Is an Internal Model of Head Orientation Necessary for Oculomotor Control?

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ABSTRACT: In order to test whether the control of eye movement in response to head movement requires an internal model of head orientation or instead can rely on directly sensing information about head orientation and movement, perceived gravity was separated from physical gravity to see which dominated the eye-movement response. Internal model theory suggests that the oculomotor response should be driven by perceived, internalized gravity, whereas the direct sensing theory predicts it should always be driven by vestibularly sensed gravity. Subjects lay on an airbed either supine or on their side and were sinusoidally translated along their dorsoventral body axis. The direction of perceived gravity was separated from physical gravity by performing the experiments in a room built on its side with the direction of its "floor" orthogonal to both physical gravity and the subject's translation. The swinging sum of the imposed sinusoidal acceleration with physical gravity was thus in a plane orthogonal to its sum with perceived gravity. Oculomotor responses to these swinging vectors were looked for and responses were found only to the sum of the acceleration with physical gravity, not perceived gravity. It was concluded that an internal model is not used to drive these compensatory eye movements.

KEYWORDS: internal model; tilt translation; vestibulo-ocular reflex; torsion; perception; eye movements; otoliths; gravity

INTRODUCTION

When the head moves it is often desirable for the eyes to move to compensate for the effect that the head movement might otherwise have on retinal stability. But in order for the eyes to move correctly, it is necessary for their controllers to know about the head movement for which they are compensating. Sensory information about the head movement can be ambiguous (see FIG. 1, for example), and so it has been proposed that appropriate oculomotor control might be achieved using an internal model of the head's position[1–4] rather than using sensory information directly. The internal model theory proposes that a representation of the movement and orientation of the head is generated using copies of motor signals,[5] sensory information, knowledge of physical laws, and expectations based on recent history. Using an internal model allows high-level principles, for example, that maintained accelera-

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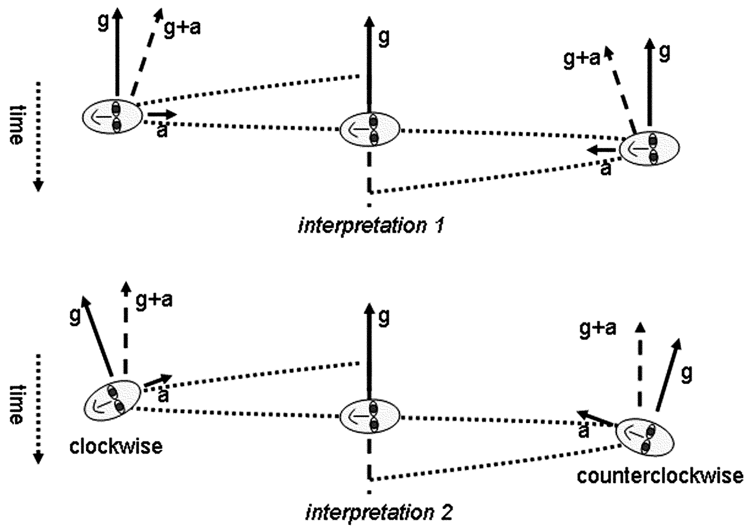

FIGURE 1. Two interpretations of the accelerations (*solid arrows*: linear acceleration "a" and the acceleration that is the equivalent of gravity "g") that are experienced by a subject oscillating along their body axis (indicated by *dotted sine wave*) while lying left ear down. The combination of physical acceleration (a) and gravity (g) is ambiguous. It could be interpreted as a linear translation (a) in a 1-*g* environment (interpretation 1). An alternative interpretation (interpretation 2) is that the entire combined acceleration (g + a) corresponds to gravity. Because gravity maintains a constant orientation in space, this interpretation is equivalent to the subject tilting in the directions shown.

tions are likely to be due to gravity rather than physical acceleration of the organism,[6] to be used in deducing the pattern of head movement. Internal model theory has been successful in explaining other aspects of motor control[7] because it overcomes problems associated with feedback delays, and allows anticipation and motor learning. Despite the success of internal model theory in describing many aspects of the oculomotor,[2] autonomic,[8] and perceptual[9] response to head movement, it remains possible that sensory processing directly, with the addition of some temporal filtering,[10–12] may be sufficient to explain the oculomotor response to head movement.

