

REVIEW

Visual perception and interception of falling objects: a review of evidence for an internal model of gravity

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Abstract

Prevailing views on how we time the interception of a moving object assume that the visual inputs are informationally sufficient to estimate the time-to-contact from the object's kinematics. However, there are limitations in the visual system that raise questions about the general validity of these theories. Most notably, vision is poorly sensitive to arbitrary accelerations. How then does the brain deal with the motion of objects accelerated by Earth's gravity? Here we review evidence in favor of the view that the brain makes the best estimate about target motion based on visually measured kinematics and an *a priori* guess about the causes of motion. According to this theory, a predictive model is used to extrapolate time-to-contact from the expected kinetics in the Earth's gravitational field.

1. Introduction

Earth's gravity accelerates all objects at the same rate. We are probably adapted to this acceleration genetically, culturally and habitually. From the moment we are born, we deal with gravity—balancing, struggling, enjoying, coping with it every minute of every day. Also, the ability to predict the time that remains before contact (time-to-contact or TTC) with a falling object, and to react quickly and appropriately as a result, is critical in many situations. In the remote past, our survival in the forest depended on the ability to avoid contact with a predator jumping off a tree. Today, we may be engaged in less dangerous but equally demanding tasks, such as saving an object that slipped off our hands by quickly anticipating its time to ground contact. Watching or playing many recreational or competitive sporting activities involves similar predictions of the law of motion of the moving ball. What are the mechanisms that the human brain has evolved that allow it to anticipate the specific acceleration due to gravity?

The computational problem that needs to be solved by the brain is apparently straightforward. Consider the free fall of an object from a starting height h_0 . Neglecting air resistance, the vertical motion will follow the standard equation of motion: $h(t) = h_0 - 0.5gt^2$ where $h(t)$ is the time-varying height of the object and g is the acceleration of Earth's gravity (about 9.81 m s^{-2} at sea level, with a <1% maximum variation by changing latitude or altitude). To estimate TTC, we must implicitly solve for $h(t) = 0$ at $t = \text{expected contact time}$. The future motion of the object can be extrapolated based on current estimates of $h(t)$ and its time derivatives. Accuracy of motion extrapolation depends on the time derivatives that are used. Thus, a zero-order extrapolation means that only position (height) of the object is used, a first-order extrapolation also uses changes of position (velocity), and a second-order extrapolation also includes changes of velocity (acceleration). The higher the order of the extrapolation, the more accurate the estimate of TTC.

If the computational problem is uniquely defined by the physics of the situation, the specific solution that is provided by the brain might vary depending on the available sources of information and the context of the specific task to be carried out. Here we review this issue for visual perception and manual interception of falling objects. These tasks rely on implicit processing of visual gravitational acceleration. However there are also tasks that require explicit knowledge about the physics of an object's motion, as when we must verbalize a judgment. Cognitive and perceptual understanding of free fall is reviewed in Zago and Lacquaniti (2005a).

2. Visual perception

There is ample evidence that the specific acceleration due to Earth's gravity is taken into account in some visual tasks. The ability to detect gravitational acceleration in visual motion can be demonstrated early in life. Between 5 and 7 months, infants begin to implicitly expect a downwardly moving object to accelerate and an upwardly moving object to decelerate (Kim and Spelke 1992, Friedman 2002). In Kim and Spelke's experiments, separate groups of 5- and 7-month-old infants were habituated to two different events in which a ball rolled either downward or upward on an inclined ramp with appropriate acceleration, speeding up as it moved downward or slowing down as it moved upward. Then infants were tested with events in which the ball moved in the direction opposite to the habituation event (upward if it had previously moved downward, and vice versa), and with an acceleration which was either novel but appropriate or familiar but inappropriate. The hypothesis is that infants who are sensitive to the naturalness of the object's motion would look longer at the test displays with unnatural motion. At 7 months, infants looked longer at the familiar but now inappropriate acceleration pattern, providing evidence for sensitivity to the effect of gravity in this situation. At 5 months, in contrast, infants looked longer at the novel, appropriate acceleration pattern, suggesting that they discriminated the two motions but were not sensitive to the inappropriateness of upward accelerating or downward decelerating motion in this situation.

