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EARLY ABRUPT RECOVERY FROM ATAXIA DURING VESTIBULAR COMPENSATION IN GOLDFISH

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Summary

1. Vestibular compensation was studied in goldfish that had had the utriculus and semicircular canal organs unilaterally removed. Characteristic postoperative behavioural deficits of postural asymmetry were quantitatively scored. Operated animals were compared with those subject to the same duration of anaesthesia and restraint during a sham operation.

2. The period of several minutes following the operation was characterized by severe postural asymmetry and locomotor ataxia. In the operated fish, but not the sham-operated ones, the eyes rolled tonically towards the operated side without nystagmus, the body was flexed towards the operated side, and any swimming was disoriented with rolling motion towards the operated side. These deficits lasted less than 30 min after revival from the anaesthesia. All three behavioural deficits ended abruptly within 1 min of each other for individual fish, and normal, nearly upright swimming was then maintained, even in the dark.

3. We interpret this recovery as one of the first stages in the central process of vestibular compensation. The unusually abrupt end of these deficits in adult goldfish compared with that in other vertebrates suggests a remarkable capacity for the central nervous system to adapt. The speed of recovery of three distinct motor outputs supports models of early compensation that utilize central modulation or gain control of existing pathways, rather than anatomical reorganization.

Introduction

One of the remarkable phenomena demonstrating functional plasticity in the brain of adult animals is the process of 'vestibular compensation' in vertebrates (von Bechterew, 1883; Schaefer & Meyer, 1974; Pfaltz, 1983; Precht, 1983). If the labyrinthine sensory organs of the inner ear are unilaterally destroyed, there are severe asymmetrical deficits in postural behaviour and locomotion. These deficits

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usually include abnormal posture, rolling or turning during locomotion, eye deviation or nystagmus, and an asymmetry in muscle tonus between the operated and the intact side. But a recovery process begins within minutes to hours depending on species, and this compensation for the asymmetrical sensory deficits may continue for several weeks or months, restoring body equilibrium towards more normal behaviour.

Flohr (1983) proposed that this compensation is 'the result of a controlled, goal-seeking process, induced by the system's error and directed to its elimination' (see also Pfaltz, 1983). A number of central nervous system structures may be involved, including the vestibular nuclei, the vestibular commissural system, the inferior olive, the spinal cord, the visual system and the cerebellum (Precht, 1983; Galiana *et al.* 1984; Igarashi, 1984). Vestibular compensation is probably not dependent on a single mechanism, but on several simultaneous ones (Igarashi, 1984; Maioli & Precht, 1985). However, it is likely that these various mechanisms involve integration in the vestibular nuclei. A recent hypothesis states that a change in gain of feedback loops involving the commissural system between the vestibular nuclei of the two sides may be a major neural mechanism for this remarkably adaptive plasticity in adult animals (Galiana *et al.* 1984). To begin to compensate for a vestibular lesion, some time must be required for central neuronal networks to execute at least three processes: (1) to compare asymmetrical signals in the bilateral vestibular nuclei, (2) to detect these asymmetries as abnormal in relation to other sensory inputs or to appropriate behaviour, and (3) to initiate central changes to restore symmetrical motor control. Behavioural deficits that occur after hemilabyrinthectomy have different time courses of recovery which suggests that different processes are involved. Some deficits end abruptly, some return gradually towards normal, and some reach a steady state that is not a full return to normal. Recovery patterns for a particular set of behavioural deficits may differ among different species. There are few reports that quantify the behavioural changes at the very beginning of compensation, in the first minutes to hours, although changes in neuronal activity levels occur during this time (Precht *et al.* 1966; Markham *et al.* 1977; Maioli *et al.* 1983; Yagi & Markham, 1984). This study analyses the changes that occur in a set of postural behaviours during this earliest stage of vestibular compensation.

Fish are especially suited for the study of vestibular compensation since postural motor output does not involve the head–neck and neck–body reflexes seen in most other vertebrates (Schaefer & Meyer, 1974; Jensen, 1979*a*). A fish swimming freely in the water also has few, if any, gravitational cues either from tactile input or from proprioceptors responding to load-bearing of the limbs, as in tetrapods (Kolb, 1955; Jensen, 1979*a*). The major sensory input for postural control in many teleost fishes, as in other vertebrates, comes from the pars superior of the labyrinth of the inner ear; this part consists of one of the otolith organs (the utriculus) and the three semicircular canal organs (von Holst, 1950; Lowenstein, 1971; Platt, 1983).

