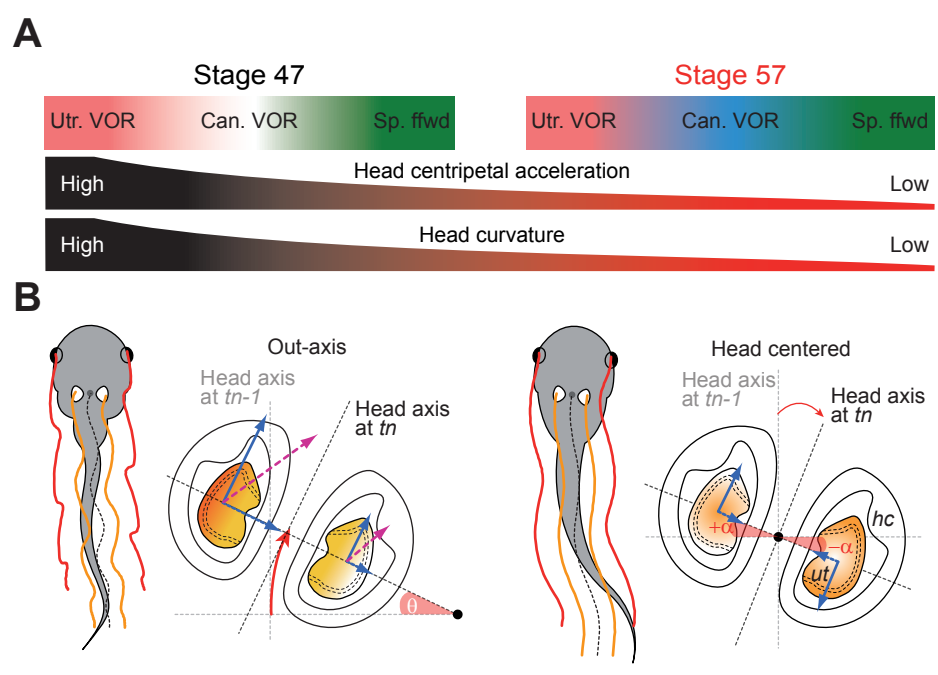


Figure 4



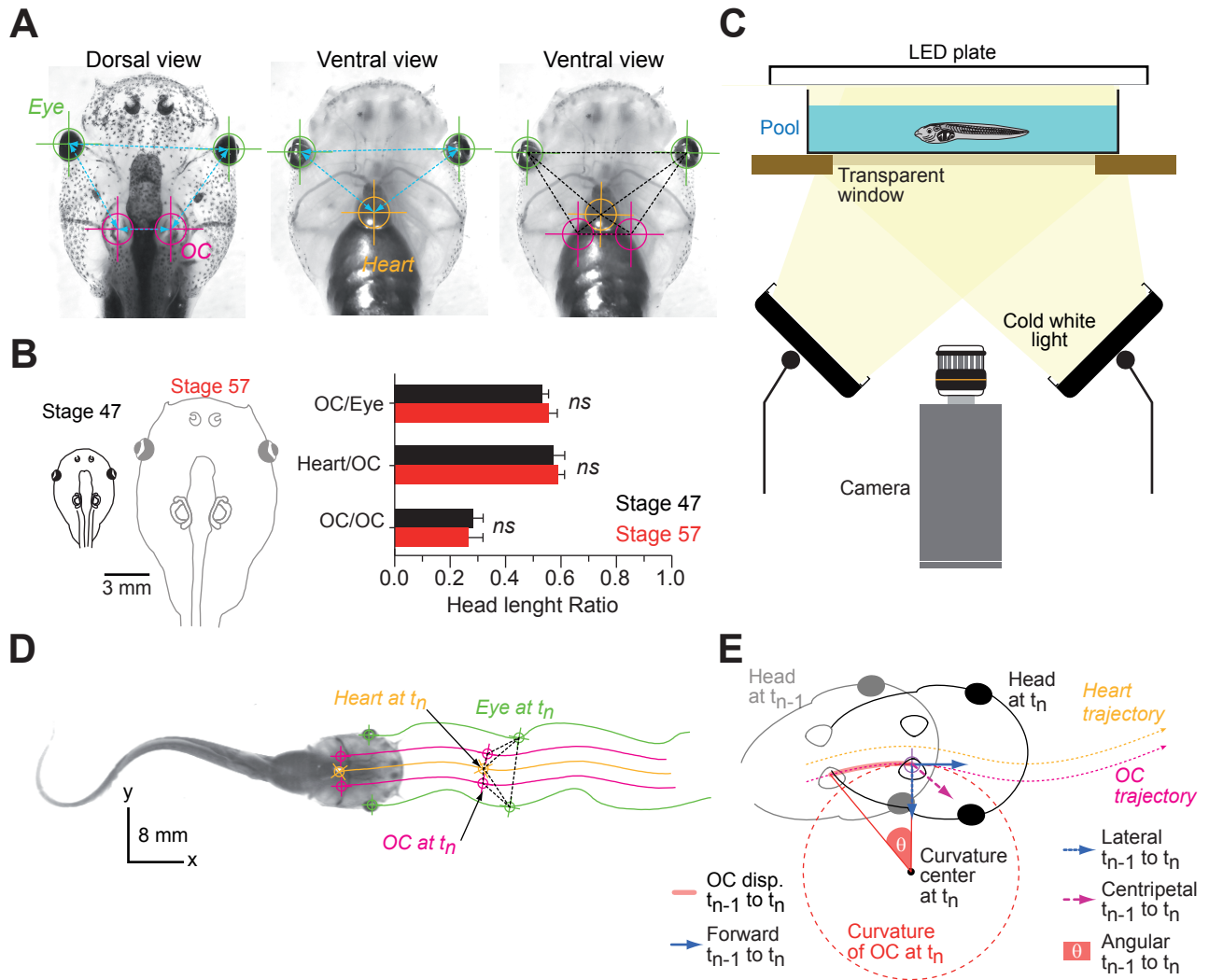


Figure S1. Morphometric analysis of anatomical features and off-line calculation of head motion kinematic parameters. Related to Figure 1 and 2.

(A) Images depicting dorsal (left) and ventral views (middle, right) of a stage 57 larvae with outlined locations and measured or triangulated relative distances between eyes (green), heart (orange) and otic capsules (OC, magenta); anatomical markers served subsequently as landmarks for tracking the head motion during swimming.

(B) Scaled drawings of the head/body at stage 47 and 57 (left) and morphometric ratios of measured or calculated anatomical markers (right); note that despite size differences, relative distances between eyes, heart, OC remain constant during development, *ns*, not significant (Mann-Whitney *U*-test).

(C) Schematic of the set-up for high speed (500 fps) video recordings of free swimming.

(D) Ventral view of video imaged swimming of a stage 57 tadpole depicting the tracked trajectories of both eyes (green) and the triangulated heart (orange) and OCs (magenta) at the time point t_n .

(E) Schematic summarizing the trajectory of the triangulated motion of the OC along with the direction and size of the forward, lateral, centripetal and angular acceleration vectors calculated from the displacement (disp.) between time point t_{n-1} (gray) and time point t_n (black); θ , angular displacement.