In adults, visual gravity cues contribute to perception of causality and naturalness of motion (Twardy and Bingham 2002), to perception of absolute distance and size for falling objects (Watson *et al* (1992), but see Hecht *et al* (1996) for an alternative viewpoint) or for biological motion (Jokisch and Troje 2003). Pittenger (1990) made a pendulum swing faster or slower than normal by driving it with a second, hidden pendulum. He found that observers detected deviations as small as 0.1–0.2 s from the natural period. Moreover, occasional experimenter errors resulting in out-of-place accelerations were detected immediately and were recognized as external forces or hidden causes. He concluded that people do not see gravity as a force at all, but as a natural part of (vertical) object behavior: they are tuned to this invariant in the environment. Gravity cues also influence the realism of special effects in cinematography (Spottiswoode 1969). Thus, cinematographers have long been aware of the problem of making miniature objects appear full-size when

filmed. Thus when a monster wrecks down a skyscraper scaled in miniature by a factor K , the scene must be filmed at a speed \sqrt{K} times the normal speed. When later projected at normal speed, it would look natural because the time of fall under gravity is related to the square root of the height of fall. In addition, gravity cues influence the memory of the last seen position of a disappeared target. When an observer views an object undergoing implied or apparent motion and the object suddenly disappears, memory for the object's final position is shifted forward in the direction of motion (Freyd 1987). Descending motion leads to larger forward displacement than does ascending motion, and the memory distortion for horizontally moving objects is also displaced downward below the path of motion (Hubbard 1995).

3. Catching a falling ball

Evidence that the gravitational acceleration is taken into account is especially compelling for manual interceptive responses under visual guidance (Lacquaniti 1996). Thus, several components of the motor responses involved in catching a free falling ball are accurately timed relative to the expected time of collision. A typical laboratory experiment involves dropping balls of different mass one at a time from a given height above the outstretched hand of a subject (Lacquaniti and Maioli 1987). In different blocks of trials, the height of fall is varied between 0.2, 0.4, 0.8, 1.2 and 1.6 m. Balls of identical external appearance but different mass are used in the range from 0.2 to 0.8 kg (in 0.2 kg steps). Under such conditions, one finds that a major build-up of electromyographic (EMG) activity in flexor and extensor muscles of the elbow and wrist joints occurs in the form of anticipatory responses whose latency increases with the height of fall. However, the onset time computed relative to the time of ball contact with the hand varies little, irrespective of the ball mass and the height of fall (Lacquaniti and Maioli 1989b, Lacquaniti *et al* 1993a). The time of onset of anticipatory activity relative to collision reflects the estimate of target TTC available to the motor system to initiate the response. The TTC and the time course of the motor responses do not change with the height of fall, nor do they depend on the ball mass. The results obtained with catching are in substantial agreement with those of studies in which subjects punch balls dropped vertically toward the head (Lee *et al* 1983, Michaels *et al* 2001). In these cases, the ball is punched by means of a ballistic limb extension whose onset time relative to collision is invariant across heights of drop (5 or 7 m above the subject), ball size and viewing conditions (monocular or binocular, Michaels *et al* (2001)).

The expected mass of the ball does not affect motor timing, but strongly affects the magnitude of the responses. Thus, in one experimental protocol, the height of fall and the mass of the ball were independently varied using a factorial design (Lacquaniti and Maioli 1989b). It was found that the mean amplitude of the anticipatory muscle activity scales linearly with the expected momentum of the ball at collision time. When the mass of the ball is unexpectedly changed, subjects scale their responses to the expected momentum instead of

the true one (Lacquaniti and Maioli 1989b, Lang and Bastian 1999). Thus, subjects take into account all three of Newton's laws of dynamics.

Not only do subjects tune the anticipatory responses parametrically, but they also gate the stretch reflex responses just around the expected arrival of the ball on the hand. A stretch reflex evoked by an external perturbation normally obeys the principle of reciprocal innervation between antagonist muscles: the muscles that are stretched by the perturbation contract, whereas the shortened muscles relax. During a catching task, instead, the responses are gated just before the collision time with the result that both stretched and shortening muscles are co-activated reflexly (Lacquaniti *et al* 1991, 1992). This reflex co-activation, along with the anticipatory contraction described above, contributes to increase the overall stiffness and viscosity of the limb around the time of collision with the incoming ball (Lacquaniti *et al* 1993b). Limb impedance was estimated by applying pseudo-random torque motor perturbations continuously during catching. It was found that the magnitude (modulus) of viscosity increases just before the collision, and the direction (argument) rotates closer to the vertical, indicating that a larger component of reactive force is exerted by the hand in the direction of the forthcoming perturbation (the vertical for free fall).