To elucidate the mechanisms that allow compensation, a behavioural baseline must be established. Compensatory behaviour has been studied in some teleosts (Schoen, 1950; von Holst, 1950), but the species used are too small for convenient physiological recording. Goldfish, however, provide hardy subjects for behavioural, anatomical and physiological studies on the function and structure of the inner ear (Manning, 1924; Furukawa & Ishii, 1967; Hama, 1969; Fay & Olsho, 1979). Some aspects of postural control and eye movements of goldfish have already been measured under several different conditions of light direction and labyrinthine input (Traill & Mark, 1970; Graf & Meyer, 1983), and the anatomy of their peripheral vestibular system has been described (Platt, 1977). There are no reports directly comparing vestibular compensation in goldfish with the data from von Holst's laboratory on other teleosts. As part of a larger study on vestibular compensation in goldfish, this report describes an unusually abrupt change that occurs simultaneously for a few behavioural measures, within the first hour after a unilateral lesion.

Materials and methods

Comet goldfish (*Carassius auratus*) were purchased locally as needed, and maintained in aquaria in the laboratory after a quarantine period to eliminate diseased animals from the study. The fish used in this study were mature (although not large) adults, 50–60 mm from snout to base of tail. Both pre- and postoperative animals were kept in fluorescent room lighting with a 12 h:12 h day:night cycle, in glass-walled 40-l fish tanks with aeration and subgravel filters, with 1–5 fish in each tank.

Operation

The operation to initiate compensation was a unilateral partial labyrinthectomy. Each fish was anaesthetized by placing it in a solution of TMS (tricaine methanesulphonate, Crescent Research Chemicals, Scottsdale, Arizona; $0{\cdot}3\,g\,l^{-1}$), then placed in a plastic trough with a built-in mouthpiece. The fish was artificially ventilated with anaesthetic solution flowing from a line through the mouthpiece. Deep anaesthesia was shown by lack of spontaneous gill movements or any reflexes in response to touching the eye or body. The fish's back was covered with a moist piece of tissue paper to keep it cool and damp.

The operation removed the whole pars superior (the three semicircular canal organs and the utricle) from the animal's right side with little if any bleeding (Fig.1). A small opening was made with a pointed no. 11 scalpel in the side of the skull above and behind the eye, just dorsal to the opercular bone articulation. Beneath this point the vestibular labyrinth could be seen lying just lateral to the cerebellum and caudal to the optic tectum of the midbrain. Using a dissecting microscope for clarity, the utricular pouch was grasped with no. 5 forceps and gently pulled, exposing the attached ampullae and short lengths of the membranous semicircular ducts. All three ducts were cut with iridectomy scissors. The