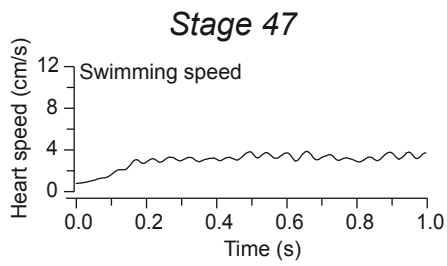
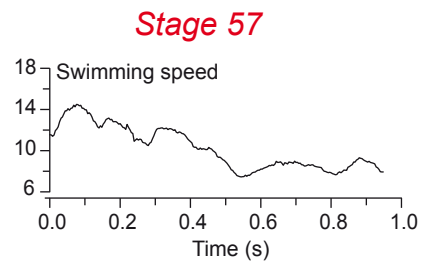
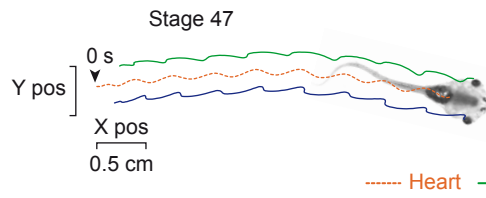
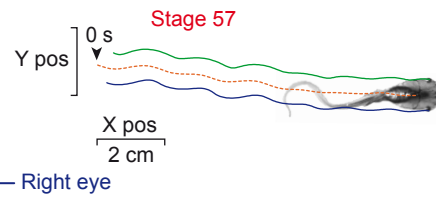
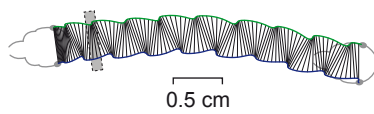
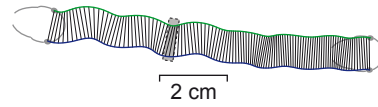
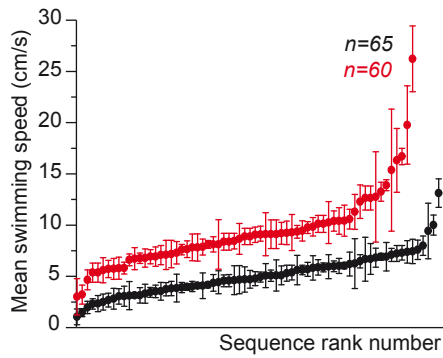
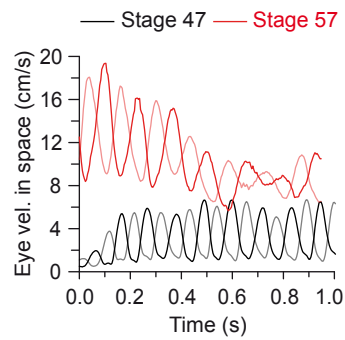
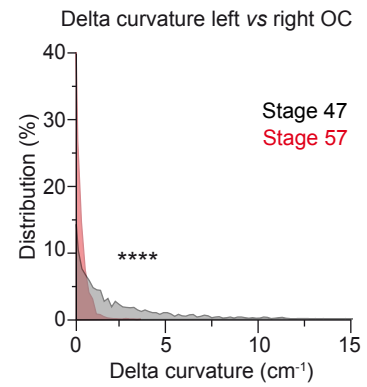
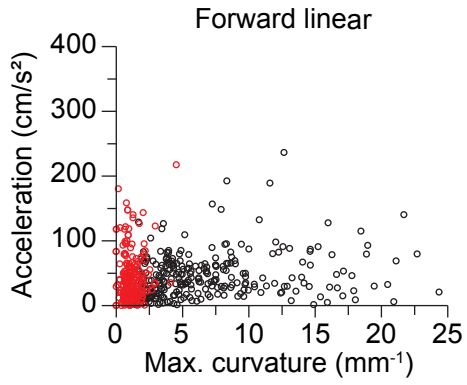
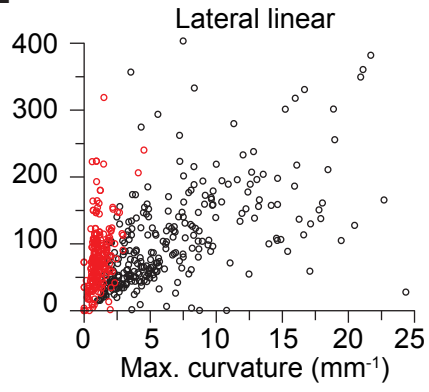
A₁**A₂****B₁****B₂****C₁****C₂****D****E****F**

Figure S2. Comparison of swimming speed. Related to Figure 2.

