

BEHAVIORAL RESPONSES TO LINEAR ACCELERATIONS IN BLIND GOLDFISH*

I: *The Gravity Reference Response*

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Abstract. Blind goldfish were subjected to linear accelerations on a motor car and on a parallel swing. Movements of the fish in a tank during the accelerations were recorded with a movie camera. During the horizontal acceleration, the fish aligns his longitudinal axis in a plane perpendicular to the direction of an apparent gravity with the fish's back pointing away from the direction of this apparent gravity vector. This is similar to the manner in which the fish usually aligns himself horizontally in response to the vertically downward terrestrial gravity and can therefore be termed 'gravity reference response'. It is concluded that blind goldfish cannot distinguish between otolith displacements caused by passive tilts and equivalent otolith displacements caused by moderate inertial forces during rectilinear acceleration. With a horizontal jerk of higher magnitude, two additional responses can occur: horizontal 180° turns following tailward jerks and straight forward darting following noseward jerks.

1. Introduction

Most vestibular physiologists now agree that displacement of the otoliths in the inner ear leads to body movements which are directed so that the original position of the otoliths, hence, of the body, is restored. Direct recordings from utricular nerve fibers indicate that displacements of the otoliths in all three planes of space can be sensed and that there are specific differences in the impulse patterns for displacements of the otoliths in different directions (Ades and Engstroem, 1965; Löwenstein, 1966; von Holst, 1950). The otolith displacement under natural conditions is usually caused by the gravitational force of the Earth (9.81 m/sec^2) in combination with any changes in the normal position of the head. The behavioral responses of animals to such stimuli are understood reasonably well (Magnus, 1924).

It is still not certain, however, what kind of behavioral responses are triggered when the otolith system is stimulated, not by changes in the direction of the gravitational pull, but by inertial stimuli following horizontal acceleration of the whole body. From a physical standpoint gravitational and inertial stimuli are indistinguishable. According to the principle of equivalence in the general theory of relativity, the gravitational and inertial masses are equivalent (Jongkees and Groen, 1946; Young, 1967). From within the utricle of the vestibular system it is impossible to distinguish between otolith displacement caused by gravitational and that caused by inertial forces. Among the relatively few experiments reported in the literature which deal

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with the problem of inertial stimulation of the otoliths are those of Jongkees and Groen (1946), who studied the subjective sensations of humans on a parallel swing, Harden Jones (1956) who studied the behavioral responses of blind goldfish to linear acceleration, and Brindley (1965) who observed rabbits' postural reflexes during free fall.

One of the many questions still open in this field is whether the central nervous system can distinguish between gravitational and inertial stimuli by comparing otolith displacements with concurrent angular accelerations as perceived by the labyrinth semicircular system (Mayne, 1969; Mayne, 1967; Young, 1967). It will be shown that blind fish cannot make this distinction and always behave as when the otolith displacement is caused solely by a passive tilt in the gravitational field of the earth.

2. Methods

The methods were similar to those we used previously to observe fish under reduced gravitational force (Von Baumgarten, 1969). Ten goldfish (*Carassius auratus*) and one guppy (*Lebistes reticulatus*) were blinded under full anesthesia, by removal of both eyes. The experiments were performed two to six weeks after the operation. The experimental setup (Figure 1) included a 36 liter aquarium measuring $30 \times 55 \times 23$ cm,

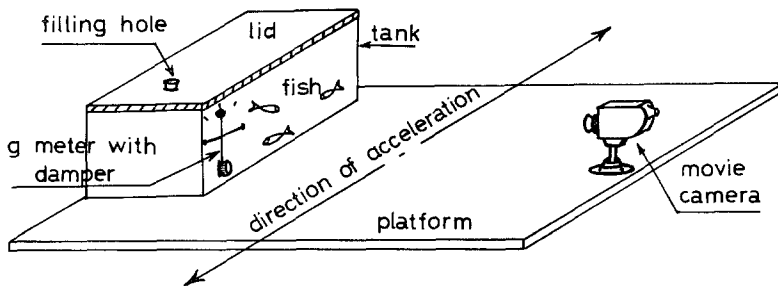


Fig. 1. Sketch of experimental set-up. See text for description.

filled with water and closed with a sealed lid. The amount of gaseous air in the tank was kept as small as possible in order to reduce water current and turbulence to a minimum. An accelerometer was fixed on the front glass of the fish tank to measure horizontal acceleration. A super-8 movie camera was mounted opposite the fish tank, on a platform which was strapped in the rear compartment of an automobile. This setup allowed the simultaneous filming of both the fish's behavior and the indications of the accelerometer before, during and after acceleration.

