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DISORIENTATION OF ANIMALS IN MICROGRAVITY

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ABSTRACT

Disorientation responses of animals exposed to microgravity produced by parabolic aircraft flights and also in-space experiments were reviewed. Disoriented postures in floating are largely species-dependent. Reflexive lowered tone of gravity-bearing extensor muscles by labyrinthectomy is not seen in mammals (hamster and monkey) and frog, though dorsiflexion of the neck and the trunk is not so remarkable in hamster and monkey as in frog. In weightlessness, fundamental vestibular reflexes may be affected (righting reflex in cat), but coordinated performance can be easily compensated by visual function (mouse, monkey and turtle). In normal birds and fish who can move three-dimensionally in their environments, exposure to parabolic flight microgravity induces irregular tumbling with the eyes open and regular looping with the eyes closed, although the loop direction is the opposite in these two animals; backward (inside) in pigeon and forward (outside) in fish. Most recently, however, it was found that normal fish (goldfish) tumbled backward when observed in prolonged microgravity in space, suggesting that microgravity effects on fish in aircraft-flight parabolas would differ from those in space. Sensory conflicts in normal fish diminish remarkably during 3—4 days of space microgravity, and the cerebellum may be involved in the recovery, lending support to the sensory conflict theory for the genesis of space motion sickness.

Key Words: Microgravity, Parabolic flight, Disorientation, Animals.

INTRODUCTION

In a terrestrial 1-g environment, a microgravity of 5—10 seconds in duration is available with a free-fall using a "drop tower", a tube-shaped facility of 100—300 meters in depth or a duration of about 20 seconds with a parabolic aircraft flight. These microgravity conditions, however, always accompany a shock of 10—15 g in the former at landing and a hypergravity of about 1.5—2.5 g in the latter immediately before and after the parabola. In this sense, microgravity in space is a unique physical condition which one never experiences on the ground.

It is now common knowledge that animals as well as human beings are able to adapt to new environments such as low or high temperature or low oxygen conditions, but there are certain limitations when such environments are severe. Our initial research on space has begun to indicate that a microgravity environment is not beyond our ability to adapt to it, but our limitations in this regard remain a matter for close investigation.

The 28-d, 59-d and 84-d flight missions of the Skylab project which were conducted during 1973—74, were launched to collect physiological data on the effects of microgravity on the human body. The results were published by NASA in 1977[1] and have provided a basis for current space medicine. Since 1983, the US space shuttles have become available, and the flights have accelerated medical examinations in orbit, which include vestibular and neruosensory, cardiovascular, endocrinological, hematological, fluid and electrolytes changes, muscle atrophy,

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bone calcium loss, and radiation experiments. These flights with space shuttles are up to 2 weeks in duration so far. Similar experiments have also been conducted on the Russian Salyut and Mir stations, with longer flight durations of up to 366 days, but the results had not published until the Mir station was opened to European researchers recently. In the latest issue of a textbook on space medicine,[2] space had been devoted to an outline of results from Russian space missions.

Since the first orbital flight of the Russian cosmonaut, Gagarin (space crew), in 1961, more than 300 space crews have stayed in space, and a variety of physiological disadvantages due to prolonged exposure to microgravity have come to light. However, because the number of those who completed a mission lasting more than one month is still less than 50, it is difficult to generalize response properties, and the study of microgravity effects has been complicated by many tasks that the crews have been called upon to perform during these missions. Furthermore, the prophylactic and therapeutic use of medicines and exercise applications as countermeasures for observed problems have masked the real microgravity effects.

Animals had been extensively used before manned space flights were realized, not only in the United States but also in Russia, but few studies have been published. The animals were exposed for a short term to parabolic flight microgravity with aircrafts and small rockets. Among orbital flights with the space shuttle, the first animal experiment was conducted in 1983 with rodents, but a reliable animal holding facility for rodents or small primates was not available until the Spacelab-3 mission in 1985. For aquatic animals, a holding facility was developed in Japan and used in the Spacelab-J mission in 1992 and also in the 2nd International Microgravity Laboratory (IML-2) mission in 1994. Thus, animal experiments in space are still in their infancy, because of the technical difficulties involved under microgravity, but will become routine in the coming era of space stations since animal experiments are indispensable to improve understanding of the mechanisms of problems observed so far in space crews.