(A, B and C) Instantaneous swimming speed (A1 and A2) obtained from the extracted trajectory of the body center (heart, B1 and B2) and extracted horizontal head movements during swimming (C1 and C2).

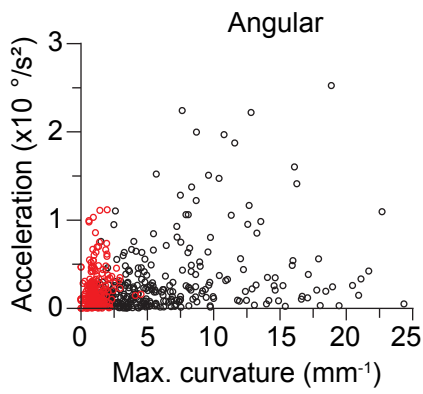
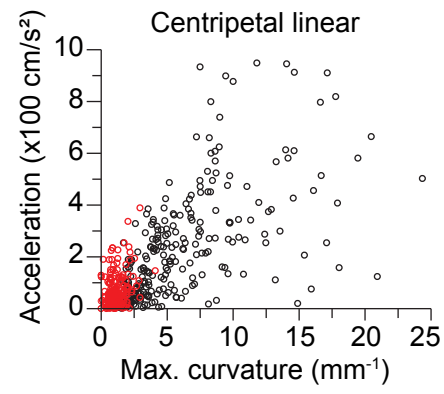
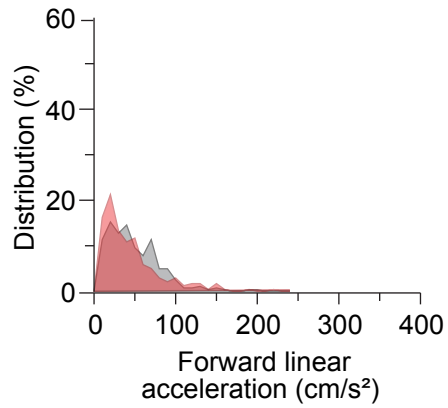
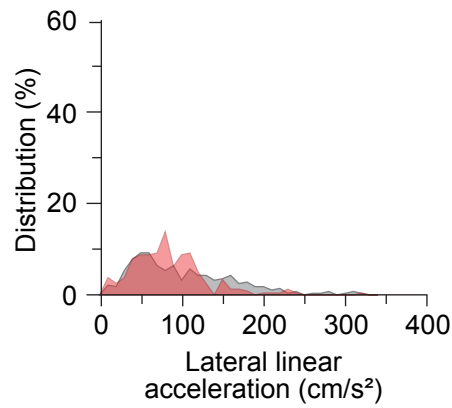
(D and E) Sequence ranked mean swim speed (\pm SD; D) and velocity of the inner side of the head turn on the left (solid lines) and right (dotted lines) side (E).

(F) Distribution of the Delta curvature (left - right inner ear curvature) obtained from all swimming sequences; **** $p < 0.0001$ (Kolmogorov-Smirnov test).