Under certain conditions, catching a falling ball with the outstretched hand can still be performed even in the absence of visual information (Lacquaniti and Maioli 1989a). When blindfolded subjects are provided with advance information about the height of drop and an auditory cue signals the time of ball release, they are normally able to catch. However, they do so by means of a strategy that differs from the normal one. Anticipatory muscle contraction is absent or diminished, whereas the reflex responses are boosted up relative to the normal. Thus, subjects are able to reach an internal estimate of the expected duration of fall even in the absence of vision, as demonstrated by the fact that they can easily detect randomly interspersed cases of inaccurate timing of the auditory cue. This demonstrates that the estimate of fall duration is distinct from the estimate of the instantaneous time-to-contact. The latter is necessary to trigger consistent anticipatory responses and depends on vision.

4. Catching in microgravity

The results reviewed above indicate that the gravitational acceleration is taken into account in timing the manual interception of a falling ball. However, they do not reveal how this occurs. The simplest explanation is that the visual system measures target acceleration and passes on this measurement to the motor system. A problem with this explanation, however, is that extant evidence shows that our visual system is bad at discriminating or even detecting arbitrary accelerations (Werkhoven *et al* 1992). It is well known that TTC estimates can be derived from several monocular and binocular cues, such as dilation of the retinal image, changes in binocular disparity, reduction of the optical gap between the target and the interception point, and pursuit

eye movements. However, these cues generally provide only first-order approximations related to the object's distance and velocity (Rushton and Wann 1999, Regan and Gray 2000, Tresilian 1995). The human visual system poorly estimates arbitrary accelerations, especially over the short viewing periods typical of interception/avoidance responses (Brouwer *et al* 2002, Regan *et al* 1986, Werkhoven *et al* 1992). For example, speed-discrimination sensitivity (i.e. detecting that two constant speeds are different) is better than acceleration discrimination sensitivity by a factor of four to five (Snowden and Braddick 1991). Also, arbitrary accelerations are not taken into account in timing manual interceptions (Port *et al* 1997). These manual responses, instead, are geared to target position and velocity. Moreover, electrophysiological recordings in the monkey show that neurons specialized for visual motion processing in cortical area MT accurately encode target direction and speed, but contain only partial information about acceleration (Lisberger and Movshon 1999).

An alternative hypothesis was proposed by Lacquaniti *et al* (1989b, 1993a), namely that, when timing anticipatory motor responses for catching, 'a priori' knowledge on the most likely path and law of motion' may be employed. In particular, they suggested that the specific acceleration of gravity is an ecological constraint that is internalized in the brain. Evidence for internalized visual gravity was provided by McIntyre *et al* (2001). They showed that, in the absence of gravity-determined sensory cues, astronauts expect the effects of Earth's gravity on a dropped object (moving at constant speed) when they attempt to catch it in the Spacelab. In orbital flight, the spacecraft and its occupants are in free fall, so there are no contact forces of support on an astronaut's body opposing the action of gravity. This means that there are no gravity-determined tactile cues related to body orientation and no gravity-determined otolith cues about head orientation (Lackner and DiZio 2000). In this experiment, the astronauts sat strapped in a chair fixed to the floor of the Spacelab module. A ball launcher attached to the ceiling projected a 0.4 kg ball 'downward' from a height of 1.6 m above the outstretched hand, with a paradigm similar to that of Lacquaniti and Maioli (1989b). 'Downward' motion in a space module means a motion directed from the ceiling toward the floor. In the absence of gravity effects, the ball descends at a constant speed. This should be the prototypical condition to which a strategy based on first-order visual information (Lee 1976, Rushton and Wann 1999) is best attuned. Instead, the inappropriate application of an internal model of Earth's gravity to microgravity would assume that the ball is accelerated by gravity, and therefore would lead to underestimates of the actual TTC. The results were crystal clear: astronauts systematically continued to anticipate the effects of gravity and their anticipatory responses started too early (McIntyre *et al* 2001). While catching responses occurred prematurely over all three test days in-flight (days 3, 9 and 15), evidence of adaptation to 0g conditions was found near the end of the mission (days 9 and 15). The amplitude and velocity of the early, erroneous movement diminished, and a new upward limb rotation with the appropriate timing developed gradually. On the whole, however, adaptation

was slow and incomplete during microgravity exposure, whereas re-adaptation to Earth's conditions occurred almost immediately. Although all subjects bobbled the first catch on Earth, the average data from early post-flight sessions (performed on the day of re-entry and the two following days) did not differ significantly from pre-flight or later post-flight sessions (Berthoz *et al* 2002).