In order to test whether an internal model is necessary or whether direct sensory information can drive the oculomotor response to head movement, we examined the eye movements evoked by a head movement for which the internal model and direct sensing theories made different predictions. The movement we used was a linear acceleration orthogonal to gravity. This ambiguous movement and two of its interpretations are illustrated in FIGURE 1. If the two accelerations, gravity and an imposed acceleration, are summed into a single gravito-inertial acceleration (GIA) and the GIA is interpreted as being gravity then, because the direction of the GIA varies with the imposed acceleration, the stimulus must be interpreted as a roll tilt (FIG. 1, bottom). Alternatively, the GIA could be interpreted as resulting from dorsoventral linear translation orthogonal to gravity (FIG. 1, top).

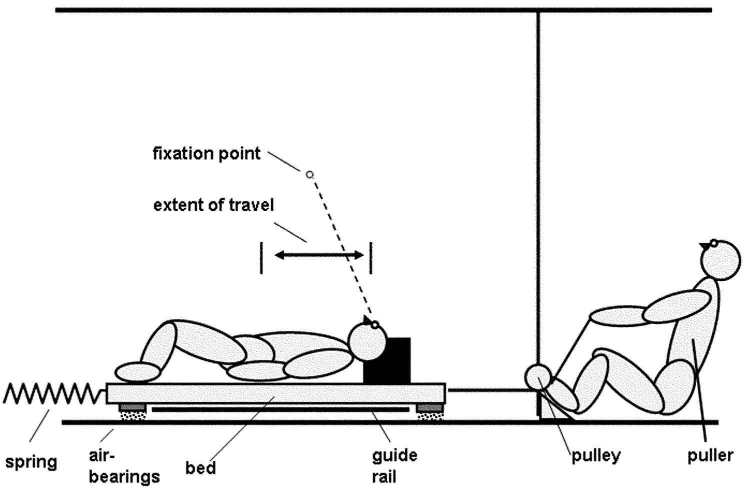

FIGURE 2. Diagram of the system used to move our subjects. Subjects lay either supine (as shown) or left or right ear down on a bed that was mounted on very-low-friction air bearings. The experimenter moved the airbed by means of a cable attached to one end. The bed was attached to the room at the other end by a spring that acted as a low-pass filter to keep the motion smooth. Also shown is the fixation point, which was viewed at a distance of 120 cm in the supine condition.

An actual tilt of the head evokes compensatory eye movements[12–15] around the tilt axis in the opposite direction to the tilt, whereas vertical eye movements would be expected from translation. Eye movements with the appropriate phase about the tilt axis can therefore be used as a signature to reveal when the brain interprets the combined GIA as indicating tilt. These signature eye movements have been found to be evoked when linear accelerations are experienced orthogonal to gravity.[11,16,17]

The different predictions of the two theories were created by performing our experiments in the York University Tilted Room Facility, a room built on its side (see FIGS. 2 and 3). The Tilted Room causes the perceived direction of gravity to align with the room,[18–21] but of course has no effect on physical gravity. The direct sensing theory predicts that physical gravity would be the only drive to eye movements, whereas the internal model theory predicts that perceived, internalized gravity would determine the oculomotor response. Because physical and perceived gravity were orthogonal to each other, the tilts that each of them caused when added to the linear acceleration were orthogonal too (see FIG. 3). We could therefore identify which tilt drove eye movements and which theory was correct.

METHODS

Subjects

Four subjects (3 male, 1 female, age range 20 to 50 years), including one of the authors (LRH), participated in this experiment. Experiments were approved by York University's ethics board.

