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Task-Dependent Rate of Recovery From Hemilabyrinthectomy: An Analysis of Swimming and Locomotor Performances[1]

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PETROSINI, L. *Task-dependent rate of recovery from hemilabyrinthectomy: An analysis of swimming and locomotor performances.* PHYSIOL BEHAV 33(5) 799–804, 1984.—Guinea pigs were hemilabyrinthectomized or hemicerebellectomized and repeatedly tested on a swimming task and in the open field. Initially, hemilabyrinthectomized animals showed impaired swimming behavior which improved over time: within 21–25 days after the vestibular damage, the animals were able to swim around the tank with coordinated motor patterns. Only a slight tendency to turn towards the lesion side continued to be displayed. Hemicerebellectomized guinea pigs were significantly less impaired in their swimming ability since the very first test session. Both groups of animals showed similar recovery time courses in their open field activity. The data demonstrate a task-dependence in the rate of recovery following a unilateral labyrinthectomy and a substantial contribution by the labyrinth to swimming function.

Hemilabyrinthectomy   Hemicerebellectomy   Swimming   Land locomotion   Recovery of function   Guinea pig

VESTIBULAR compensation represents an advantageous model for the study of a rapidly developing plastic process [10]: in fact unilateral lesions of the peripheral vestibular apparatus result in gross disturbances of posture and movement, which over time undergo a rapid functional recovery [14–16]. Vestibular compensation deals with oculomotor, postural and locomotive deficits and then cannot be treated as a homogeneous process, since the different hemilabyrinthectomy symptoms are compensated for to different degrees and with different time courses [16]. The recovery of static and dynamic reflexes is not necessarily correlated in each animal, probably due to the different functional contributions of the motor systems controlling postural tone and dynamic reflexes [1].

Among advanced locomotor performances, such a differentiation could also exist. Among the locomotor symptoms which follow a unilateral vestibular injury, a severe impairment of swimming behavior has been described [9]. Swimming ability requires the integration of multisensory inputs and a rapid processing of information [17] and in particular a subtle balance control. Therefore, it may be a productive model for studying functional integration of a coordinated series of reflexes and their plastic potentialities [17]. Recently for example swimming ability has been considered to be a very sensitive test for assessing the effects of motor cortex damage in rats, which is otherwise difficult to reveal [4]. On the other hand the role that task variables may play in evaluating brain lesion effects has been widely described [6,12].

The purpose of the present investigation was to determine whether guinea pigs would display different time courses in their recovery from different locomotor abilities known to be seriously affected by a hemilabyrinthectomy (HL). To this end, swimming and land locomotion recoveries were analysed in animals with acute HL. The shift from terrestrial to aquatic environment could evidence task-dependent differences in evaluating the consequences of a vestibular lesion and the degree of functional recovery regained.

Furthermore, time courses of recoveries of swimming and land locomotion behaviors following hemicerebellectomy were analysed in order to compare time course and extent of recovery following different lesions which induce motor impairment and asymmetry.

METHOD

The present experiments were performed on guinea pigs weighing 400–600 g. The subjects were randomly assigned to one of 3 experimental groups: guinea pigs in group 1 (n=10) were used as controls; guinea pigs in group 2 (n=10) underwent a right HL; guinea pigs in group 3 (n=7) received a left hemicerebellectomy. In the animals of group 2, under ether anaesthesia, the labyrinth was destroyed by injecting 0.5–0.8 ml of a solution of chloroform and vaseline oil in the middle