The limited adaptation observed in microgravity could depend on two factors. (a) The early responses were compatible with adequate performance, as all subjects always caught the ball. Therefore, lack of significant error feedback might have not generated enough pressure to improve the response timing. (b) Microgravity conditions induce several changes in arm motor behavior (Lackner and DiZio 2000). Movements tend to be slower and muscle tone (limb impedance) is lower than on Earth. It could be that, under 0g conditions, when a muscle has not been previously active to maintain arm posture, earlier muscle activation is required to achieve the same limb impedance as under 1g conditions at expected ball impact time.

5. Parametric adaptation of the internal model of gravity on Earth

To address the issues left unresolved by the microgravity experiments, Zago *et al* (2004) carried out a series of experiments on Earth where different gravity levels were simulated for a visual target by means of a computer controlled projection system. In this paradigm, a sphere moves vertically downward on a wide empty screen with different laws of motion. Because there is no visual feature other than the target and the starting box, nor is there any structured background projected on the screen, the sphere represents a virtual target. Subjects are asked to punch a ball that falls hidden behind the screen and arrives in synchrony with the visual target. Initial speed of the visual target is randomized to make flight duration unpredictable from trial to trial. The timing requirements of punching are more stringent than those of catching: the tolerance window allowed to punch the falling ball with the finger knuckles is only about ± 15 ms relative to the correct interception time. Using this paradigm, Zago *et al* (2004) confirmed the previous findings of the microgravity experiments by McIntyre *et al* (2001). Subjects systematically time their motor responses very differently when the visual target moves with an acceleration equivalent to gravity (1g) as compared with when the target moves at constant speed (0g). Motor responses generally are time-locked to the arrival of 1g targets, whereas the responses to 0g targets are premature. On average, subjects correctly intercept 85% of 1g targets at the first attempt, but only 14% of 0g targets, consistent with the application of an internal model of Earth's gravity.

This study also established an important point: the internal model of target motion depends on the sensory and cognitive context of the task. In fact, when the same virtual targets are presented in the absence of the real ball falling behind the screen but subjects are required to intercept the visual target by clicking a mouse button, the internal model of gravity is

no longer applied. Subjects time their responses consistent with the assumption of uniform motion in the absence of forces, even when the target actually accelerates. In contrast with the previous protocol, here subjects correctly intercept a significantly higher proportion of 0g targets than that of 1g targets (on average, 95% and 84%, respectively). The observation that the relative performance with 1g and 0g targets in the virtual interception is almost the reverse of that in the punching experiment demonstrates that interception performance does not depend exclusively on the characteristics (accelerating versus constant speed) of the visual targets.

Recent research focuses on the issue of whether multiple internal models are learned and switched to cope with a variety of conditions or single general models are adapted by tuning the parameters. According to one view, a collection of specific internal models is stored in motor memory, and sensory or cognitive information provides the identifying cues to select the appropriate internal model (Wolpert and Kawato 1998). For instance, after subjects learn to manipulate two different tools (a rotated mouse and a velocity mouse), they can easily switch between the two, while distinct, spatially segregated regions are engaged in the cerebellum by each tool (Imamizu *et al* 2003). According to a different view, however, subjects may not employ separate models and switch between them according to the sequence context, but they may represent different environments with a single internal model (Martin *et al* 1996). Thus, Karniel and Mussa-Ivaldi (2002) taught subjects, on separate days, to move in two different velocity-dependent force fields applied at the hand by a robot. Even after this experience, subjects were unable to move accurately when the same two fields alternated after each movement.

Zago and Lacquaniti (2005b) tested between alternative strategies for learning to deal with the novel environment of visual targets descending at 0g on Earth. One possibility is that extensive training results in the development of a 0g model appropriate for the new situation. The alternative possibility is that subjects continue using the internal model of Earth's gravity throughout the exposure to 0g targets, but adapt its internal parameters. The gravity model belongs to the class of threshold-based TTC models (Lee *et al* 1983, Port *et al* 1997, Tresilian 2004). It predicts that the interceptive movement is centrally triggered when TTC reaches a given threshold value λ (see figure 1). λ is equivalent to a time margin before the expected collision time, and is necessary to compensate for signal transmission delays that include both central processing times and peripheral movement time. The control of interception is under on-line visual control up to λ , by comparing the visually derived estimate of target TTC with the preset threshold value. The threshold value is specified by information about target distance and velocity, under the assumption that the target is accelerated by gravity (Lacquaniti and Maioli 1989b, Lacquaniti *et al* 1993a, McIntyre *et al* 2001, Zago *et al* 2004). At time λ before the expected collision, the action is launched with little (if any) correction based on feedback. The formal prediction of the model is as follows:

$$\text{TTC}(t) = \frac{-\hat{v}(t) + \sqrt{\hat{v}(t)^2 + 2\hat{g}\hat{h}(t)}}{\hat{g}} \quad (1)$$