After a control record was made of the fish's behavior at rest, the car was accelerated to a speed of 40–70 mph within a period of between 3 and 8 sec, corresponding to horizontal accelerations of between 0.5 and 0.8 g. After reaching the final velocity and maintaining it for several seconds, the car was brought to a quick stop by applying the brakes, reaching a 'negative' horizontal acceleration of between 0.5 and 0.9 g. The

total distance covered by one run was between 50 and 300 m. Several times horizontal acceleration was intentionally applied when the fish were in different initial positions.

No essential difference in the behavior of the fish was observed when comparing positive forward accelerations of the car with negative accelerations due to braking, provided the inertial force caused by these 'positive' or 'negative' accelerations had the same direction relative to the body of the fish. Since the effects of optokinetic stimulation can be excluded in our blind goldfish, we concluded that whether the acceleration was due to increasing or decreasing the forward speed of the car was irrelevant to the outcome or to the interpretation of the experiment, and that it is possible hereafter to refer to the stimulus only as causing tailward, noseward, side-ward, upward or downward displacement of the otoliths.

In another series of experiments, the fish tank was placed on a parallel swing and horizontally accelerated either by the pendulum action of the swing or by gently pushing the swing from both sides at the reversal points of movement. Similar results were obtained.

3. Results

Horizontal acceleration was almost invariably followed by a systematic, predictable change of the tilt of the fish's longitudinal axis when the fish's longitudinal axis was initially parallel to the imposed acceleration. When the acceleration forced the otoliths tailward, the fish tilted nose downward and approached the bottom of the fish tank (Figures 2a and b). When the acceleration was such that the otoliths were forced noseward, the fish tilted nose upward and swam forward towards the surface (Figure 2b). These responses were observed during increases of the forward speed of the car as well as during braking; the reaction of the fish depended solely on the initial position of the fish with respect to the direction of the acting acceleration. When the direction of acceleration was sideward, as was the case if the fish's nose or tail was pointed towards the camera, the fish rolled around his longitudinal axis so that his back was tilted against the direction in which the inertial force acted on his otoliths (Figure 2c).

Confirmation that this response to inertial stimuli was systematic, not random, came from experiments in which several fish in one tank simultaneously displayed this response. Fish which pointed in the same direction also tilted in the same direction, and fish which opposed each other with their heads displayed reciprocal tilting. During the tilting the fish showed a remarkable simultaneity of movement and, most often, a parallel position in the fish tank (see the figures).

Further confirmation of the systematic nature of this phenomenon was obtained in experiments in which the direction of the inertial force on the otoliths was suddenly changed. This could be achieved by shifting from positive acceleration to braking. The fish, provided that they did not change their heading, switched from a dive to a climb or from a climb to a dive. In Figure 3a and b the mirror-like curves represent the movement of two fish which opposed each other and were subject to a directional change of the horizontal acceleration.

A similar change in the tilt of the longitudinal axis occurred when the direction of the acceleration of the fish tank remained the same, but the fish spontaneously turned around in the horizontal plane to head in the opposite direction. Then, too, climbing fish started to dive (Figure 4) and vice-versa according to the direction in which the acceleration acted on their bodies. ('Apparent gravity' and 'theoretical tilt' are also plotted in Figure 4; these items will be further defined under Discussion.)