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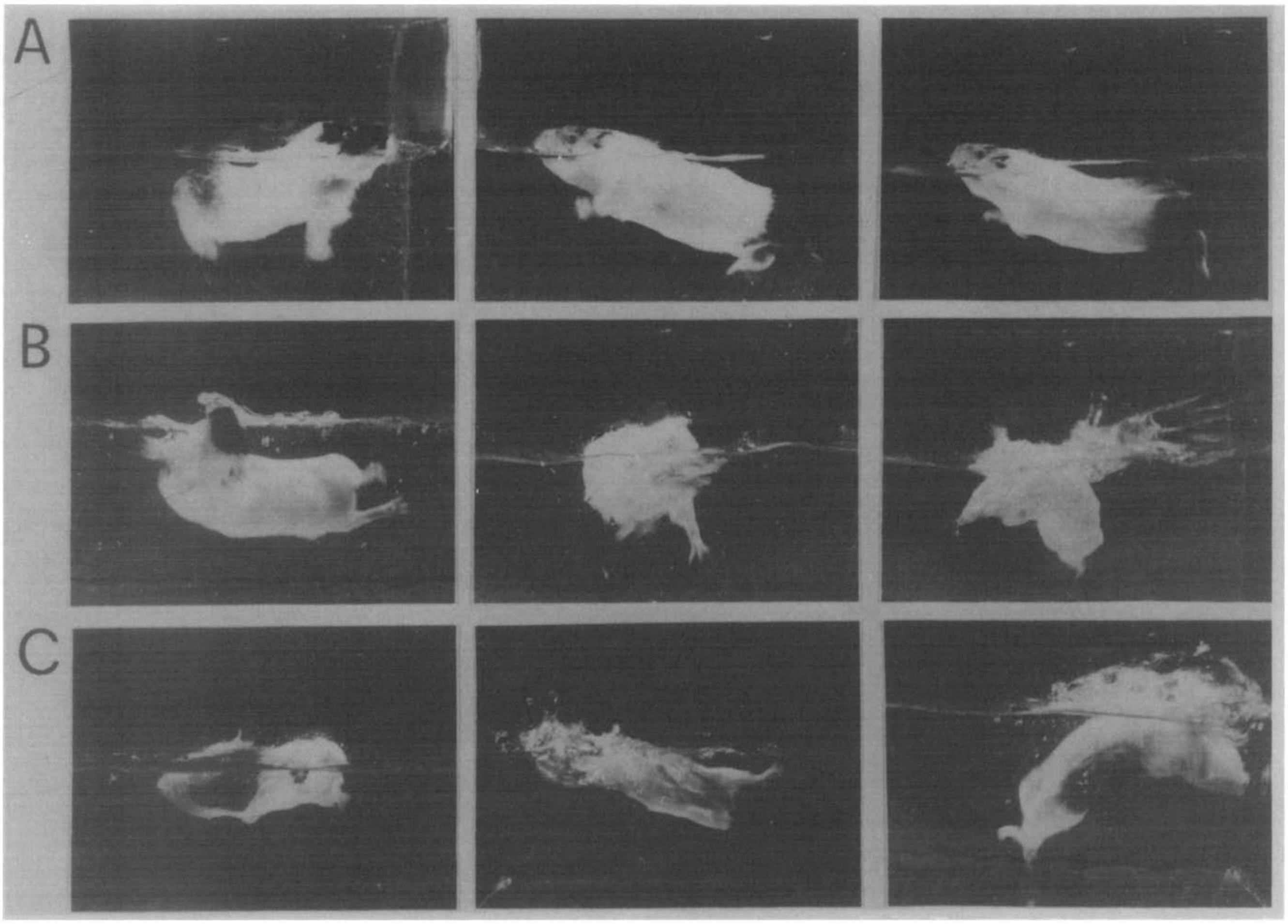

FIG. 1. Swimming behavior patterns in a normal (A) and in two acutely hemilabyrinthectomized (B,C) guinea pigs. Note in lesioned animals rolling swimming and the difficulty to maintain their noses out of water.

ear. Post-lesion testing began the day after the HL and was repeated every 4th day for a total of 7 sessions, the last of which was performed the 25th day after the lesion. Each animal was immersed in a 60×45×19 cm glass tank filled, except for 8 cm, with 37°C water; at this level, the guinea pigs could not make contact with the tank bottom. The animals were gently released by hand in the water and allowed to swim freely about the tank. Since it has been found that neuromuscular coordination and head-body position are maintained well-adapted to effective swimming, when the guinea pig's nose is kept above water, two parameters of swimming were evaluated: (a) swim-time; (b) swim-directionality. Swim-directionality (or direction bias) was defined as the number of movements towards the right side/the total number of movements × 100%. For swimming without a dominant direction, this ratio would be equal to 50%. Regarding swim-time, the worst performance exhibited by a normal animal of a pilot study on 10 subjects had been to swim for at least 30 sec. Therefore, a 30-sec period has been chosen as the cut-off period distinguishing control-like from impaired performances.