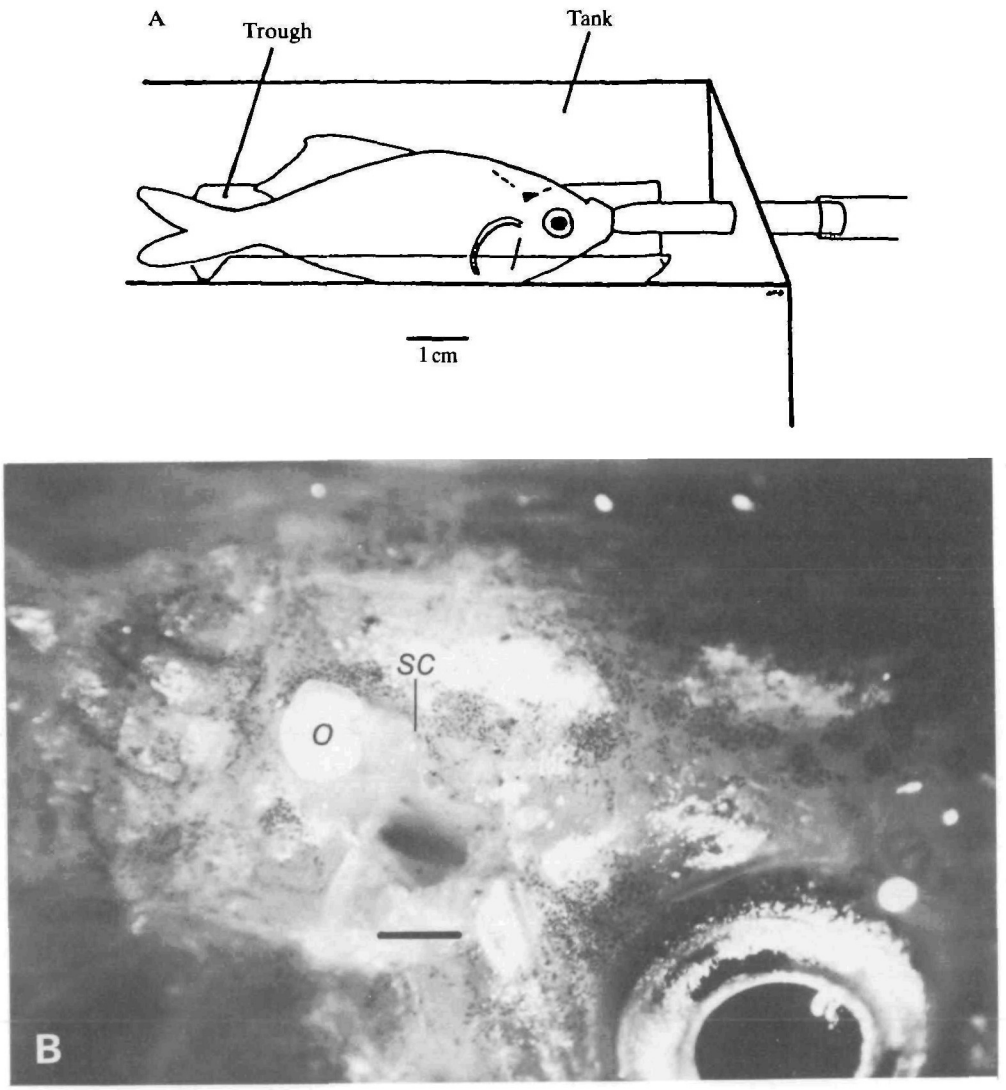

Fig. 1. Surgery. (A) The anaesthetized fish is supported in a trough in a tank; the dark triangle shows the site of surgery. (B) The utricular pouch with its otolith (*o*) and attached semicircular canal ampullae (*sc*) is shown after removal from the hole above and behind the eye.

utricular pouch containing its otolith and sensory macula and the three attached ampullae with their sensory cristae and ducts were pulled upwards to free them from the bony labyrinth. The trailing eighth cranial nerve branch to the pars superior was cut using the scissors and the end-organs were pulled clear of the skull. Fluid was cleared from the hole by a wick of tissue paper, and a warm (33 °C) solution of sterile agar (2 % in fish saline) was injected gently into the cavity (Platt 1973). This agar immediately cooled to form a plug that after many days became

incorporated with ingrowth of connective tissue. After the operation, the anaesthetic flow was replaced by fresh water, and when the fish started spontaneous breathing movements, it was placed in an observation tank in normal room lighting. Times were noted for duration of anaesthesia, and time to revival of spontaneous respiration after switching from anaesthetic to freshwater ventilation. The whole operation required less than 15 min, from beginning of anaesthesia to revival.

A sham operation consisted of making the same surgical opening in the skull as for utricular removal, and clearing enough tissue to locate the utricle. The horizontal canal was inevitably severed because it lies within the bone across the surgical opening. To control for the effects of anaesthetic on behaviour, these sham-operated fish were kept under anaesthetic for as long as the average time of anaesthesia for operated fish. The opening was plugged with agar and the anaesthetic solution switched to water. From that point on, the methods then paralleled those for the labyrinthectomized animals.

Behaviour

When spontaneous respiratory movements began, the fish was placed in the observation tank. This time became the zero mark for measuring a number of other parameters for eight fish: (1) the time that the operated side of the fish stayed flexed; (2) the time that the eyes remained deviated to one side; (3) the time until the fish swam continuously without further rolling (we found that once a fish could swim for 1 min without rolling, it did not roll any more unless disturbed); (4) the total number of body rolls when swimming; (5) the percentage of time spent lying on the operated side, when resting. The same measurements were made on four sham-operated fish. Averages of each behaviour for sham and operated fish were then calculated, as were the average time spent under anaesthetic and the time to revival.