Several species of animals have been employed for microgravity experiments over the past 50 years. Most of the experiments were for observation of disorienting response of animal in microgravity. In the present paper, species differences in animal disorientation under microgravity were reviewed, though referable papers were limited. Such information will be not only helpful to develop an improved or new animal holding facility for space experiments, but also serve to improve understanding of the neurovestibular problems of man in space.

DISORIENTATION OF MAMMALS EXPOSED TO MICROGRAVITY

Mouse and Hamster

The first physiological experiment in microgravity was conducted in small monkeys and mice aboard sounding rockets; heart and respiratory rates of the monkeys and balancing behavior for normal and labyrinthectomized mice were observed.[3] No evidence of cardiovascular or respiratory disturbances was observed, and performance was not disturbed as long as a foothold was available to these animals during a microgravity period lasting for two to three minutes.

Animals apparently were able to maintain their posture almost normally as long as a foothold was available. According to observations by our colleagues during 20-sec parabolic aircraft flights,[4,5] all of the hamsters remaining on a foothold could maintain their posture as if they were on the ground, suggesting that tactile and proprioceptive information from the legs might be sufficient to adjust their orienting performance adequately. On the other hand, once floating in air, the normal hamsters were almost in a state of panic. They extended their extremities, trunks, claws and tails and struggled to find a foothold (Fig. 1). This panic attack was less intense in the labyrinth-lesioned hamsters both of whose labyrinths had been lesioned 6—7 weeks

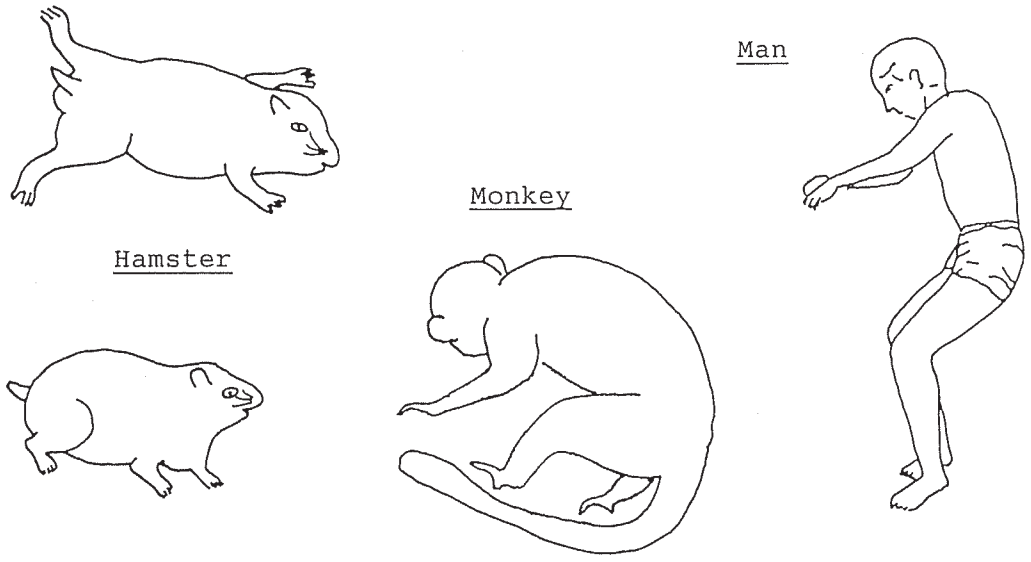

Fig. 1. Posture of animals and man in microgavity. Hamster floating and on a foothold, and monkey floating during parabolic aircraft microgravity. Man in space microgravity.

before the flight experiemnt. Possibly, other factors than lowered tone of the gravity-bearing extensor muscles due to loss of otolith inputs would have forced the normal hamsters reflexibly to assume such flying posture, and the illusion of falling might have caused them to panic, while in the hamsters without labyrinthine function, gravity changes might have affected them less. The hamster operated only on one side rotated in the air toward the lesioned side in microgravity.

Cat

The postural righting reflex of cats is one of the best-known reflexes for posture adjustments which the gravity force exerts on. When a cat, blindfolded and lying on its back, is dropped, it immediately turns into normal position to land on its feet, indicating that a visual cue is not involved in this spatial orientation. Function of such orientation response of cats was examined during microgravity produced by aircraft parabolic flights.[6] The three-week-old kittens whose postural righting reflex was not developed, floated upside-down in air during weightlessness, whereas in the eight- and twelve-week-old ones whose reflexes were well established, the reflex acted for the initial several seconds but ceased thereafter during the weightless state, with or without blindfold; this was not discussed by the authors, but their conclusion was only that the visual cue did not affect the basic reflex.