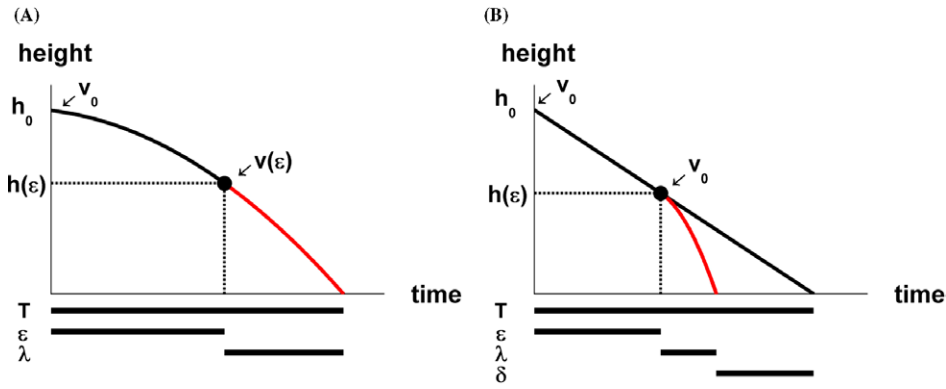


Figure 1. Predictions of the 1g model for timing ballistic interceptions of a descending target. The instantaneous height of the target above the interception point is plotted as a function of time. T denotes the total flight duration of the target. Subjects trigger the interception at time λ before the expected collision, corresponding to time ε after the onset of target motion. The red curve denotes the target trajectory extrapolated from current position $h(\varepsilon)$ and velocity $v(\varepsilon)$ on the basis of the 1g model. The punch occurs at the time of expected collision $\varepsilon + \lambda$ (corresponding to the intersection of the red curve with the time axis). (A) The application of the 1g model correctly estimates the time of arrival of 1g targets. (B) The application of the same model underestimates the time of arrival of 0g targets by δ , and the punch occurs at time δ before target arrival. Modified from Zago and Lacquaniti (2005b) with permission.

where t is the time elapsed after the onset of target motion, $\hat{h}(t)$ and $\hat{v}(t)$ are the visually estimated height of the target above the interception point and target velocity, respectively, both measured at time t , and \hat{g} is the neural estimate of gravitational acceleration. In the default case of targets accelerated by Earth's gravity, $\hat{g} \approx 1g$. To distinguish between a physical variable and its corresponding neural estimate, we put a 'cap' over the latter.

According to the model of equation (1), the interceptive response is launched when $TTC(\varepsilon) = \lambda$ and we denote the elapsed time until the hand moves as time ε . For a successful punch, the hand must reach the interception point at the same time as the target does. By definition, the hand arrives at time $\varepsilon + \lambda$ after the onset of target motion, whereas the target arrives at time T (figure 1(A)). For a successful interception: $\varepsilon + \lambda = T$. For simplicity, here we neglect the existence of possible margins of error for the interceptive action. If present, these margins would result in a temporal tolerance window (μ) around the ideal trigger time. This window depends on the spatio-temporal configuration of the moving hand relative to the moving target. Thus, for 1g targets, $T - \lambda - \mu^- < \varepsilon < T - \lambda + \mu^+$. The gravity model correctly estimates the time of arrival of 1g targets if $h(\varepsilon)$ and $v(\varepsilon)$ are measured reliably by vision, and the punch is timed exactly on T as a result. In fact, for some targets (especially very slow or very fast ones) $\hat{v}(\varepsilon)$ may be inaccurate and the corresponding interception may be in error (Regan 1997, Zago et al 2004).