The time count started from the moment of immersion and stopped when the animal's nose was below the surface of the water or when the animal exceeded the cut-off time. More cognitive measures, such as reaching a tank corner or swimming according to particular directions, were deliberately excluded to avoid components of disorientation or low motivation that might bias the results.

After being tested, each animal was removed from water, towel dried and allowed a 30-min rest period, before being tested in the open field apparatus.

It consisted of a 150×150 cm arena with the floor divided into 36, 25×25 cm identical squares. This arena was surrounded by 35 cm high wood panels. A 100 W incandescent lamp was suspended 1.5 m from the field centre, so that illumination of the surface was uniform. The entire field was wiped down with disinfectant (Citrosil, Italchemi Pharma) after each trial. Open field test sessions lasted 5 min. The animal was placed on the middle point of one side of the field. The number of quadrant crossings, when all four paws entered the new quadrant, was recorded. Squares of the row nearest to the starting point were scored with the lowest value (score 1), while those of the farthest row with the highest value (score 6).

In the 7 animals of group 3 the cerebellum was unilaterally removed under ketamine hydrochloride (Ketalar, Parke-Davis) 24 mg/kg IM anaesthesia. The left hemicerebellectomy was performed either by splitting the vermis (classical

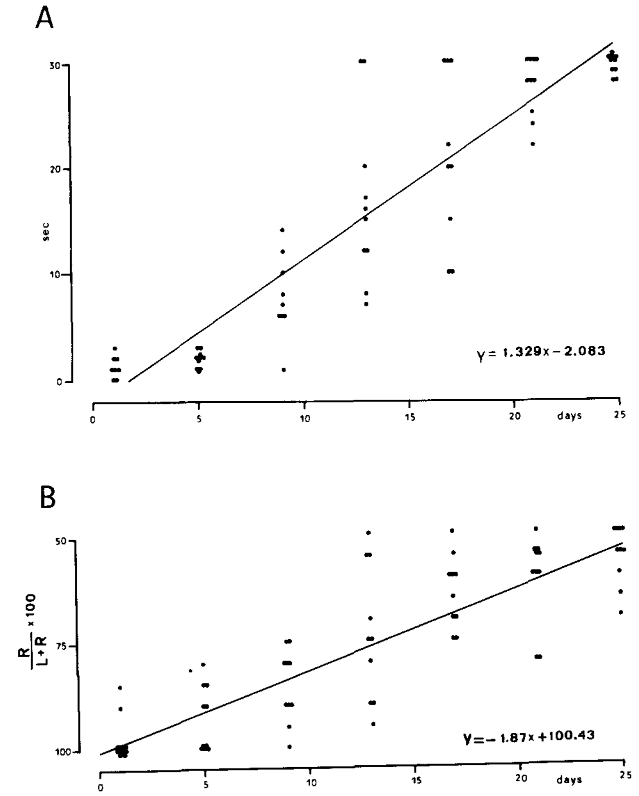

FIG. 2. Scatter diagrams of measurements of swim-time (A) and swim-directionality (B) in relation to days from hemilabyrinthectomy. The correlation coefficients are respectively r=+0.91 and r=+0.84. Regression lines with their equations are also shown. In B swim-directionality was calculated as the ratio between the number of movements to the right and the total number of movements, expressed as percentage.