In a different series of experiments, the fish were accelerated on a parallel swing. The fish in this experiment showed responses which were comparable to those de-

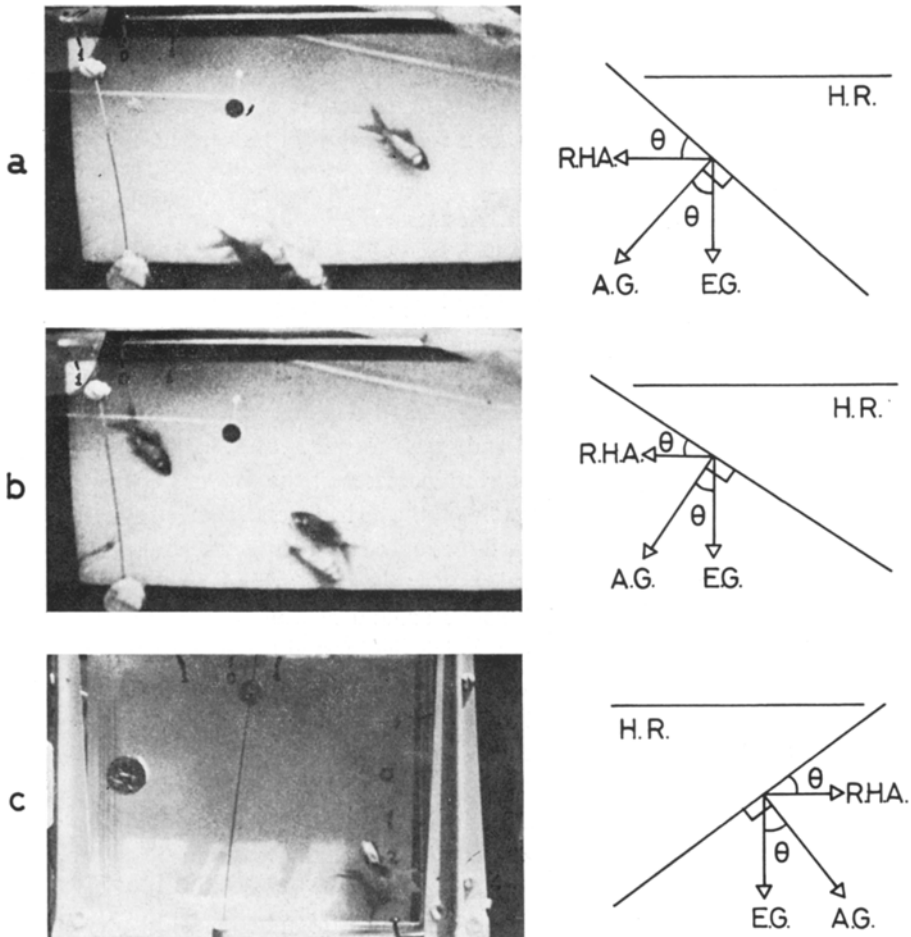


Fig. 2. Gravity reference response. The pictures at the left are single frames taken from super-8 mm movies. The g -meter marks are in the left top corner of the pictures. The diagrams at the right indicate the horizontal reference line HR, the earth gravity EG, the reactive horizontal acceleration RHA, the apparent gravity G and the theoretical tilt angle θ . Note the parallel tilt of the fish in all experiments. The noseward accelerated fish in a and b dive, the tailward accelerated fish in b climbs. The fish pointing towards and away from the camera in c are leaning sideways. The observed tilts approximate the theoretical tilt angles.

scribed before in the experiments with an automobile. The longitudinal axis of the fish oscillated with the individual excursions of the swing and closely paralleled the acceleration curve and the tilting curve corresponds closely to the latency period of the response. It averaged 270 msec (Figure 5).