It is of interest that well-developed cats could maintain their orienting reflex for the initial few sconds even under microgravity. A possible explanation would be that the otolith organs of the cat onboard would have been affected by the preceding hyper-gravity and its effect continued for several seconds in the microgravity phase, implying that gravity-change signals could be briefly stored in the central nervous system (CNS). This idea is just an extension of a velocity storage mechanism which has been proposed for the regulation of semicircular canal signals on eye movements; that is, velocity-change signals from the semicircular canal organs will be stored in the CNS during a horizontal rotation and the post-rotatory after-nystagmus, characteristic eye

movements, which can be typically induced by a rapid stop in rotation, is attributable to neural discharges out of the storage.

Squirrel Monkey

Clear differences in free-floating adapting behavior and in recovery of the food reinforcement reaction (a bar press) were found between normal and labyrinthectomized squirrel monkeys, when the animals were extensively subjected to repeated parabolic flights (total 127 parabolas for 4 days).[7] The labyrinthectomy had been performed approximately one year earlier.

The normal monkeys in a small box for bar pressing were observed to turn upside down or somersault repeatedly during the first few parabolas, but none of the operated ones did, resulting in a low response rate (11% of the ground control) in the former animals, whereas the rate remained considerably higher (74%) in the latter. However, after 120 parabolas, the normal ones improved their response rate considerably up to 80%, whereas the operated animals maintained the same level. Corresponding to these changes in reinforcement reaction, the normal monkeys free floating in a large box demonstrated severe disorientation with frantic scrambling for a toehold, extending the lower limbs, and curling the tail ventrally (Fig. 1). In the adjusted stage, the monkeys smoothly drifted back and forth with a tail flick or a body twist to approach the wall softly, or jumped around skillfully from this wall to another. On the other hand, the operated monkeys did not show any pattern of panic from the initial stage and could improve gradually in floating, but their lack of coordination in locomotion adjustment persisted until the end of the experiment.

These findings in the monkeys, as also described by the authors, are comparable to observations made on normal subjects and deaf persons with bilateral labyrinthine defects (LD subjects) under parabolic flight microgravity, where some of the normal but none of the LD subjects experienced an illusion of reversal (upside-down) in their orientation.[8] Another point to be noted in this experiment is that the functional recovery attained in the normal monkeys was higher than that of the lesioned animals. It implies that the vestibular organs would have played a supplementary role for establishing orientation adjustment during repeated microgravity exposures. Expanding on this possibility, it is conceivable that normal function of the otolith organs may be still important for the space crews to facilitate their adaptation to a microgravity environment, although there has been no supporting evidence to date in space experiments.

DISORIENTATION OF PIGEONS EXPOSED TO MICROGRAVITY

With parabolic aircraft-flights, King[9] first observed disorientation of normal pigeons, and loss of the control was detailed further by Oosterveld and Greven.[10,11] When the g-force was lowered, normal pigeons always spread their wings at 0.06 g and took flight at zero-gravity (0 g). They showed random movements with their head swung up or horizontally, and when the g-force became negative transiently during the parabolic flight, they immediately turned and and flew upside down, normal to gravity. When their eyes were covered, flying birds tumbled into a backward loop with a diameter of about one foot, their head and tail bent back, and continued in this posture and loop as long as the weightlessness lasted (Fig. 2). When their legs were strapped, the onset time of flying-up of unblindfolded birds was delayed until the g-load became completely zero, while any fly-reaction was suppressed in the birds with their eyes covered. In blindfolded birds, however, after a few parabolas they spread their wings at zero-gravity and started tumbling into a backward loop, with their heads showing random movements.