Results

The period of severe deficits following the operation lasted 15–30 min beginning immediately after revival from anaesthesia, which we defined as the time when the fish started to breathe on its own, when it was moved to the observation tank. This period was characterized by the following features (Fig. 2). (1) The muscles of the operated side were contracted so that the body was flexed. (2) Both eyes were held in a position directed strongly towards the operated (right) side, deviated clockwise (to the fish's right) in the transverse plane of the animal; the eye on the operated (right) side was rolled to look down towards the mouth and the contralateral (left) eye looked up dorsally. The eyes remained fixed in this extreme position without the oscillations of nystagmus. (3) While swimming, the fish rolled around its longitudinal axis towards the operated side (i.e. clockwise looking forward, rolling the dorsal fin towards the right). (4) Most of the time instead of swimming the animals were 'resting' on the bottom of the tank, always lying on the

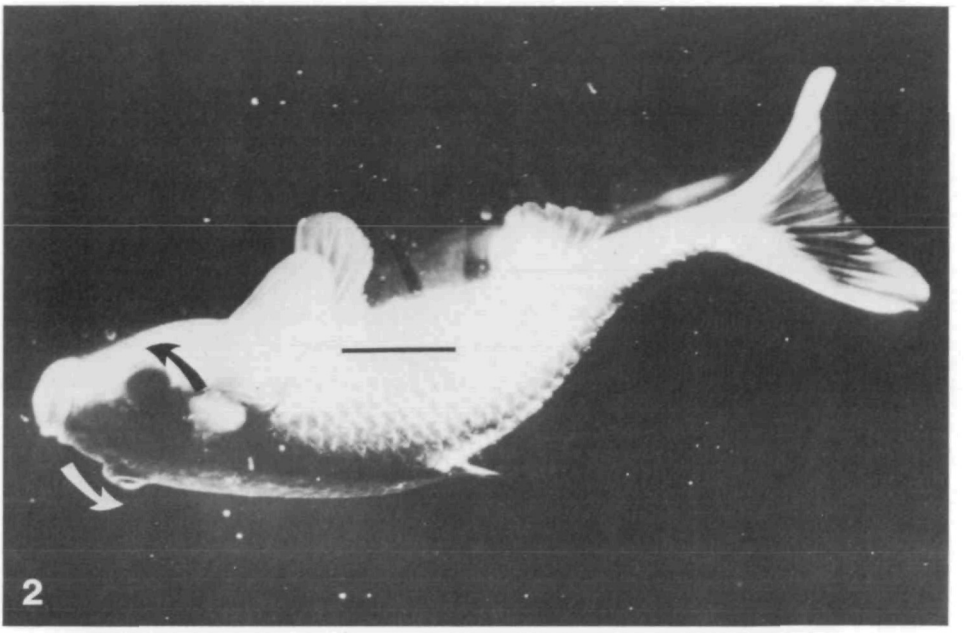

Fig. 2. Ataxic behaviour. Disoriented swimming, often upside-down as shown here, is characteristic immediately after unilateral partial labyrinthectomy. Note the rolled position of the eyes and the curling of the fins that roll the animal towards the operated side. Scale bar, 1 cm.

operated (right) side. On rare occasions when a fish was upright and still for a few moments, either floating or touching the bottom, the muscles on the operated side remained flexed.

There was no significant difference between operated and sham-operated fish in either the duration of anaesthesia or the time until the fish began breathing (t-test, $P < 0{\cdot}05$) (Fig. 3). The operated fish showed drastically larger values than the sham-operated fish for body flexion, eye deviation and disoriented swimming. In operated fish, the eyes returned to normal by abruptly 'unlocking' from their deviated position. Often this change was accompanied by 1–3 ventrally directed 'flicks' by both eyes. Then within 1 min the body flexion relaxed and swimming became normal. Since these three deficits all ended within 1 min of one another in each fish, the means for the three timed parameters are nearly equal. However, the fish remained tilted slightly towards the operated side, and this tilt lasted for many days.

Sham-operated fish showed few of these deficits. There was no flexion of the body. There was some deviation of the eyes. While swimming, a few fish rolled for less than 1 min. Further swimming was continuous and upright. Sham-operated fish sometimes rested on the bottom, either upright or lying on one side, but there was no preference shown for lying on one side or the other.