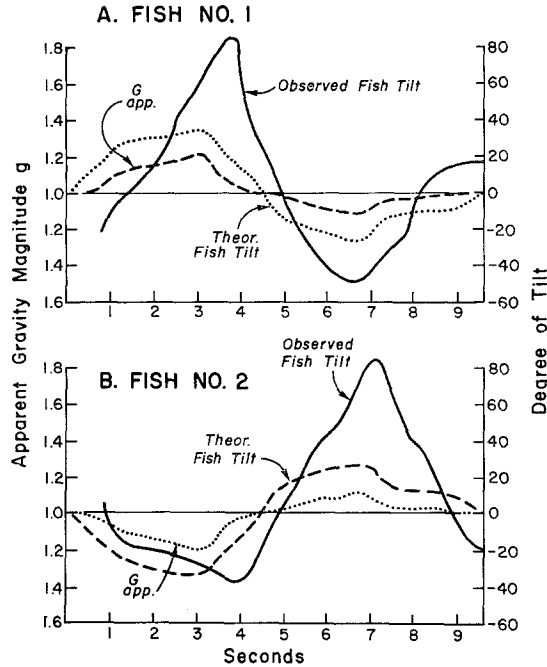


Fig. 3. Graph showing gravity reference response of opposed fish during directional change of horizontal acceleration. The 'observed tilt', the theoretical tilt and the apparent gravity are plotted against time during one experimental run. Two fish were studied simultaneously in the same tank. The plottings were obtained by single frame analysis of a movie. Apparent gravity was calculated as the vector of earth gravity with horizontal acceleration. The changes of apparent gravity were caused intentionally by acceleration or deceleration (braking) of the sports car. Note the mirror-like correlation of the tilting movements of both fish. The fish are overshooting the theoretical tilt angle.

When the horizontal g load was increased at a fast rate of more than 4 g/sec (jerk) two additional responses of the fish were observed, each depending on the direction of the acceleration in respect to the fish: tailward acceleration of the fish (equivalent with noseward displacement of the otoliths), caused the fish to turn 180° around in the horizontal plane. A noseward jerk (equivalent with tailward displacement of the otoliths) resulted in forward darting response from most fish. These two responses will be dealt with in more detail in a following paper.

4. Discussion

It is assumed in the following that the observed reactions of goldfish to rectilinear accelerations were caused by otolith displacements, since the otoliths are known to

be part of a highly specialized and sensitive receptor organ for gravitational (hence also inertial) stimuli. However, we cannot disregard the remote possibility that other sense organs provide additional sensory stimuli which could participate in the initiation of the observed reflexes. Since the density of our goldfish was not always

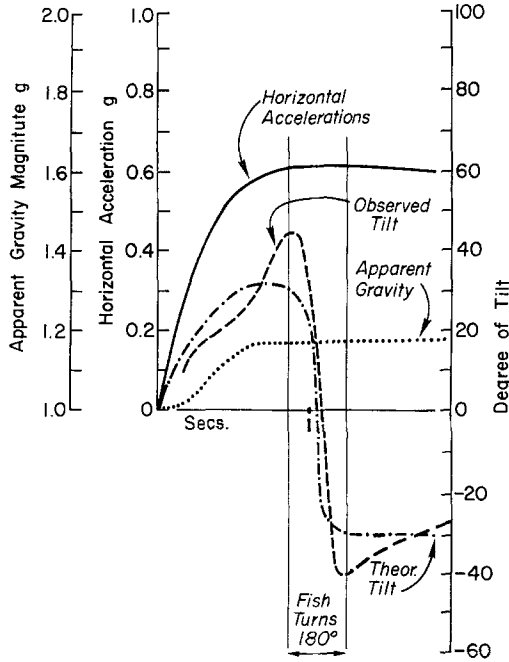


Fig. 4. Change of the gravity reference response following a spontaneous 180° horizontal turn of the fish during acceleration. The response changes from a climb to a dive after the fish makes a spontaneous horizontal turn, while the direction of the horizontal acceleration remains the same.

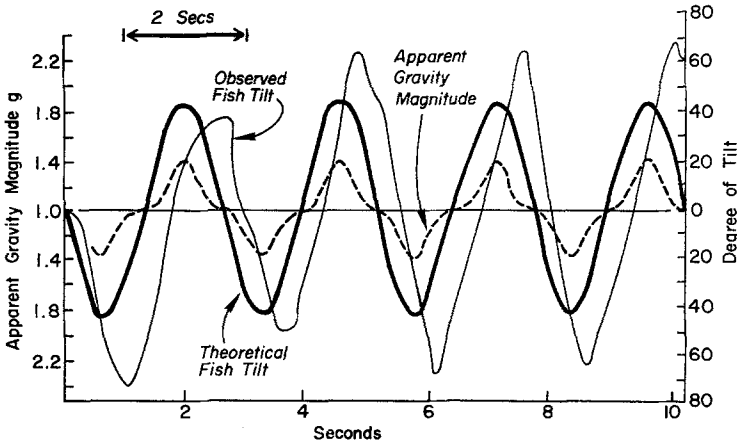


Fig. 5. Gravity reference response of a fish on a parallel swing. The longitudinal axis of the fish oscillates with the excursions of the swing and follows the acceleration curve closely.

equivalent to the surrounding water, the whole goldfish body could be passively displaced by acceleratory stimuli and such movements, relative to the water, could be detected by the lateral line system.