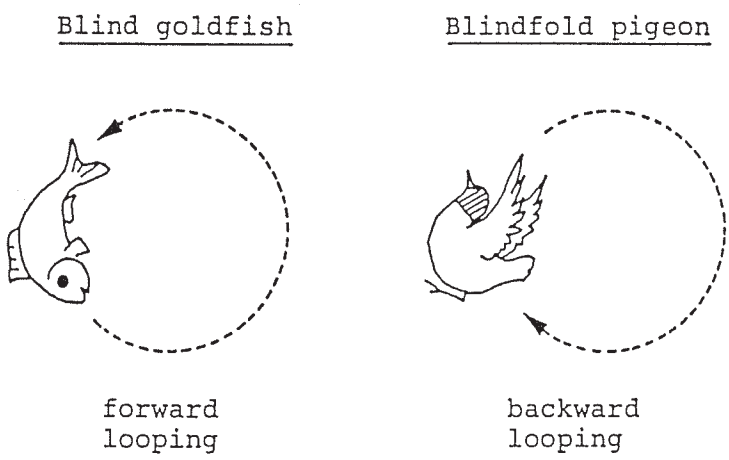

Fig. 2. Characteristic looping behaviors in fish and birds exposed to parabolic flight microgravity. Note that direction of loop is different among these animals.

Birds are animals who subject themselves, in daily life, to the lowered or zero-gravity state of free-fall for periods lasting over a few seconds. They must correlate the otolith information with the other senses differently from other animals who live on the ground. The above findings visualized such characteristic sensory-sensory interactions peculiar to birds through their disorientation patterns under microgravity. In addition, these findings demonstrated clearly that gravity-change inducing disorientation is strongly compensated by visual inputs, and this regulation is modulated further by other sensory inputs.

Oosterveld and Greven[10,11] thought that the backward looping response in the blindfolded pigeon under microgravity might be a reaction to the tumbling-forward illusion that had often been experienced in man as an inverted illusion during parabolic flight[8] and also by cosmonauts (Russian space crews) immediately after insertion into orbital flights.[2] Alternatively, the pigeon might have attempted to produce a gravity-like force on its head with this tumbling motion. These ideas, however, conflicts with evidence that has a hurdle to be cleared since a blind fish makes a forward instead of a backward loop during parabolic flight microgravity, as will be shown later (Fig. 2).

Pigeons with one or both sides of the labyrinth obstructed were also observed in parabolic flight.[12] The birds with one side obstruction showed a barbecue spin rotation with movement toward the obstructed side. The birds whose both labyrinths were obstructed with an interval of 6 weeks between each operation, showed a barbecue spin rotation at first. The direction of the rotation was towards the most recently obstructed labyrinth during the first week and then switched gradually to outside (forward) looping during the next several weeks, just the opposite of normal birds in parabolic flight microgravity. This would suggest that it is not the semicircular canal organs but the otolith organs that contribute to the looping behavior.

DISORIENTATION OF AMPHIBIANS EXPOSED TO MICROGRAVITY

Frog

A characteristic posture similar to hamsters in air[4,5] has been reported in normal frogs under

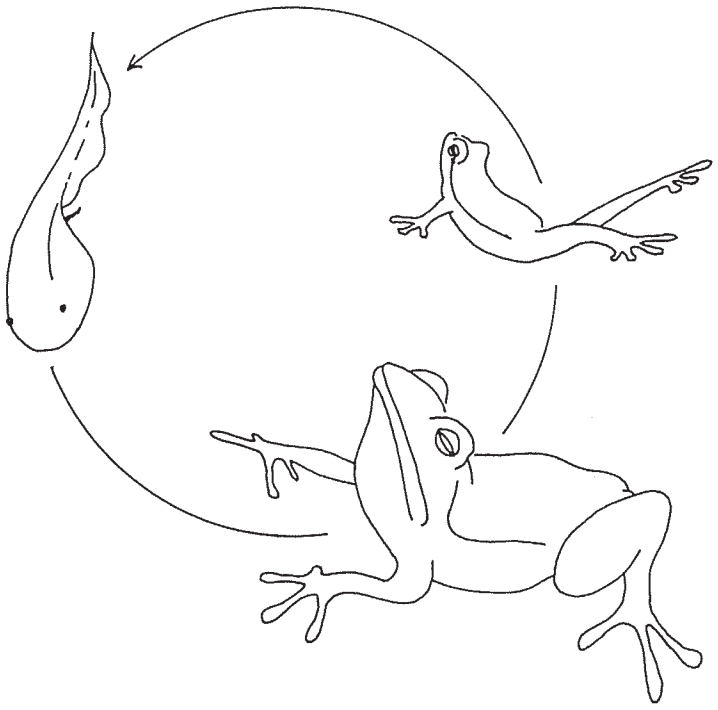

Fig. 3. Posture of frogs in microgravity. Frog on a foothold and when floating in space microgravity. Tadpole tumbles in forward loop during parabolic flight microgravity.