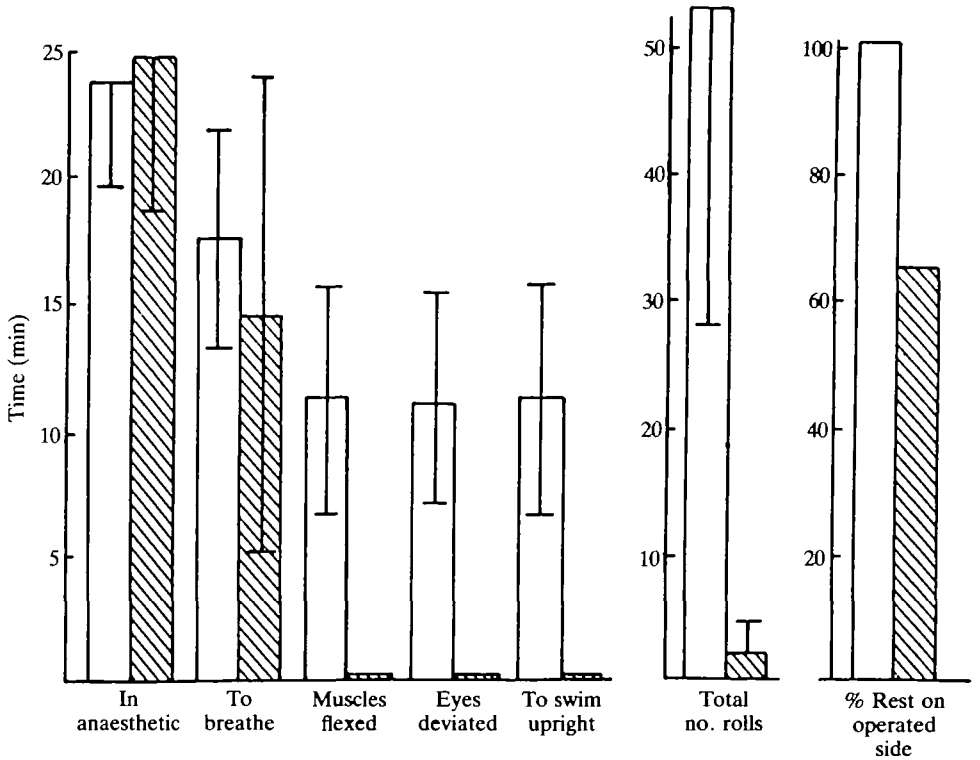

Fig. 3. Behavioural deficits. The features of the early postoperative period are shown as data bars for time, number, or percentage, as indicated; error bars show standard deviations. Clear bars are data from operated animals, cross-hatched bars for sham-operated ones. 'Time in anaesthetic' was the time during which the fish was ventilated using anaesthetic solution. 'To breathe' was the time from the ventilation switch to fresh water to the point of revival at which the fish could breathe on its own. 'Muscles flexed' was the length of time after revival that the operated side was flexed to an angle greater than 30°. 'Eyes deviated' was the time after revival that the eyes were not facing symmetrically laterally, but instead rolled, 'leading' to the operated side at an angle greater than 15°. 'To swim upright' was the time after revival until the fish could swim forward without rotating for a period greater than 1 min – that is, the duration of ataxia. 'Total number of rolls' was the number of rotations of the fish during the ataxic period. The '% rest on operated side' was the proportion of time that the fish spent on the operated side when the fish was not swimming during the ataxic period.

After each fish had been swimming normally for several minutes in the observation tank, it was transferred to a normal aquarium. Every operated fish rolled again several times on release in the aquarium. Similar rolling with the eyes leading and the body flexed towards the lesioned side could be reinduced for up to 3 days after the operation by startling the fish with a sudden tap on the tank, although the number of rolls executed decreased with time. Rolling was occasionally induced when food was placed in the tank, but this response was extremely variable.

Discussion

The abruptness of the early recovery shown here suggests certain features for models of vestibular compensation. However, before considering those implications, the form of the operation and the role of vision in the recovery period are both important factors to discuss.