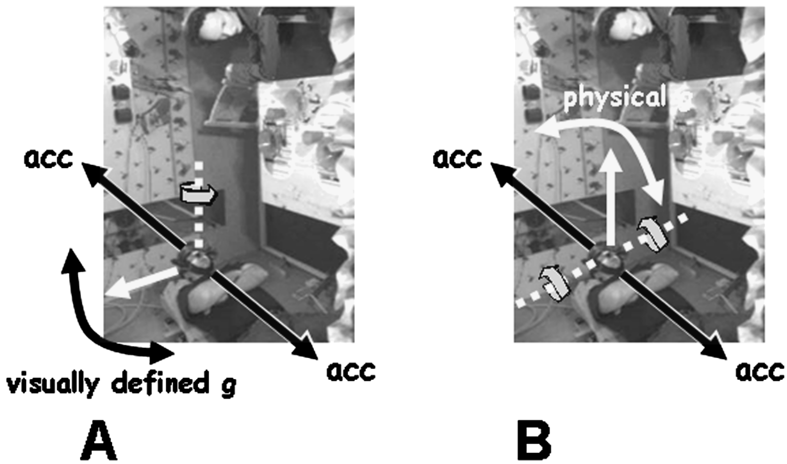

FIGURE 3. Subjects lay in the York Tilted Room, which is built on its side. The contents of the room, including manikins, are visually highly polarized to provide strong intrinsic cues about a visually defined direction of gravity that is orthogonal to physical gravity. Physical motion was always orthogonal to both visually defined (**A**) and physical gravity (**B**). Therefore, the vectors produced by combining linear acceleration with either perceived gravity (**A**) or physical gravity (**B**) each lie and move in the plane determined by the directions of their two components (shown by the *curved arrows*). By orienting the subject relative to these vectors, we looked for their effects in evoking eye movements. In the configuration shown here (supine relative to physical gravity), the acceleration plus perceived gravity vector (**A**) could generate torsional eye movements as indicated by the *arrow* curling around the dotted line. When subjects lay with their left or right ear down, then it was the sum of the acceleration with physical gravity that could evoke torsional eye movements.

The York Tilted Room Facility

The perceived direction of gravity was manipulated by the York University Tilted Room. The York Tilted Room is 2.4 m^2 on each side and decorated like an ordinary room with many objects placed in their natural intrinsic relationships with each other, except that everything is arranged to indicate "down" at 90° to the normal orientation (see FIG. 3). The wallpaper has a strongly polarized pattern; there are books on the bookshelves, knick-knacks on the windowsill, and place settings on the table. The room has been constructed so that the visual "floor" of the Tilted Room is one of the physical walls, and one of the visual "walls" of the Tilted Room appears on the physical ceiling. In accordance with this arrangement, the direction of visually defined gravity in this room is orthogonal to both physical gravity and the movement of the subject (see FIG. 3).

Physical Movement of the Subject

Within the room, subjects lay on a bed that floated on air bearings and was guided by a rail along which it glided on linear bearings. The bed was attached to the wall by a large spring and to a cable at the other end that passed through the wall of the Tilted Room. The experimenter could manually move the airbed on which the subject was lying by pulling on this cable, as shown in FIGURE 2. The position of the airbed was recorded using a potentiometer.

Procedure

Subjects lay on the airbed either on their back (supine) or on their side (left or right ear down; LED, RED, respectively) inside the Tilted Room either in the light or in the dark. Their heads were held firmly in a custom-made close-fitting cushioned container that supported the eye-movement recording helmet and kept their heads in a constant orientation. They were then oscillated manually ±10 cm along their dorsoventral body axis sinusoidally at 0.4 to 0.7 Hz. The peak acceleration was therefore in the range 0.06 to 0.2 g which, when combined with physical gravity, provided the equivalent of 4° to 11° of tilt. Subjects maintained fixation on an illuminated earth-fixed point that was suspended on an invisible wire 120 cm away from them and about half-way to the wall of the room beyond. The fixation point was positioned to be straight ahead at the midpoint of the subjects' traverse.

The direction of translation, the direction of physical gravity, and the direction of perceived gravity (when the lights were on) were always orthogonal to each other (FIG. 3). When the person was held in different orientations, the gravity and perceived gravity vectors swung in different planes relative to the person and therefore could potentially generate eye movements around various subject-defined axes.

Eye-Movement Recording and Analysis

The positions of both eyes were recorded using video-oculography (Chronos). This system recorded eye movements in Fick coordinates relative to the straight-ahead position with a resolution of about 0.1° in each dimension. These values were converted into head-frame-defined quaternions (relative to the straight-ahead eye position) using a conventional right-hand rule for the roll, pitch, and yaw axes (where positive corresponds to clockwise from the subject's point of view, down, and left).[22] Sine waves were fitted to the three orthogonal, head-defined components of the rotation velocities using the frequency of the stimulus oscillation. During dorsoventral translation the dominant eye movement was a pitch rotation to maintain fixation on the fixation point provided. We report the characteristics of the torsional component relative to this pitch response.