microgravity in parabolic flight and also on the Mir station;[13,14] extreme dorsiflexion of the neck in either perching or floating and full extension of the hindlimb in floating (Fig. 3). According to a brief communication, most frogs demonstrated inflation of the abdomen during floating, indicating fear or excitation, and the neck-dorsiflexion was mostly accompanied by stepping-back behavior on a perch, implying that the frogs might have been attempting to get rid of an irresistible sensation induced by their own reflex mechanism due to loss of input from the otoliths. This characteristic posture persisted in frogs throughout seven days of the Mir mission. Interestingly, tadpoles in parabolic flight microgravity tumble into forward looping (personal communication from K. Souza) (Fig. 3), opposite to the behavior of blindfolded pigeons and just like the blind fish as shown later.

Turtle

Food-catching behavior is fundamental for animals, and a visual cue is most important in its performance. This response of the turtle under microgravity was examined by von Beckh.[15] Under a normal gravity condition, turtles strike like snakes at their food, projecting their necks with pin-point accuracy at the bait. He compared the response of normal ones with a turtle whose labyrinth had been injured by accident in an overheated aqua-terrarium. This turtle had learned to compensate for his loss of labyrinthine cues by developing his visual orientation during three weeks after the accident and regained almost its normal response in taking the bait by the time of flight. During parabolic aircraft-flight weightlessness, the turtle without labyrinthine

function completed the bait-catching as on the ground, while the normal ones moved only a little and slowly and were unable to attack the offered bait or failed to take it when striking. However, the failure in the normal ones was considerably improved after twenty to thirty flights, possibly due to acquired visual compensation.

The author also demonstrated a similar pattern of disturbed orientation and muscular coordination in human subjects who had to mark crosses appropriately on the target in front of them, with their eyes open or closed during the same parabolic flights. The improvement started already after several flights. Visual compensation should have played a main role for the improvement. It is now accepted that visual cues are most reliable under microgravity in space, and the predominant contribution of visual sense has been commonly experienced by space crews.[2)]

DISORIENTATION OF FISH EXPOSED TO MICROGRAVITY

Like birds, fish swim around three-dimensionally in the water. The cochlea is missing but the vestibular (semicircular canal and otolith) organs are well developed. The utricular otolith has a relatively large body, probably for sensing a gravity force against buoyancy. The visual function is also well developed and has been studied extensively.

Parabolic Flight Experiments

When blind goldfish were exposed to parabolic flight, the lowered g load caused the fish rapidly to dive with head down and continued microgravity resulted in forward looping,[16,17)] just opposite the direction observed in the blindfolded pigeon (Fig. 2). As the fish showed an opposite head-up (climbing) response in transition from a lower to a higher g load, the authors considered these diving and looping responses could be used to counterdirect the otolith displacements caused by gravity force. However, since the otolith displacement should be in the same direction either in fish or birds under microgravity, it seems strange that the direction of the looping response would be different between these animals. The neck, which is absent in fish but a powerful structure in birds for maintaining balance, may be a key to resolving this issue. Alternatively, the contribution of some as yet unidentified gravity sensing organ(s) other than the otolith organ may be involved in the different responses.

As described in the above reports, normal vision changes the loop pattern from a vertical circle to an irregular turn, in both fish and birds during parabolic flights, suggesting a suppressive effect of vision on vestibular function. There is good evidence that the strength of visual suppression may vary depending on the animal species and strain. In the IML-2 space experiment on Medaka reproduction under microgravity undertaken by a team of Japanese researchers in 1994, a special species of Medaka fish, which do not have looping responses in light under microgravity, were used. In this case, the Medaka chosen possessed strong visual dominancy in swimming behavior, and the characteristic was strain-dependent.[18,19)]

Unilateral labyrinthectomy in blind goldfish results in continuous rotation towards the lesion side. If this rotation were simply driven by signals from the second, intact otolith action, the fish exposed to diminished g-force would cease the rotation or reduce the rotation speed. Contrary to this expectation, however, the rotation of lesioned fish in parabolic flight low-gravity increased in speed, though the speed returned to the pre-exposed rate during the parabola.[20)] This finding suggests that the rotation induced by labyrinthectomy would result from signals highly biased in the integration center for equilibrium.