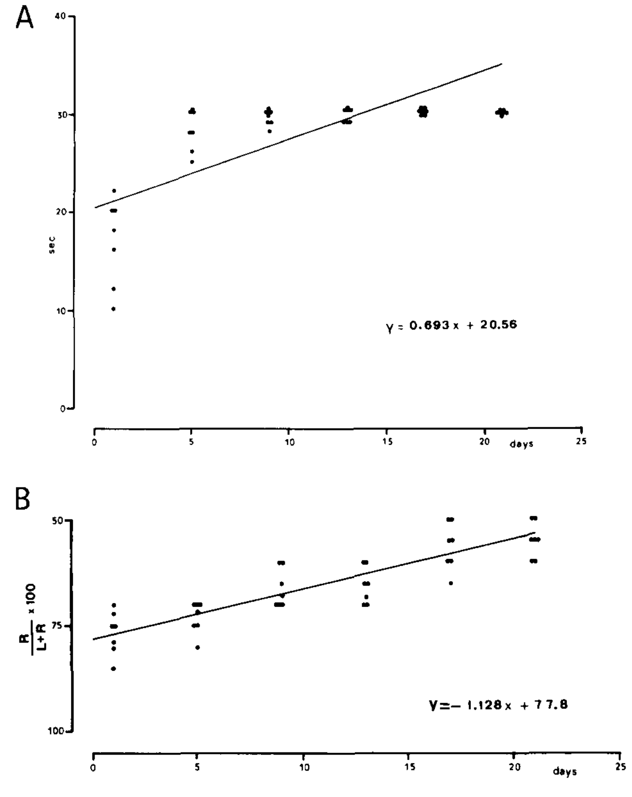

FIG. 3. Scatter diagrams of measurements of swim-time (A) and swim-directionality (B) in relation to days from hemicerebellectomy. The correlation coefficients are respectively r=+0.72 and r=+0.86. Regression lines with their equations are also shown.

hemicerebellectomy) or by removing the left hemisphere only (functional hemicerebellectomy) [3,11]. Following the surgery, the animals were allowed 24 hr to recover. Postoperative testing was identical to that for hemilabyrinthectomized animals, and had the same schedule, except that the last test session was performed the 21st day after the lesion, because by that time all animals had reached control-like performances. After the last test session, the animals were sacrificed and the extent of the cerebellar lesion was histologically determined from Nissl-stained sections.

Statistical significance of the results was calculated by analyses of variance followed by multiple Tukey's tests.

RESULTS

Swimming in Hemilabyrinthectomized Animals

At the beginning of testing (1 day after HL), the hemilabyrinthectomized guinea pigs displayed uncoordinated movements almost immediately after submersion in water; the animals leaned towards the lesion side and rotated around their longitudinal axis with a corkscrew-like movement. The loss of coordinated swimming resulted in a gradual but inexorable sinking. Sometimes, the animals did not exhibit this rotatory activity but they leaned more and more towards the lesion side, floated motionless and finally remained submerged. As days went by, the animals were capable of more coordinated movements sufficient to directionally propel them, even if they swam in circles towards the lesion side. At this stage (9–13 days from HL), the guinea pigs were able to keep their noses out of the water for 8–16 sec. A coordinated swiming was restored within 21–25 days after HL. The swimming activity involved all four limbs with well-performed sequences of flexion and extension. Also in this late stage the guinea pigs still exhibited a preferred directionality towards the injured side. These results are summarized in Figs. 1 and 2.

A separate group of 5 animals was tested for its aquatic behavior, for the first time, 15 days after the labyrinthine lesion. This procedure was used to determine whether trained animals swam better than naive ones, to test the hypothesis that learning phenomena could cooperate in the gradual improvement of swimming patterns shown by hemilabyrinthectomized guinea pigs. This group of animals showed the same swimming abilities as the guinea pigs with the same post-operative intervals that were tested more than once. Furthermore, the behavior of this group allowed to dismiss the possibility that the aquatic environment might

TABLE 1

DIFFERENCES BETWEEN MEAN VALUES OF SWIM-TIME AT DIFFERENT STAGES OF COMPENSATION IN HEMILABYRINTHECTOMIZED AND HEMICEREBELLECTOMIZED ANIMALS

Time*	Differences between mean values of swim-time†
1	15.75
5	26.24
9	21.42
13	12.87
17	9.2
21	2.5

*Time expressed as post-operative days.
†Tukey's test $t(0.01)=8.18$ (minimal significant difference at the 0.01 level of significance).

represent an emotional stimulus capable of handicapping the animal, and that as a consequence, it might be responsible for the severe impairment of swimming behavior exhibited in the first test sessions. In conclusion, the time course of recovery of swimming ability was unaffected by prior swimming experience and by emotional components in the present experimental conditions.