For reasons of simplicity, we assume in the following that only one 'standard' otolith is displaced during the experiment, either tailward or noseward. Such simplification, which disregards the complex geometry of the different otolith organs of the fish, seems permissible if the problem to be discussed here concerns not the details of the receptor mechanisms in the statocysts but the behavioral responses of the whole fish which are caused by inertial forces of noseward or tailward direction.

The tilting of fish during horizontal linear accelerations was very stable and appeared invariably in all fish tested. Forward acceleration of the fish, causing a tailward displacement of the otoliths, led to a nose-down tilt of the fish. Backward accelerations of the fish, connected with a noseward displacement of the otoliths, led to a nose-up tilt of the fish. The explanation of this phenomenon seems to be that the blind fish which cannot recognize its real attitude and tilt, relies on the otolith system as the only cue left to him for perceiving his attitude in space. During rectilinear accelerations, of course, this system provides wrong information concerning the real tilt. The fish whose otoliths were displaced tailward consequently 'concluded' that he has suddenly been passively tilted head up. In other words, his CNS obtained from the otolith organ the input signals keyed to initiate a compensatory, forward tilting rotation around the transversal axis. The reciprocal movement would result in the fish being accelerated tailward. Its otolith would be displaced noseward, giving the fish the illusion that it was tilted downward. In this case, the input signals to its CNS would be keyed to initiate an upward tilt. A similar scheme can be applied in the cases when acceleration hits the fish from the side. Otoliths of both sides would then move against the direction in which the fish was accelerated, simulating a passive sideward tilt which would initiate counter-rolling.

Figure 2, pictures a, b and c with corresponding diagrams on the right side, shows that the fish align themselves with their longitudinal axes in a plane perpendicular to the direction of an apparent gravity vector with the fish's backs pointing away from the direction of this apparent gravity vector. Apparent gravity is the vector sum of the vertically downward earth gravity vector and the *reactive* inertial horizontal acceleration which is opposite to the applied horizontal acceleration of the fish tank. The manner in which the fish aligns itself to the apparent gravity vector is the same as the manner in which the fish normally aligns itself horizontally in response to the vertically downward earth gravity. In this response, two accelerations, gravity and inertial reactive, appear to be vectorially summed by the otolith to establish a new apparent gravity to which the fish aligns himself as if responding to earth gravity alone. This response in the following is referred to as 'gravity reference response'.

It should be mentioned, that the observed tilting movements in the gravity reference response were achieved actively, not passively by the fish. Frame by frame analysis of the movies revealed the up or down deflections of the tailend of the fish, which initiated in conjunction with forward swimming, the observed tilting movements.

The center of gravity in goldfish is high near the spine and if any passive gravity reference response would be present it should be of opposite direction than the observed one. Dead or anesthetized fish do not display the gravity reference response as described here.

Figure 3 illustrates the magnitude of the apparent gravity and the theoretical tilt angle (the instantaneous direction of the apparent gravity vector) of each fish No. 1 and No. 2. The apparent gravity and theoretical tilt angle plots are oriented to correspond with the heading of each fish. Similarly in Figures 4 and 5 the apparent gravity magnitudes and the theoretical fish tilt angles are shown along with the actual fish tilt angles. From these illustrations it appears that the fish follow the theoretical tilt with a delay of $\frac{1}{4}$ to 1 sec. The fish generally overshoot the maximum tilt angle.