In contrast with 1g targets, the time of arrival of 0g targets is underestimated by the model (figure 1(B)), and the punch occurs before target arrival even with correct measurements of $h(\varepsilon)$ and $v(\varepsilon) = v_0$. The value of this temporal error δ is derived as follows. For a constant speed target:

$$T = \frac{h_0}{v_0} \quad (2)$$

$$\varepsilon = \frac{h_0 - h(\varepsilon)}{v_0} \quad (3)$$

$$\delta = T - \varepsilon - \lambda. \quad (4)$$

From simple algebra one obtains

$$\delta = \frac{\hat{g}\lambda^2}{2v_0}. \quad (5)$$

Note that equation (5) shows the temporal error that results from the application of the gravity model to 0g targets; in other words, we assume that TTC is still computed by the brain using equation (1) with $\hat{g} = 1g$.

In principle, there are alternative strategies for learning to deal with 0g targets. Training might result in the development of a 0g model appropriate for the new situation. According to the 0g model:

$$TTC(t) = \frac{\hat{h}(t)}{\hat{v}(t)} \quad (6)$$

and once again the interceptive response is triggered when $TTC(\varepsilon) = \lambda$ and we denote the elapsed time until the hand moves as time ε . If subjects were able to use a 0g model with the 0g targets, they would estimate the time of arrival of these targets correctly, and produce motor responses time-locked to target arrival. Alternatively, however, subjects might continue using the gravity model throughout the exposure to 0g targets, but they would adapt its parameters. An adaptive gravity model has two internal parameters, λ and \hat{g} . λ has been defined above as the time margin for triggering the interceptive action, and \hat{g} as the internalized estimate of target acceleration.

It has previously been hypothesized that interceptions of moving targets are based on visually measured kinematics and an *a priori* hypothesis about the causes of target motion (Zago et al 2004). In the language of estimation theory, the posterior probability (the probability of a target kinetics given the visual measurements of target kinematics) would be computed from the likelihood of target kinematics and from the prior using Bayes' rule: $P(g|v) = P(g)P(v|g)$, where $P(g)$ is the prior of target kinetics (force acting on the target), $P(v|g)$ is the likelihood of target kinematics (conditional probability