Experiments on Space Shuttle

Contradicting the above findings in fish exposed to parabolic aircraft flights, not only the normal goldfish but also the goldfish without the otoliths showed backward looping, instead of forward looping, throughout the 15-day IML-2 mission, though the loop frequency was reduced later in the flight.[21] Furthermore, in this same experiment, the goldfish whose otolith organs had been removed unilaterally and compensated for the dysfunction by the time of lift-off, bent their body and rolled towards the operated side again onboard, though the body flexion and the rolling disappeared by the 5th–8th day of the flight. Additionally, it was found that the time after labyrinthectomy was an important factor which could modulate the response pattern. These striking differences between findings from parabolic aircraft flights and those from prolonged microgravity suggested both data could not be discussed simply as microgravity effects. It may be reasonable to consider that the data from parabolic flight belong to dynamically changing responses to be defined as transitional effects caused by gravity changes.

When a fish is illuminated from the side, it tilts its body vertically 20–30 degrees, so as to turn its back toward the light source. This tilt response is called the "dorsal light reaction (DLR)" of fish, and is known as a good model for visual vestibular interaction.[22,23] In fact, when the otoliths are removed (vestibulectomized), the fish turns its back completely toward the light. The otolith-removed fish, however, regains the DLR tilt angle a few months after surgery, rapidly in a few days and then gradually later.[24] Since these fish can maintain the upright position in darkness, there must be unidentified graviceptor(s) other than the otolith organs which compensates for the otolith dysfunction; the swim bladder may be a candidate graviceptor organ since gas buoyancy can be a cue for gravity sensation.[25]

In Skylab 3, a 59-day flight mission in 1973, von Baumgarten and group[26] observed that two fingerling fish in a polyethylene bag swam in tight and irregular circles during the first 3 days, but gradually returned to their normal swimming pattern thereafter. A similar phenomenon was observed in the killifish at 16–17 months of age during the 9-day mission of the Apollo-Soyuz Test Project (ASTS).[27] Interestingly, in this latter experiment, one group of fish with a 32-hour developmental stage at the time of launch were hatched after the flight was completed. These hatched fish were less disoriented when exposed to parabolic aircraft microgravity, and more sensitive to its hyper-gravity periods, suggesting a specific effect of gravity on fertilizing cells at their critical development stage. Furthermore, the fry of fish hatched from eggs flown for 19.5 days aboard the biosatellite Cosmos-782, showed slightly increased creatine kinase activity in the cortex of the vestibular cerebellum, suggesting microgravity-induced modification of functional activity at the structure which normally receives inputs from graviceptors.[28]

On the basis of these findings in fish, a working hypothesis was proposed by our group that disorientation and recovery processes in normal fish should be demonstrable during the initial days of microgravity exposure, in the form of a disturbance and restoration of DLR, respectively. In addition to this, we considered that these processes might reflect in EEG activities of the cerebellum, since DLR is largely integrated in the cerebellum.[29,30] This experiment was conducted during the 8-day flight of the Spacelab-J mission in 1992.[31] Two carp, one normal and the other labyrinthectomized, were placed aboard, each mounted with a pair of ball-tipped electrodes and a miniature preamplifier with a lead cable on the head for EEG recording. The results showed that, in the normal carp, the DLR was unstable for the first 3 days inflight but gradually recovered thereafter. The recovery was characterized by gradual restoration of the DLR tilt speed. A spectral analysis of the EEG revealed changes on day 2 at first and again on day 4,[32] corresponding to the time of the worst deterioration of the DLR and the phase of DLR recovery, respectively (Fig. 4).

These findings provided a good evidence of the sensory conflicts and readjustment occurring