It was argued in the literature (Mayne, 1967, 1969; Young, 1967) that the semicircular canal system could provide additional cues which could help the CNS to distinguish otolith displacement caused by gravitational stimuli from that caused by inertial stimuli. While theoretically such a possibility seems feasible, the experiments show that this is not the case in fish. So far as the gravity reference response is concerned, any change or lack of change in the impulse pattern of the semicircular canal system, at least in our experiments, did not suppress the otolith reflex. Moreover, the active tilt, which in our experiments followed rectilinear accelerations, was obviously not inhibited or compensated for by the semicircular canal system. The fish were even overshooting the theoretical tilt angle. We do not know at the present time whether the observed tilt would be larger or smaller without the semicircular canal system. The solution of this question would require experiments with intact otoliths and destroyed semicircular canal systems, or at least more quantitative comparisons between the theoretical tilt and the observed tilt for any given horizontal acceleration. The gravity response following inertial stimuli is in reality an earth gravitational counter-rolling response in which the stimulus is altered by inertial forces. Earth gravity and the inertial reaction to horizontal acceleration are vectorially summed to form a resultant apparent gravity to which the fish aligns himself. Thus in the gravity reference response the fish does not separately recognize the inertial horizontal acceleration stimuli.

One may conclude that fish are unable to distinguish between gravitational stimuli and inertial stimuli where the applied inertial acceleration is constant or near constant. However if the inertial stimuli change at a sufficient rate (jerk vector threshold) the fish will demonstrate his recognition of this inertial stimulus by means of fast turns (as observed already by Harden Jones, 1956) or by a forward darting movement. The threshold jerk for this response was approximately 4 g/sec *horizontal* or less for the individual fish involved. Tests to be conducted in the near future should more specifically define this escape response jerk vector and threshold.

It does not appear that gravity reference response during horizontal linear accelerations has great, if any, functional significance for the fish. Strong horizontal accelerations were very rarely encountered during the long evolutionary epochs and probably did not exert sufficient survival pressure to develop a neural pattern which

allows to suppress such meaningless reactions. With the entrance of man in the era of modern technology however, strong and quickly changing linear accelerations are encountered in vehicles such as cars, boats, airplanes and spacecraft.

Nausea and other autonomic responses can occur indicating that the human vestibular system is not perfectly matched to such stimuli. Human volunteers, subjected to linear accelerations on a parallel swing reported tilting illusions at the endpoints of the excursions of the swing (Jongkees and Groen, 1946). These subjective sensations seem to be a human correlate of the gravity reference response in fish, indicating that our human vestibular system has essentially the same difficulties to distinguish gravity from externally imposed horizontal acceleration.

References

- Ades, H. W. and Engstroem, H.: 1965, in 'The Role of the Vestibular Organs in the Exploration of Space', NASA Publication SP-77, U.S. Naval School of Aviation Medicine, Pensacola, Fla., National Aeronautics and Space Administration, Washington, D.C., 23.
- Brindley, G. S.: 1965, *J. Physiol.* **180**, 20-21.
- Harden, Jones, F. R.: 1956, *Nature* **178**, 642-643.
- Jongkees, L. B. W. and Groen, J. J.: 1946, *J. Laryngol. Otol.* **61**, 529-540.
- Löwenstein, O.: 1966, in 'Second Symposium of the Role of the Vestibular Organs in Space Exploration', NASA Publication SP-115, AMES Research Center, Moffett Field, California, 1966. National Aeronautics and Space Administration, Washington, D.C., 73.
- Magnus, R.: 1924, *Körperstellung*, Springer, London, New York, Berlin.
- Mayne, R.: 1967, Discussion to the paper to T. R. Young and J. L. Merry, in *Third Symposium on the Role of the Vestibular Organs in Space Exploration*, Naval Aerospace Medical Institute, Naval Aerospace Medical Center, Pensacola, Fla., p. 367.
- Mayne, R.: 1969, *Vestibular Systems*, in *Handbook of Sensory Physiology*, Vol. VI: Springer-Verlag, Berlin/Heidelberg/New York.
- Von Baumgarten, R. J., Atema, J., Hukuhara, T., and Rocker, M.: 1969, *Space Life Sci.* **1**, 554-564.
- Von Holst, E., 1950, *Z. Vergleich. Physiol.* **32**, 60.
- Young, J. L. R., 1967, in *Third Symposium on the Role of the Vestibular Organs in Space Exploration*, Naval Aerospace Medical Institute, Naval Aerospace Medical Center, Pensacola, Fla., p. 389.