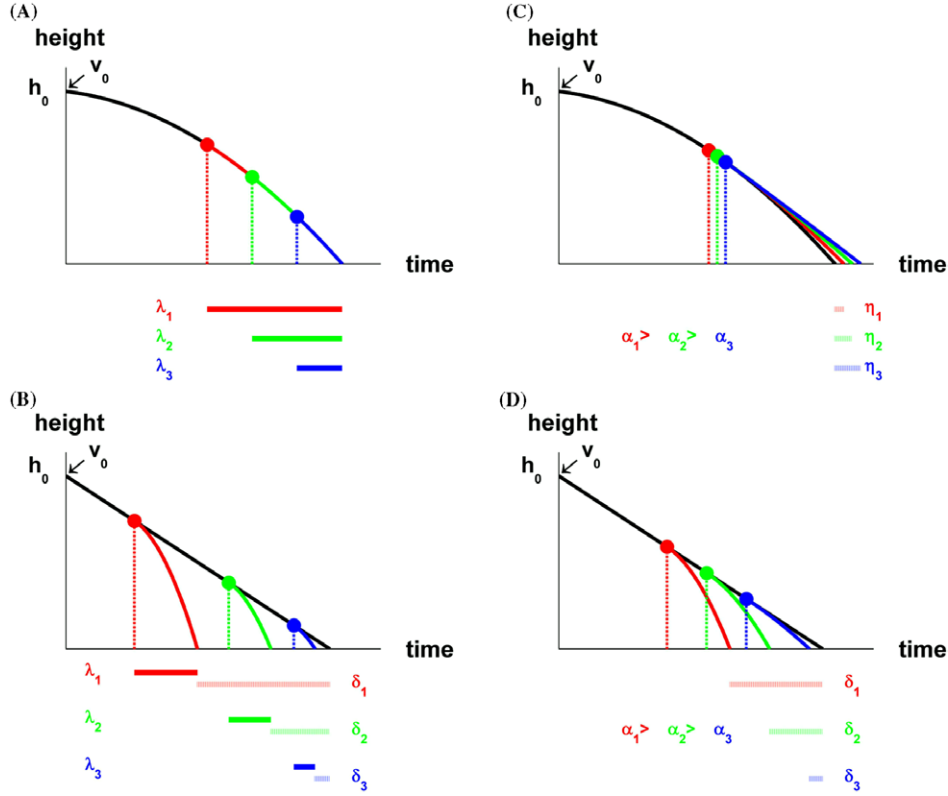


Figure 2. Simulation of adaptation of the internal parameters of the 1g model with prolonged exposure to 0g targets. λ is the time margin before the expected collision. \hat{g} is the internalized estimate of target acceleration. (A), (B) Simulations of adaptive reduction of the time margin λ , keeping $\hat{g} = 1g$. Red, green and blue traces correspond to $\lambda_1 = 300$ ms, $\lambda_2 = 200$ ms, $\lambda_3 = 100$ ms, respectively. Decreases of λ do not affect the responses to 1g targets (A), but reduce the error δ with 0g targets (B). (C), (D) Simulations of adaptive reduction of $\hat{g} = \alpha g$, keeping $\lambda = 300$ ms. Red, green and blue traces correspond to $\alpha_1 = 0.7$, $\alpha_2 = 0.4$, $\alpha_3 = 0.1$, respectively. Decreases of \hat{g} lead to overestimates of the time of arrival of 1g targets by η (C), while reducing the error δ with 0g targets (D). In (B), (D) $\delta_1 > \delta_2 > \delta_3$. In (C), $\eta_1 < \eta_2 < \eta_3$. Modified from Zago and Lacquaniti (2005b) with permission.

of target velocity given different values of target kinetics) and $P(g|v)$ is the posterior probability of target kinetics given the visual measurements of target velocity. In the current context, \hat{g} would represent the prior for target kinetics. In line of principle, the value of this prior could depend on the probability distribution of target accelerations within any one experiment. In the default case of targets accelerated by gravity, $\hat{g} = 1g$. Otherwise, \hat{g} could take any arbitrary value, depending on the neural estimate of target acceleration. In the limit case that $\hat{g} = 0$, the adapted 1g model becomes identically equal to the 0g model considered above.

Thus, as is apparent from equation (5), for any given v_0 , the error δ with 0g targets could be reduced by decreasing either λ or \hat{g} or both. A decrease of λ could result from a compression of central processing times up to minimum values dictated by physiological constraints. In this case, one would expect that the error δ with 0g targets decreased, but did not go below the minimum signal transmission delays (figure 2(B)). Performance with 1g targets should not be affected by a physiological decrease of λ , as long as $h(\varepsilon)$ and $v(\varepsilon)$ continue to be correctly estimated (figure 2(A)). In contrast with the adaptation of λ , there are no *a priori* physiological limits for the adaptation of the internal estimate of target acceleration (\hat{g}). In line of principle, the brain could

adjust this estimate up to the true acceleration ($\hat{g} = 0g$), and succeed in zeroing the error δ for 0g targets (figure 2(D)). Note, however, that progressive adaptation of \hat{g} to values smaller than 1g (as well as simultaneous adaptation of both \hat{g} and λ) would affect the responses to both 0g targets and 1g targets. Responses to 0g targets would improve according to equation (5). At the same time, responses to 1g targets would worsen. An internal estimate of target acceleration to $\hat{g} < 1g$ overestimates the time of arrival of 1g targets by η , and the punch would occur at time η after target arrival (figure 2(C)). The value of this temporal error is derived as follows:

$$\eta = \lambda + \varepsilon - T \quad (7)$$

$$T = \frac{-v_0 + \sqrt{v_0^2 + 2gh_0}}{g} \quad (8)$$

$$h(\varepsilon) = h_0 - v_0\varepsilon - 0.5g\varepsilon^2 = (v_0 + g\varepsilon)\lambda + 0.5\hat{g}\lambda^2 \quad (9)$$

$$\varepsilon = -\frac{v_0}{g} - \lambda + \frac{\sqrt{v_0^2 + (g^2 - g\hat{g})\lambda^2 + 2gh_0}}{g} \quad (10)$$

From simple algebra, one obtains

$$\eta = \frac{\sqrt{v_0^2 + (g^2 - g\hat{g})\lambda^2 + 2gh_0} - \sqrt{v_0^2 + 2gh_0}}{g} \quad (11)$$