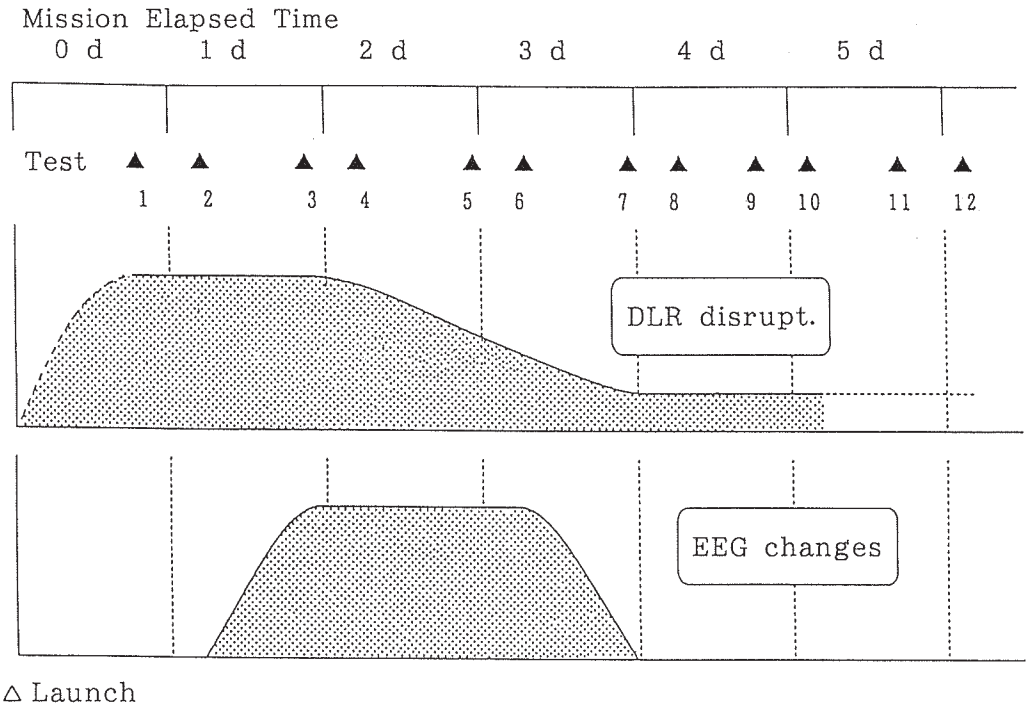

Fig. 4. Time course of sensory conflicts and recovery in fish under space microgravity. Degrees of disruption in the dorsal light response (DLR) and deviation in the EEG activity are illustrated arbitrarily (shaded areas), based on results in the normal carp data obtained from Spacelab-J experiment. Spectral power of cerebellar EEG changed significantly between the 2nd and 3rd tests and again between the 6th and 7th tests.

in the early days of microgravity, and also supported the sensory conflict theory as to the genesis of space motion sickness (SMS). According to the theory, SMS is attributable to sensory conflicts primarily caused by loss of vestibular input, and the recovery process corresponds to rearrangements of neural circuits in the CNS taking place during an initial few days of microgravity. Actually, SMS episodes have rarely been reported after 4 days in space.

The lesioned fish whose otoliths had been removed two months before the flight maintained DLR in the first inflight test (22 hrs after launch), but the DLR was disrupted at 2 days as in normal carp. The recovery process could not be evaluated in the fish, because the EEG cable became tightly twisted so as to immobilize the fish for the remainder of the experiment. However, our working hypothesis that the disruption of DLR should also occur in the lesioned fish, since neural compensation following labyrinthectomy on earth would have to be readjusted in microgravity, was partly ascertained.

CONCLUSION

Before practical means of producing the state of microgravity were available, some physiologists suspected that a short period of microgravity might be enough to result in prolonged disturbances in performance and even to induce motion sickness, because of the strong conflict

between normal vision and changes in vestibular and proprioceptive apparatus. This notion of sensory conflict has further gained favor in current space physiology and medicine, and is now taken to be the most promising theory to explain the genesis of space motion sickness.

On the other hand, although disturbances in performance under microgravity were not actually as serious as suspected, a new problem arising from loss of vestibular inputs was possible reorganization of sensory and sensory-motor integration in the CNS and threshold changes in the peripheral sensing systems. These must be physiologial changes of adaptation to microgravity, but may distort the body reference coordinates originally established on earth, resulting in mistaken operation and incorrect sensory-motor responses during space flights. The key issue is first of all to determine the general features of such disorientation and its time course under microgravity.

In order to proceed with investigations on this subject, further animal experiments in space are indispensable. As reviewed in the present paper, a short-term exposure to microgravity produced by aircraft is sometimes valuable to know responses to gravity change, to assess the species difference of the response, and to determine whether or not the observed response is rapidly adaptive in nature. However, an exposure so short is virtually useless to attempt to predict real responses and processes in space microgravity. Past experience and experiments in man and animals in space microgravity suggest that the sensory and sensory-motor functions may change rapidly at first in a matter of minutes or hours, and then gradually over the days and weeks that follow.

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