RESULTS

Combining Linear Acceleration and Physical Gravity

When subjects were translated dorsoventrally while left or right ear down, the direction of the combined GIA swung in the coronal plane and therefore potentially evoked torsional eye movements. When subjects were left ear down and at the most ventralward extent of their travel (FIG. 1, left side), the linear acceleration (directed dorsally in the body) and physical gravity combined such that if the combined vector (FIG. 1, dotted line) were to be interpreted as gravity, this would correspond to the body being oriented head up: that is, a positive rotation around the subject's naso-occipital axis. Such a positive rotation of the body around this axis would evoke an oppositely directed (negative, i.e., counterclockwise from the subject's point of view; see METHODS) torsional eye displacement. At the same point in the movement (subject most ventralward), compensatory eye movement would be in the upward or negative pitch direction. The prediction is thus that eye movements due to the swing of the GIA during left-ear-down translation evoke torsional and vertical movements that are in phase. Exactly the same argument can be applied when the subject is lying right ear down, where the prediction is that the torsional and vertical eye-movement components will be out of phase.

FIGURE 4 shows the three components of the eye-movement velocity during translation while on either the right or left side. Preliminary analysis showed no difference in the responses to left and right eyes, and so data from both eyes have been pooled. The major feature of the response was the vertical eye movement evoked by the translation that was necessary for the subject to maintain fixation during the movement. However, there was also a strong torsional component, the phase of which depended on subjects' orientation relative to gravity. The torsional component was close to in-phase with the vertical component when left ear down, and close to out-of-phase when right ear down. Fitted through the data are sinewaves with the frequency of the stimulus.

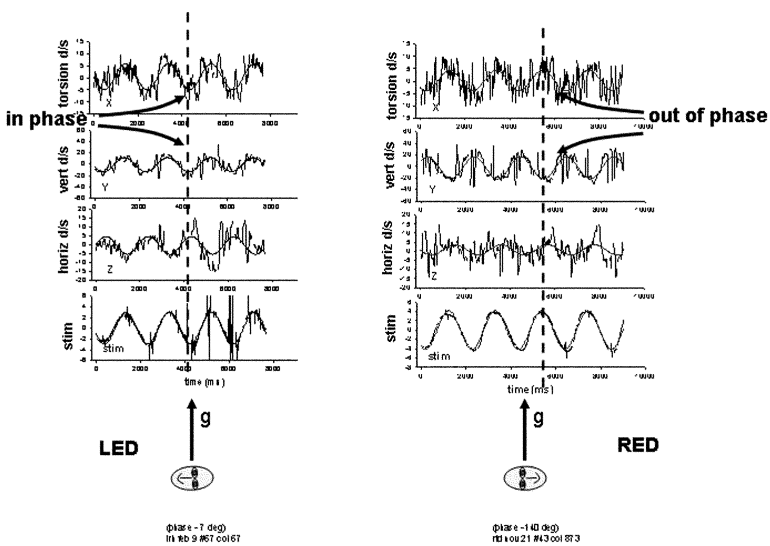

FIGURE 4. Data records of the three components of eye velocity during z-axis translation while subjects lay with their left (LED) or right (RED) ear down. The traces are, in order, X (torsion), Y (vertical), Z (yaw), and the stimulus. The eye signals are in °/s, and the stimulus is in arbitrary units. Also shown are the best-fit sinewaves, forced to have the frequency of the stimulus, and a reference line to aid in assessing phase relationships.

Summaries of all the responses recorded in multiple runs of the four subjects lying in both orientations in the light or dark are shown in separate plots in FIGURE 5A. In these polar plots the length of the lines corresponds to the peak torsional eye velocity, and the orientation indicates the phase relationship relative to the vertical eye-movement component. Zero (straight up) corresponds to in-phase, 180° (straight down) corresponds to out-of-phase, 90° means that the torsion leads the vertical and –90° means that the torsion lags the vertical.