A₁**A₂**

Stage 47

Stage 57

A₃**A₄****B₁****B₂**

Stage 47

Stage 57

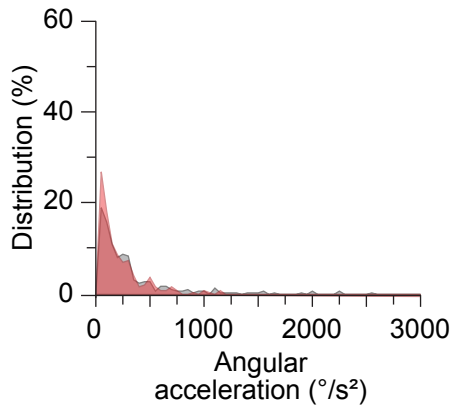
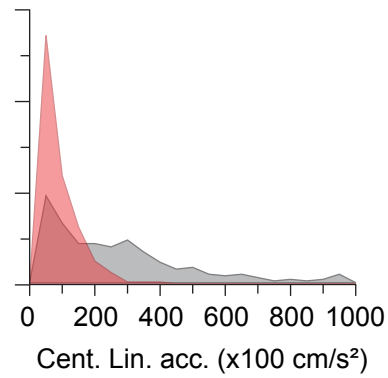
B₃**B₄**

Figure S3. Magnitudes and distribution of head acceleration components during swimming. Related to Figure 2.

(A and B) Scatter plots (A) and relative distributions (B) of forward linear (A1 and B1), lateral linear (A2 and B2), angular (A3 and B3) and centripetal linear (A4 and B4) acceleration components, calculated for the OC at the peak curvature of each swimming cycle; note the marked difference in the distribution profile of centripetal linear acceleration components of stage 47 and 57 tadpoles.