Swimming in Hemicerebellectomized Guinea Pigs

At the beginning of swim-testing (1 day after the surgery) hemicerebellectomized guinea pigs showed a rather coordinated pattern of movement, which allowed them to swim for about 15 sec. Their trunks were not perfectly horizontal, the operated side being deeper in water than the unoperated side. In the second test session, the animals kept their noses out of the water for about 30 sec. The animals tended to swim in a circle towards the unoperated side, however this directionality was less compulsive than the one shown by HL animals. No rolling movement was shown (Fig. 3).

To obtain a reliable estimate of the effect of the two lesions on swim-time, a 2×6 (lesion×time) analysis of variance was performed. Since the numbers of observations in each cell were unequal, the Winer's ANOVA model for a "p×q" factorial experiment with unequal cell frequencies was used [18]. There was a significant difference between hemilabyrinthectomized and hemicerebellectomized animals $F(1,90)=174.1$; $p<0.001$; the effect of time was significant, $F(5,90)=24.62$; $p<0.001$ as well as the interaction of time and lesion, $F(5,90)=36.00$, $p<0.001$. To compare the effect of the lesions on swim-directionality, a 3×6 (3 lesions: none, hemilabyrinthectomy, hemicerebellectomy×6 times) analysis of variance was used. A significant difference in swim-directionality among groups was found, $F(2,144)=247.36$, $p<0.001$. The time effect, $F(5,144)=36.37$, $p<0.001$, and interaction, $F(10,144)=11.02$, $p<0.01$, were significant. Subsequently multiple comparisons between the mean values of swim-time or swim-directionality at the different stages of compensation were performed by Tukey's tests. These analyses revealed significant differences in swimming deficit compensation between groups (Tables 1 and 2).

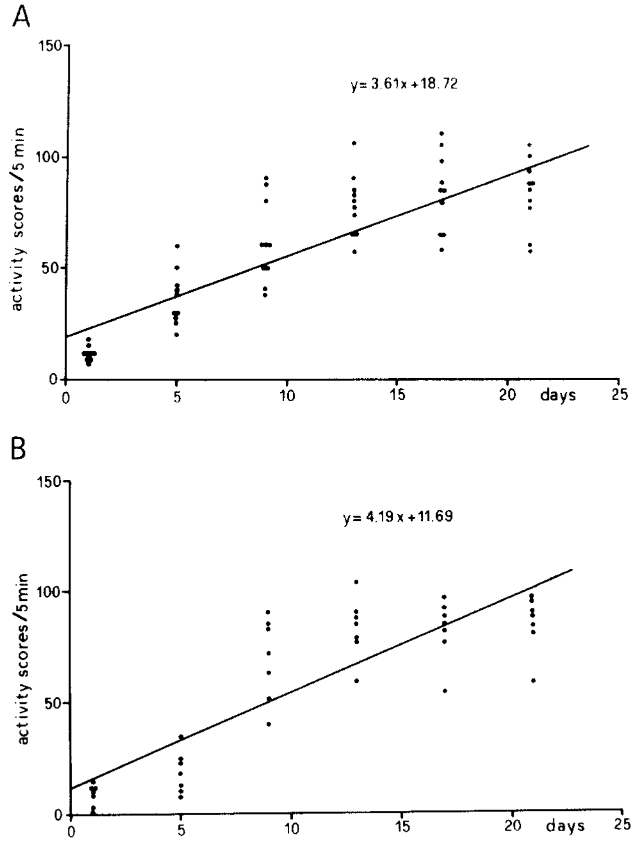

FIG. 4. Scatter diagrams of measurements of open field activity in relation to post-operative days in hemilabyrinthectomized (A) and hemicerebellectomized (B) animals. The correlation coefficients are respectively $r=+0.80$ and $r=+0.84$. Regression lines with their equations are also shown.

