

### The Development of the Static Vestibulo-Ocular Reflex in *Xenopus*

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The relation between the amount of the static vestibulo-ocular reflex arc and the developmental stage is characterized by an optimum function. The reflexes occur before the labyrinth is completely developed, but at this time, bilateral connections of the labyrinth with the oculomotor centers are efficient.

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Although the morphological development of the labyrinth is well investigated [1, 2], very little information exists about the functional development of the vestibular system. In *Xenopus laevis* Daudin, Horn and Rayer [3] started to investigate the functional development of the vestibular system using the central compensation of defects caused by hemilabyrinthectomy. The following experiments are a further contribution to the study of the functional development of the vestibular system in the clawed toad.

Tadpoles from stage 41 to stage 66 and juvenile toads two and four months after metamorphosis (for the definition of the developmental stages see [4]) were tilted around their longitudinal axis. The relation between the tilt angle  $\gamma$  and the position  $\alpha$  of both eyes were determined by measuring the angle between the body's dorso-ventral axis and the diam-

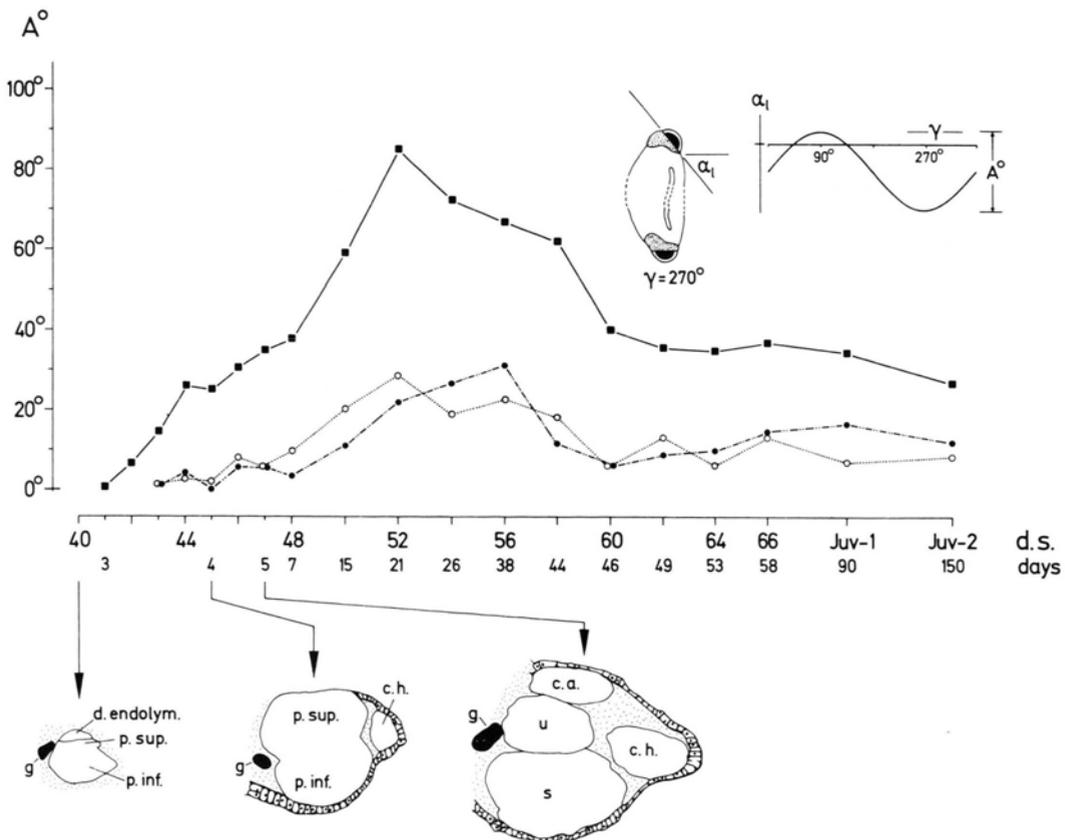


Fig. 1. The relation between the magnitude  $A^\circ$  of the vestibulo-ocular reflex and the developmental stages *d. s.* of the clawed toad.  $A^\circ$  is defined by the term  $A_{l,r}^\circ = \alpha_{l,r}(\gamma = 90^\circ) - \alpha_{l,r}(\gamma = 270^\circ)$ .  $\alpha_{l,r}$  is the position of the left and right eye, respectively. The lowest row of numbers are the days after fertilization. The figures below the graph demonstrate the development of the labyrinth for the developmental stages 40, 45 and 47. *c. a.* canalis anterior; *c. h.* canalis horizontalis; *d. endolym.* ductus endolymphaticus; *g* ganglion VIII; *p. inf.* pars inferior; *p. sup.* pars superior; *s* sacculus; *u* utriculus. ■—■ intact animals, mean of both eyes; ○ ··· ·○ right eye and ● ··· ·● left eye of the leftside hemilabyrinthectomized animals.



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eter of the pupil (see inset figure in Fig. 1). For each eye, the angular difference  $A$  between the eye positions  $\alpha$  for  $\gamma=90$  and  $270^\circ$  were used to characterize the development of the vestibulo-ocular reflex. The experiments were performed with intact, hemilabyrinthectomized on the left side and bilaterally labyrinthectomized animals.

In intact tadpoles, the reflexes are clearly visible at stage 43. During this period, the labyrinth is not completely developed (Fig. 1).  $A$  increases rapidly up to stage 52. After reaching the maximal value,  $A$  decreases gradually to an almost constant value for tadpoles at stage 60 and older.

In all hemilabyrinthectomized stages,  $A$  is smaller than the half the value of the intact ones. But  $A$  also reaches a distinct maximum in stages 52 to 54. The differences between the values of  $A$  for the left and right eye are not significant.

In bilaterally labyrinthectomized animals, which have been investigated beginning from stage 46,  $A$  is always about zero in all stages. The loss of the reflex after this operation proves the great importance of the labyrinth to elicit the vestibulo-ocular reflex.

The increase in the magnitude  $A$  of the reflex up to stage 52 may be caused by the increasing efficien-

cy of the structures involved in this reflex arc, including the sensory cells, the central neurones and the eye muscles. The decrease of  $A$  for stages older than 52 may be due to an increasing formation of the efferent innervation of the labyrinth which could originate from the brain stem and the basal zones of the cerebellum [5]. On the other hand, intensified inhibitory processes via the vestibulo-ocular loop or the vestibulo-cerebello-oculomotor loop [6, 7] may cause the marked decline of  $A$ . It is not very probable that the structural changes of the head during the metamorphosis are responsible for this decline because  $A$  decreases before these morphological changes occur.

The experiments with hemilabyrinthectomized animals prove that bilateral connections of the labyrinth with the oculomotor centers exist when the static reflexes appear. But in tadpoles younger than stage 48, the input from both labyrinths seems to be necessary to produce a suprathreshold excitation of the motor neurones of the eye muscles.

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