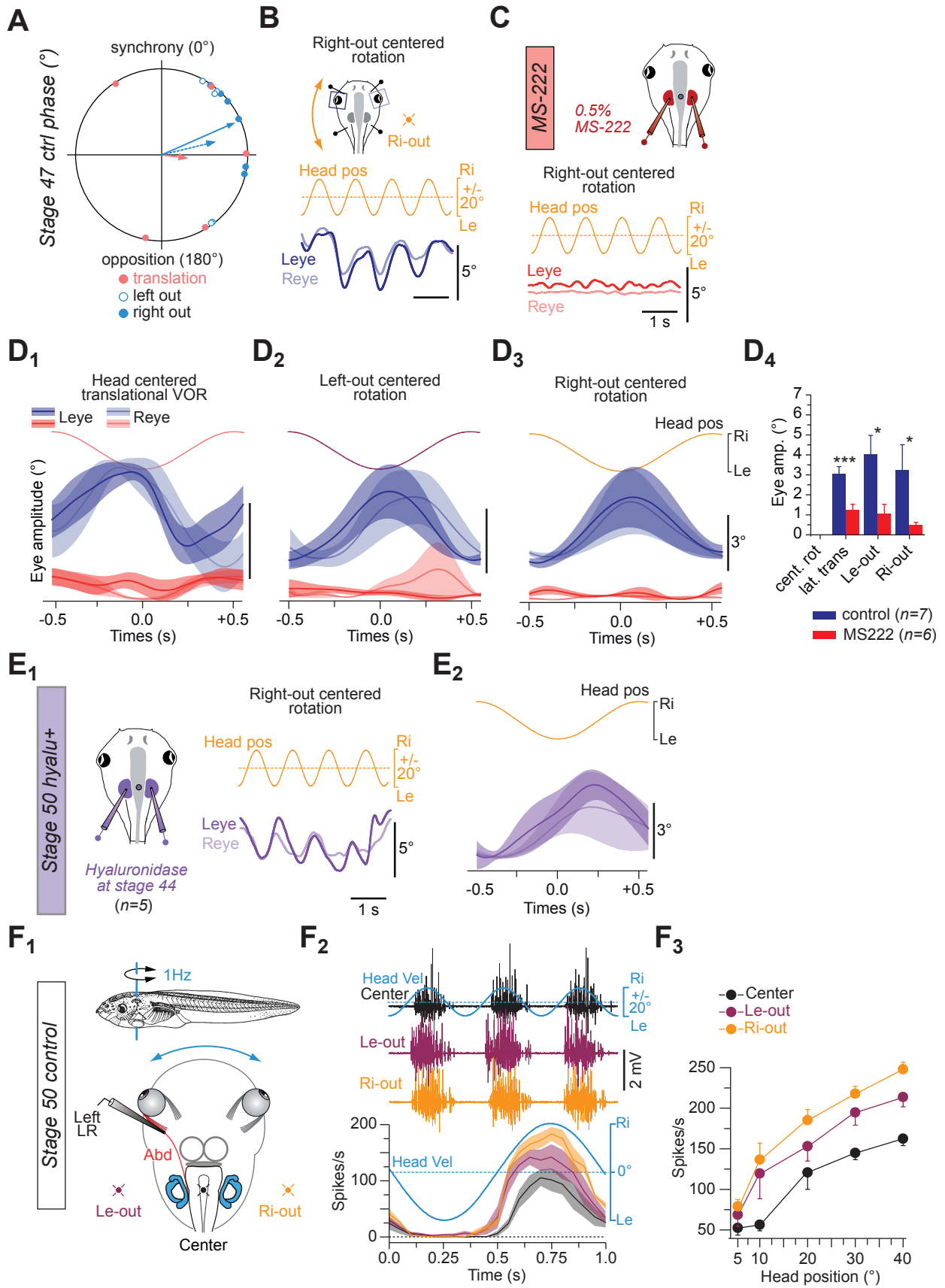


Figure S4. Eye movements and extraocular motor discharge under control conditions and after impairment of the sensory transduction. Related to Figure 3.

(A) Phase relation of cyclic eye movements during translation and rotational motion around off-center axes positioned on the left (le-out) and right side (ri-out) at stage 47 under control condition.

(B, C and D) Movement of the left (dark traces) and right (light traces) eye at stage 47 during horizontal rotation with the vertical axis off-center (Ri-out, orange) under control condition (B) and after injection of 0.5% MS-222 into both inner ears (C); note that eye movements were completely abolished by the local anesthetic. See supplemental videos 3A2 and A3.

(D) Average over a single cycle (mean \pm SEM) of the left and right eye during translational motion (D1) and horizontal rotation with the position of the off-center vertical axis left-out (D2) or right-out (D3) before (blue traces) and after injection of 0.5% MS-222 ($n = 6$) into both inner ears on stage 47 tadpoles; note the significant reduction of the respective eye motion amplitudes after the injection (D4); * $p < 0.05$, *** $p < 0.001$ (Mann-Whitney U -test);

(E) Four successive motion cycles (E1) and average over a single cycle (mean \pm SEM, E2) of the left and right eyes during horizontal rotation with the vertical axis off-center (Ri-out) in semicircular canal-deficient stage 50 tadpoles ($n = 5$); note the persistence of eye movements.

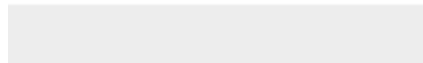
(F) Schematic of a semi-intact stage 50 whole-head preparation of larval *Xenopus* (F1) depicting abducens motor nerve recordings during horizontal rotation around a vertical axis in the center (black) or off-center on the left (Le-out, purple) or right side (Ri-out, orange); single sweeps of abducens nerve discharge during sinusoidal horizontal rotation (blue trace) around the le-out axis (top, purple), center (middle, black), and ri-out axis (bottom, orange) at 1 Hz and $\pm 120^\circ/\text{s}$ peak velocity (top traces in F2); average abducens nerve firing rate modulation (\pm SEM, shaded areas, bottom traces in F2) over a single motion cycle (blue trace) and firing rate (mean \pm SEM) as function of peak head velocity (F3) during 1 Hz rotation around the three different axes; note that the LR nerve spike discharge, phase-timed with contraversive head peak velocity, was modulated during rotations (1 Hz; $\pm 30 - 240^\circ/\text{s}$) around on- and off-center axes; however, peak firing rates were consistently larger for rotations around an eccentric compared to the centered axis with larger responses following rotations around the eccentric axis contralateral to the recorded LR nerve.



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Video S1.mp4

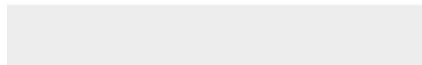




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