There is a statistically significant difference between the eye movements recorded in the left- and right-ear-down orientations (F(1,6), –8.27, $P < .05$). The average

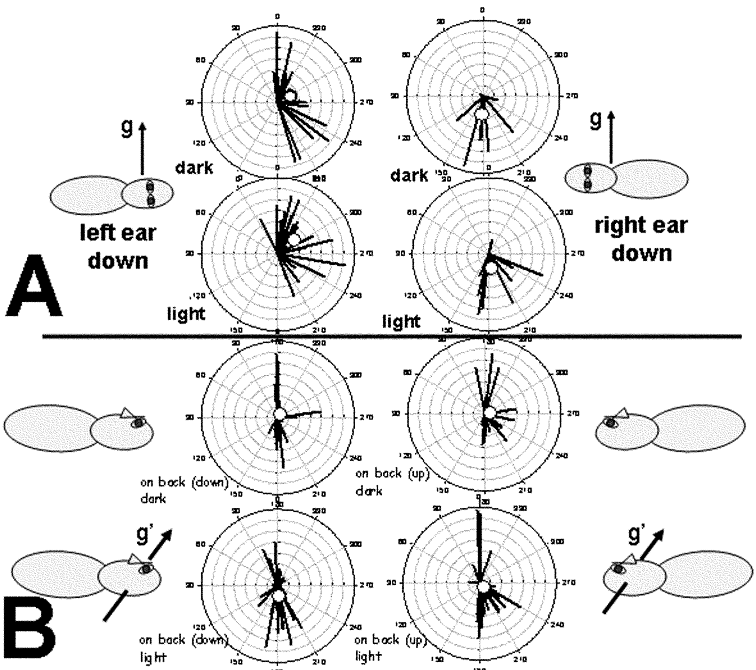

FIGURE 5. Summary of all data collected in this project for the eight body orientations and illumination conditions. The length of each line represents the peak torsional eye velocity, which is plotted in polar coordinates. The concentric circles are spaced at 1°/s intervals. 0° is in-phase, 90° is a lead, and 270° is a lag (–90°) relative to the vertical eye velocity response. The left column represents conditions that predict a torsional response in phase with the vertical eye velocity and the right column represents conditions that predict an out-of-phase response. The top four plots (**A**) compare torsional eye movement where the combination of applied accelerations and physical gravity shifted the GIA in the torsional plane. There was a clear difference between the left-ear-down and right-ear-down conditions (compare left and right diagrams). The lower four plots (**B**) show the torsional component of the response when the subjects were supine. The upper two diagrams of this set are data collected in the dark where there was no reason to expect a difference between them. In the lower pair, the combination of applied acceleration with perceived gravity shifted the GIA in the torsional plane. There was no difference between light and dark conditions or between the two directions.

response (FIG. 6) had a magnitude of 1.5°/s. When recorded left ear down, there was an average phase lag of torsional velocity relative to vertical velocity of –56°; when right ear down, there was a lag of –175°. For each record the average torsional eye velocity was expressed as a ratio of the peak tilt velocity of the stimulus (obtained from the amplitude and frequency). The mean values, which can be taken as the gains of the tilt interpretation response, were 0.15 in the dark and 0.16 in the light.

Combining Linear Acceleration and Perceived Gravity

When subjects lay supine in the York Tilted Room such that their movement was orthogonal to the direction of visually defined, perceived gravity, the same argument as outlined earlier applies if the linear acceleration was summed with perceived gravity. When supine, both perceived gravity and the linear acceleration are in the coronal plane (FIG. 3) and therefore might evoke torsional eye movement. As for physical gravity, the phase of the torsional eye movement would depend on whether visually defined gravity was to the left (equivalent to right-ear-down, out-of-phase) or right (equivalent to left-ear-down, in-phase). FIGURE 5B compares the torsional components evoked while moving with perceived gravity to the left or right. There should be no difference, dependent on which way subjects lie in the dark. In the light, however, if perceived gravity were swung by the imposed acceleration, we might expect a difference between the two body orientations. No such difference was seen,