Various operations involving vestibulectomy, nerve cutting and chemical lesion of the maculae have been used to initiate compensation. The operation used here was a unilateral partial labyrinthectomy intended primarily to remove the utricle, since it is the major gravistatic end-organ of the inner ear in the vertebrates (von Holst, 1950; Lowenstein, 1974). Canal ampullae were removed along with the utricle to ensure a consistent lesion, rather than risk variable damage caused by cutting or blockage of canal organs or ducts. Thus the whole pars superior was removed from one side. This report deals only with the behavioural changes within the first hour following this lesion; changes over longer times will be described in the following paper.

We do not consider that the other two otolith organs, the saccule and lagena, have a major functional role in goldfish compensation. The saccule and lagena of goldfish are considered to be primarily auditory (Furukawa & Ishii, 1967; Fay & Olsho, 1979), and removal of the saccule alone has little effect on posture (Manning, 1924). Removal of just the saccule in other teleost fishes (Werner, 1929; Lowenstein, 1932; von Frisch, 1938; von Holst, 1950) has little measurable effect on postural control, except in the atypical flatfish (Shöne, 1964; Platt, 1973). The lagena is usually considered to have some auditory or vibratory sensitivity in teleosts (von Frisch, 1938; Lowenstein, 1971; Platt & Popper, 1981), but it may also have a minor role in modulating posture (Schoen & von Holst, 1950). In mammals, the saccule appears to have a relatively minor role in postural control compared with that of the utricle (Igarashi & Kato, 1975; Goldberg & Fernandez, 1975). Additional removal or neurectomy of the saccule and lagena would have required much deeper surgery right behind the gills and under the brain. The utriculosaccular duct is narrow in goldfish (Platt, 1977), and individual otolith organs still function well after selected removal of others in fishes (Lowenstein, 1971). So we feel that the removal of the pars superior here does not have much effect on the remaining otolith organs, and that this partial labyrinthectomy is sufficient for this study.

In these experiments the fish recovered in the light. Long-term vestibular compensation is known to be affected by blinding or by recovery in the dark for several different species (Kolb, 1955; Jahn, 1960; Courjon *et al.* 1977; Jensen *et al.* 1979). Even in normal animals it is well known that visual input in certain conditions can predominate over vestibular input for postural or locomotor control (see Henn *et al.* 1980). The abrupt recovery of these fish thus might represent an abrupt change from vestibular to visual control. However, when postoperative fish were placed in the dark and their posture checked by a strobe flash, they retained the recovered upright orientation seen in the light (Ott & Platt, 1988). Since they did not show a deficit in the dark immediately after this abrupt

recovery, we believe the recovery is an early stage in vestibular compensation and not just a simple shift to visually guided control. We have not yet determined whether the visual input is necessary during the brief recovery to recalibrate the vestibular 'upright'.

We do not know how important active movement is for vestibular compensation in fish. Recovery in these experiments allowed free movement to the fish. If a fish was immobilized for 1 h after the operation, either mechanically by surrounding it with hardened agar or pharmacologically by using a low dosage of Flaxedil, we found the fish still recovered from ataxia within a few minutes after release from the agar or recovery from the Flaxedil. This recovery time was not notably shorter or longer than that for unrestrained fish. The speedy recovery from ataxia in both cases suggests that the mechanism for this earliest stage of vestibular compensation does not depend on extensive locomotor experience.

Compensation during the time immediately after a lesion has received relatively little attention compared with quantification of the long-term changes during the later stages of compensation. The behavioural changes occurring during the earliest period of vestibular compensation in many vertebrates are defined as an acute stage in the recovery process (Schaefer & Meyer, 1974; Pfaltz, 1983). Some features seen in goldfish, such as body flexion towards the operated side, also commonly occur in other vertebrates (Schaefer & Meyer, 1974). In goldfish, the non-moving deviation of the eyes is similar to that in frogs (Kolb, 1955; Jahn, 1960), although different from the nystagmus occurring in birds and mammals (Schaefer & Meyer, 1974). The fin placement and rolling during locomotion are analogous to the limb placement and turning in tetrapods.

The postoperative time, usually known as the acute stage of compensation, is considered to begin at the time of operation, and extend for a few days, depending on species. In mammals, this period is characterized by severe ataxia and marked nystagmus, and there is a spontaneous nystagmus as well as that induced by positional change (Schaefer & Meyer, 1974; Jensen, 1979*a*; Pfaltz, 1983). These signs then show a graded decrease, believed to result from central suppression mechanisms, during additional stages that occur in a series, and have been called accommodation, multisensory compensation and recovery (Pfaltz, 1983). There is a gradation and overlap in the timing for these stages and correction of these different deficits.