Open Field Activity

In contrast to swimming data, both groups of lesioned animals were markedly impaired in their open field behavior, during the early post-operative period (days 1–5), as evidenced by their achieving very low scores. In particular hemilabyrinthectomized animals showed a compulsive circling towards the lesion side, which prevented them from reaching the most distant squares from the starting point. Hemicerebellectomized animals exhibited abnormal locomotion with distortion of the body axis, waddling gait and falling on the lateral flank. Both impairments improved during the intermediate and late post-operative periods (days 9–21). At the last test sessions both groups of animals were significantly more active than in the first sessions (Fig. 4). A 3×6 (lesion×time) analysis of variance revealed a significant lesion effect, $F(2,144)=85.82$, $p<0.001$; and a significant time effect, $F(5,144)=95.88$, $p<0.001$. Also interaction of time and lesion was significant, $F(10,144)=25.13$, $p<0.01$. Subsequent Tukey's analyses showed significant differences between groups (Table 2).

DISCUSSION

The results of this experiment demonstrate a task-dependence in rate of recovery following a unilateral vestibu-

TABLE 2

DIFFERENCES BETWEEN MEAN VALUES OF SWIM-DIRECTIONALITY OR OPEN FIELD ACTIVITY AT DIFFERENT STAGES OF COMPENSATION IN CONTROL, HEMILABYRINTHECTOMIZED (HL) AND HEMICEREBELLECTOMIZED (HC) ANIMALS

	Swim-directionality†			Open field activity‡		
Time*	Control vs. HL	Control vs. HC	HL vs. HC	Control vs. HL	Control vs. HC	HL vs. HC
1	47.6	26.53	21.07	70.9	74.09	3.19
5	43.3	23.44	19.86	46.7	64.05	17.35
9	35.5	16.14	19.36	20.8	13.3	7.5
13	23.5	15.42	8.08	5.0	1.16	3.84
17	15.0	7.43	7.57	1.5	0.7	2.2
21	11.4	5.4	6.0	0.6	1.48	2.08

*Time expressed as post-operative days.

†Tukey's test $t(0.01)=13.17$ (minimal significant difference at the 0.01 level of significance).

‡Tukey's test $t(0.01)=21.50$ (minimal significant difference at the 0.01 level of significance).

lar lesion. For open field activity, a 10-day period was sufficient to reach control-like performances; in contrast, coordinated swimming was restored only after 20–25 days following the lesioning. Therefore, vestibular compensation does not follow the same time course for all functions. Since swimming and land locomotion are generally assumed to be based on a similar neural arrangement [7], the disparity in the two performances requires some comment. Different explanations can account for such a result. The first one takes into consideration the degree of difficulty of the two tasks. Generally, the more difficult the motor task (i.e., the more it departs from the usual movement pattern), the more laborious and time consuming its acquistion [10]. Swimming could be more difficult than walking for a terrestrial animal like guinea pigs, and therefore, requires more time for its recovery. If so, the same tendency should have been shown in the motor learning which follows any lesion inducing motor impairment and asymmetry [5]. This is not the case of hemicerebellectomy. In fact, an effective swimming was displayed after 5 days from the surgery; conversely the open field activity recovery followed a very similar time course as the one after an HL. Previous researches report that swimming is already present in puppies still unable to stand and to walk [13], and that it is maintained in guinea pigs after intercollicular decerebration [2]. This dissociation between swimming and walking recoveries has been observed also in rats with hypothalamic lesions [6]. These latter results have been interpreted as an indirect demonstration that "swimming ability and locomotor activity are mediated by at least partially separated neuronal substrates." Then it seems reasonable to take into account the neuronal circuitries involved in the movement rather than the complexity of the movement itself. The data of the present research indicate that swimming needs a very elaborate regulation by the labyrinth and a longer time of recovery in comparison with gait. Therefore, they indicate swimming as a function more labyrinth-dependent than gait is. From this point of view, it may represent a very demanding task for a hemilabyrinthectomized animal. Finally, it cannot be dismissed that systems with even slightly different neuronal networks may be characterized by different plastic properties and thus may exhibit different times of development or recovery [8].

The present findings, indicating a gradual vestibular compensation, suggest the occurrence of a hierarchy of functions. First, static functions are compensated for and then the dynamic ones. Interestingly, even among these latter performances, a hierarchy appears to exist that can be as different in the various species as is the general organization of movement. Therefore, when a hemilabyrinthectomized animal is defined "compensated" it should be specified with respect to what symptom. The data reported here suggest that the choice of post-operative tasks may be an important factor in evaluating the degree of achieved compensation.

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