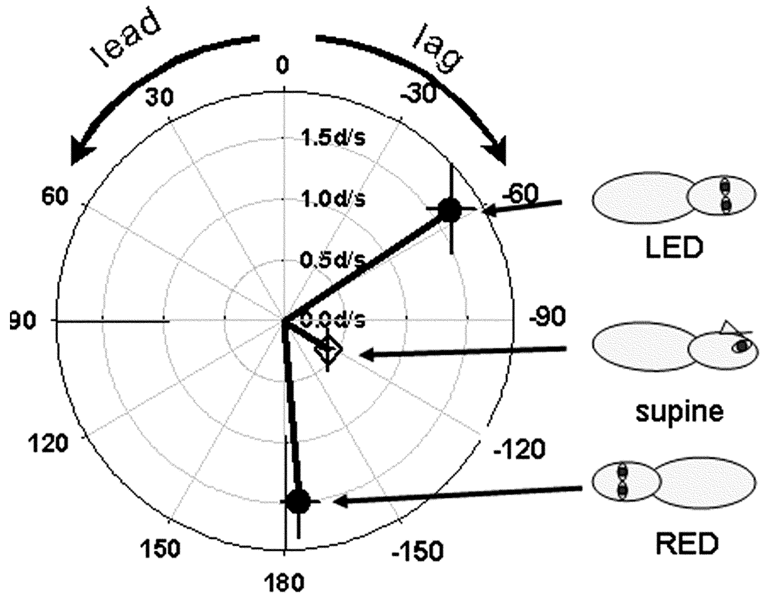

FIGURE 6. The mean response averaged for the left-ear-down, right-ear-down, and supine conditions, indicated by the cartoon inserts. Also shown are the standard errors of these means. Phase is expressed relative to the recorded vertical eye-movement response. Convention as for FIGURE 5.

either in the dark (where none was predicted F(1,2), 0.13, n.s.) nor in the light (F(1,2), 3.1, n.s.).

There was a torsional component to the eye movements recorded supine in the dark (FIG. 5) with an average velocity of 0.4°/s and phase lag of −124° (FIG. 6). If the data from the left and right-side-down configurations are expressed relative to this, the phases become lags of −41° (left side down) and −190° (right side down), respectively. Using this reference point increases the significance of the left-/right-side-down comparison (F(1,6), 14.6, $P < .01$). Relative to the "expected" values of 0 and 180° the left-/right-side-down data lag by −41° and −10°, respectively.

DISCUSSION

This study has demonstrated an oculomotor response to a swinging GIA caused by adding sinusoidal dorsoventral linear acceleration and gravity. No such oculomotor response could be demonstrated to a swinging sum of perceived gravity with the same oscillation. An internal model of the head's orientation is responsive to the perceived direction of gravity. These data are therefore compatible with the direct sensing theory of oculomotor control and not the internal model theory, which predicts that eye movements would be generated by the swing of perceived gravity.

Eye movements commensurate with a swing of the GIA have been reported before,[11] but they have generally been reported for lateral translation[1,16,17,23,24] and have appeared stubbornly resistant to the actual swing of the GIA, seeming instead to be generated in response to an anticipated swing.[16] The oculomotor response implies that the forces experienced while accelerating linearly were at least partially interpreted as a fused GIA that changed its orientation in the head as the linear acceleration waxed and waned. That is, the ambiguous force environment was interpreted as including some *tilt*. The fact that this response was not altered in the light suggests a surprisingly limited role for vision, as vision should have invalidated the tilt interpretation.[25] The predominant oculomotor response was, however, a vertical movement, and thus there were responses to *both* interpretations—tilt and translation—at the same time.

In previous experiments it has been difficult to distinguish physical forces from their possible internal representation as the drive for eye movements. By arranging perceived and physical gravity to be orthogonal to each other, we were able to show that only the combination of physical gravity with linear acceleration evoked eye movements compensatory for the tilt—not the perceived direction of gravity. The York Tilted Room has proven highly effective in influencing perceptual judgments dependent on the direction of gravity. For example, identifying shape-from-shading requires a perception of "up" to determine the most likely direction of illumination.[18–20] Similarly, distinguishing a "p" from a "d" requires a defined frame.[21] Using these tasks, the direction of perceived gravity, provided by the tilted room, was found to contribute to the perception of up with a weighting approximately equal to physically defined gravity.

Our conclusion is that, although the perceived direction of gravity is important for perceptual tasks, suggesting an internal model underlying perceptual processes, for the parameters tested in this study, eye movements seem to be under the control of directly sensed information about head movement. Head-movement information, at least in the frequency and amplitude range used in this study, seems to be used differently by perceptual and oculomotor systems.[9] Consequently, models that attempt to resolve tilt-translation ambiguity need to distinguish directly sensed gravity from its internal representation.

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