Goldfish have an acute stage which appears to be very brief. Although the postoperative responses of goldfish described here are similar to those in other vertebrates, the initial changes are remarkably fast and end with unusual abruptness. In goldfish we would include in the acute stage the early brief period characterized by the features described above that all end abruptly, within less than 30 min from the end of anaesthesia. We call this period the ataxic stage, indicating that whereas some locomotion may be possible, it is extremely disoriented and rarely executed. These initial behavioural characteristics all end at once, after only a few minutes, and do not carry over for hours or days.

We do not know whether this period exactly corresponds to the acute stage in

other animals because little work has been done on this early period. Other measures of response might show that the acute stage in goldfish extends longer than the ataxic stage alone. After the sudden recovery from this ataxia, the main residual deficit in goldfish from the first postoperative hours until the end of the first few days is a postural bias in body tilt towards the side of the lesion. The only evident postoperative behaviour that remains longer in goldfish is an increase in the relative effect of directional light on posture, compared to the effect of gravity (Traill & Mark, 1970; Ott & Platt, 1988). In other vertebrates, many of the initial behavioural signs show much more gradual recovery towards normal. Asymmetrical limb placement, head turning and ocular nystagmus can end at times ranging from hours up to 5 days, and in mammals some eye deviations and head turning may persist permanently (Schaefer & Meyer, 1974). Unlike fish, most tetrapods have a range of other somatosensory cues including limb contact and neck torsion that can influence compensation (Jensen, 1979*a*).

One difficulty in interpreting data from this period within the first hour after the operation is the possibility of lingering effects from the anaesthetic. However, because the sham-operated fish were kept anaesthetized for a time equivalent to operated fish, such effects would be felt equally by both sets of fish. In some operated individuals the ataxia ended within less than 5 min of revival, although others took more than 10 min. Some of this recovery time and variability we include under 'compensation' may depend simply on recovery from anaesthesia. But then the true times for recovery from ataxia may be even faster than we report.

Responses very similar to those seen immediately postoperatively can be restored suddenly by a process called decompensation (Azzena *et al.* 1977). If a unilaterally operated animal is handled, startled or given certain drugs after some compensation has occurred, the early asymmetrical disturbances can reappear briefly (Kolb, 1955; Schaefer & Meyer, 1974; Azzena *et al.* 1977; Jensen, 1979*b*; Bienhold & Flohr, 1980; Semenov *et al.* 1980). In teleosts, the presence of food in the water can affect postural responses even during compensation (von Holst, 1949; Traill & Mark, 1970). The goldfish used in this study, if stimulated, also showed reappearance of the ataxic stage for up to 3 days postoperatively. The restoration of this set of uncompensated acute behaviours, with a sudden onset long after the operation, suggests that the acute effects can be 'switched on' or that the compensatory mechanism can be suddenly inactivated or 'switched off'. Control of vestibular activity during compensation has been suggested to originate from many possible sites, including the spinal cord (Kolb, 1955; Jensen, 1979*b*) and cerebellum (Schaefer & Meyer, 1974; Robinson, 1976; Dieringer & Precht, 1979*b*; Courjon *et al.* 1982).

The first postoperative minutes or hours seem too brief a period for early compensation to depend on anatomical reorganization by extensive sprouting. It is not yet clear whether some structural changes may be involved in long-term compensation, but the appearance of sudden decompensation suggests that the restored symmetry may not be consolidated firmly by a structural reorganization.

Some neuronal mechanisms for establishing compensation have been suggested, including modulation of activity of vestibular neurones by the cerebellum at the beginning of compensation (Dieringer & Precht, 1979*b*; Courjon *et al.* 1982) or change in gain of feedback loops dependent on commissural interactions between the vestibular nuclei of the two sides (Dieringer & Precht, 1979*a*; Galiana *et al.* 1984). Long-term changes in activity and responsiveness in the vestibular nuclei could be exerted by neurochemical modulation of vestibular centres (Bienhold & Flohr, 1980).

The special properties of early compensation shown here for goldfish may provide a useful model for analysing the anatomical, physiological and biochemical mechanisms for this remarkably rapid plastic adult behaviour.

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