The development of the static vestibulo-ocular reflex in the Southern Clawed Toad, *Xenopus laevis*

III. Chronic hemilabyrinthectomized tadpoles

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Summary. The static vestibulo-ocular reflex was investigated in tadpoles at different times following unilateral destruction of the labyrinth during the period of early organogenesis and premetamorphosis. Balance compensation is completed after a few weeks, while gain compensation only occurs partially (Figs. 2–4). Tadpoles hemilabyrinthectomized in the age of 2.5 days (stage 38) develop no vestibular nuclei on their lesioned side, while tadpoles operated later in their life, possess these nuclei (Figs. 5, 6) even if they were not detectable at the operation day (Fig. 7). For their dorsal vestibular nucleus (DVN), the number of neurons is usually larger on the intact than on the lesioned side; while for the ventral vestibular nucleus (VVN), there is either numerical symmetry or a transient decrease of cell number on the intact side (Fig. 5).

The results demonstrate that vestibular compensation occurs even if vestibular nuclei have developed only on one side, i.e. the vestibular commissure is not a prerequisite for a successful compensation process. It is discussed whether the use of extra-vestibular error signals for balance but not for gain compensation may cause the differences in time courses of both compensation processes.

Introduction

Unilateral labyrinthectomy causes behavioural defects in adult as well as in young animals (cf. review of Schaefer and Meyer 1974). These defects disappear after some time completely or partially (vestibular compensation). As the acute symptoms of the behavioural defects as well as their elimination are so clear, vestibular compensation is one of the best known examples of neuronal plasticity.

In looking for basic mechanisms of vestibular compensation in vertebrates, one fundamental observation is that older animals need a longer time to compensate for these defects than young ones (Schaefer and Meyer 1973; Horn and Rayer 1978; Maioli et al. 1983; Rayer et al. 1983), for which the increasing complexity of the vestibular nervous network may be responsible. Recent experimental observations also indicate that pathways interconnecting the bilateral vestibular nuclei may be a prerequisite for successful compensation, by providing positive feedback-loops for signals across the midline (Bienhold and Flohr 1978; Galiana et al. 1984).

The analysis of vestibular compensation has, however, to consider two aspects: balance and gain compensation. Balance compensation concerns the restoration of normal body symmetry, normal pattern of eye movements, etc., which can be detected under "stimulus-free" conditions. Gain compensation deals with the restoration of normal function, i.e. normal response to a well-defined stimulus. In amphibians, balance compensation is investigated for both body and eye posture (Flohr et al. 1981; Rayer et al. 1983). Axonal sprouting was considered as the anatomical basis for the underlying processes (Dieringer and Precht 1979a, b).

There is, however, no observation concerning the gain compensation in the static vestibulo-ocular reflex of amphibians. The aim of the present study was, therefore, to give insight in this type of neural plasticity.
of vestibular plasticity using the static VOR. Additionally, neuroanatomical investigations were incorporated in this study, to explore also the effect of early labyrinth removal on the formation of the medullary projection areas of the VIIIth nerve. Young tadpoles are most suitable for these experiments because unlike adult toads they compensate for their eye posture defect in a reasonable short time (Rayer et al. 1983), and the formation of the vestibular nuclei occurs during pre- and prometamorphic stages (Horn et al. 1986a).

Materials and methods

Tadpoles of Xenopus laevis were taken from the stock of the Zoological Institute of the University of Karlsruhe. Details concerning apparatus, operation techniques, collection and treatment of data, and definitions are given in Horn et al. (1986a). Some remarks about handling of animals are necessary.

When tadpoles from the same brood have reached a certain developmental stage, they were divided into three groups. One group was hemilabyrinthectomized immediately (chronic group). The other two groups were kept intact, and handled as the chronic group till the experimental day. At this day, one group was operated, and tested one hour later (acute group). The third group was only exposed to MS 222 treatment (intact group).

For the behavioural experiments, three chronic groups were prepared. One was operated during the developmental period of 36–38 when swimming occurs. The second group was operated at stage 41/42, immediately before the static vestibulo-ocular reflex develops. The third group was operated at stage 50, after the dorsal vestibular nucleus (DVN) has separated from the ventral vestibular nucleus complex (Horn et al. 1986a).

For the anatomical investigations, tadpoles were hemilabyrinthectomized at stages 38, 42, 48, 54, and 58, and sacrificed at stages 54 or 66. The Klüver-Barrera staining (Romeis 1968) was chosen to determine number of large and small neurons in the dorsal vestibular nucleus (DVN) and the lateral and medial ventral vestibular nucleus (VVN). The statistical treatment of the anatomical data was restricted to the comparison between cell numbers on the intact and lesioned side because only two animals were taken for each experiment. For this calculation, the $\chi^2$-test (Sachs 1974) was used.

Definitions. $\alpha$ eye angle = angle between the dorsoventral axis of the animal and the reference line of the eye. $+\alpha$ ($-\alpha$) the reference line is tilted to right (left) (Fig. 1, right side). $\gamma$ roll angle = angle between the spatial vertical and the dorsoventral axis of the animal.

$A$ amplitude of the response with $A = \alpha(\gamma) - \alpha(360-\gamma)$ for the roll angle $\gamma$, (Fig. 1, left side). $G$ gain of the response with $G = 0.5$

$\Delta \alpha$ balance of the response; it is defined by the angular difference of the eye angles for the right ($\alpha_r$) and left ($\alpha_l$) eye at the normal, horizontal position, i.e. by $\Delta \alpha = \alpha_r(\gamma=0^\circ) - \alpha_l(\gamma=0^\circ)$.

$L_{XX}$ chronic tadpoles or juveniles, hemilabyrinthectomized at developmental stage XX.

Results

Behavioural investigations

Experiment 1. This experiment was performed to determine the time course of balance and gain

![Fig. 1](image_url). Basic features of changes in the static VOR following hemilabyrinthectomy with definitions of the amplitude $A$ of the response and the balance determining angles $\alpha_r$ and $\alpha_l$ at the horizontal, normal position of the tadpoles (left side). The right part of the figure presents the definition of the eye angle $\alpha$ and the roll angle $\gamma$ under horizontal and roll condition for both, intact and hemilabyrinthectomized tadpoles. Lesion is indicated by the black dot in the tadpoles. DV dorsoventral axis.