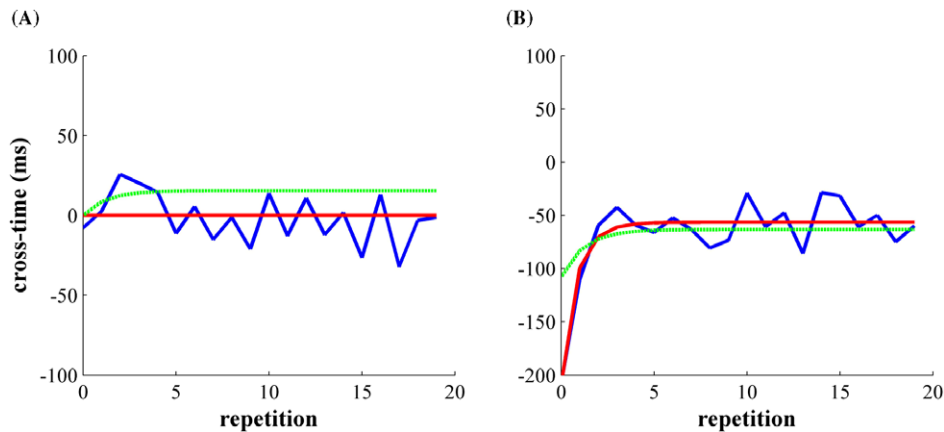


Figure 3. Adaptation of the 1g model in a protocol with 50% probability of 1g trials and 50% probability of 0g trials. The time of occurrence (cross-time) of the zero-crossing of hand acceleration relative to the *interception time* was averaged across all subjects. Mean cross-time values are plotted as a function of repetition number, for 1g and 0g data in (A) and (B), respectively. Best fits ($P < 0.05$) with exponentially decreasing values of λ or \hat{g} of the 1g model are plotted with *red lines* or *green lines*, respectively. Initial and steady-state values of λ are 326 and 170 ms, respectively, learning constant of 1.0 repetitions. Initial and steady-state values of \hat{g} are 1g and 0.59g, respectively, learning constant of 1.2 repetitions.

Note that equation (11) shows the temporal error that results from the application of the gravity model, when we assume that TTC is computed by the brain using equation (1) with $\hat{g} \neq 1g$.

These different predictions were tested by Zago and Lacquaniti (2005b) by using different protocols. One protocol involved fully immersive presentation of 0g targets over two consecutive experimental days. In this protocol, we found no evidence for the 0g model. In another protocol, 1g and 0g trials were randomized with the same probability (50%) within the same session (at different initial speeds to make flight duration unpredictable from trial to trial, figure 3). Thus subjects expected either type of target equally. Adaptation of λ with repetition (*red line*) fits the interception timing (cross-time values) of 0g trials better than does adaptation of \hat{g} (*green line*, mean $r^2 = 0.87$ and 0.69 for λ and \hat{g} adaptation, respectively, see figure 3(B)). The major difference between the predictions of the two adaptation schemes involves the 1g data (figure 3(A)). Adaptation of \hat{g} with repetition (*green line*) predicts progressive, systematic delays of the cross-time for 1g trials that should parallel the changes of timing for 0g trials as a function of repetition. No such trend was present in the experimental data (one-factor ANOVA, $P = 0.21$), in contrast with the hypothesis of adaptation of \hat{g} and in agreement with the hypothesis of adaptation of λ (*red line*).

A decrease of λ could result from a compression of central processing times up to a minimum value dictated by physiological constraints. Accordingly, the timing error with 0g targets decreases, but cannot go below the minimum signal transmission delay. By contrast, performance with 1g targets is not affected by a physiological decrease of λ , as long as target distance and velocity continue to be correctly estimated by vision. The estimated value of λ was ≈ 200 – 300 ms before adaptation. Training with 0g trials resulted in a rapid drop to values between ≈ 80 and 160 ms, depending on the protocol. These values are close to the

shortest visuo-manual delay times for ongoing target motion (Brenner *et al* 1998, Lacquaniti and Maioli 1989b, Port *et al* 1997). This may explain why the adaptation process tends to saturate early on, and the responses to 0g trials remain premature throughout the rest of training. A decrease of λ results from a reduction of signal transmission delays. Mechanical delays in ballistic interception are probably at a minimum from the outset. Central processing delays, instead, could be compressed by reducing reaction times through more efficient visuo-motor transformations. When response speed is at a premium (as in the present experiments), feedforward visual mechanisms may suffice without resorting to top-down feedback modulation (Fabre-Thorpe *et al* 2001). Although the signal transmission delays estimated here are short (less than 200 ms), they appear compatible with fast processing of on-going visual stimuli. It has been suggested that, under continuous conditions of stimulation, changes of target position can be extracted from an image on the basis of the first wave of information passing through the visual system, resulting in considerable efficiency and rapidity of processing (VanRullen and Thorpe 2002).

6. Event-dependent adaptation of the internal model of fall

A different study (Zago *et al* 2005) addressed the question of how the internal gravity model for manual interception adapts as a function of the probability and temporal distance of 0g versus 1g targets within one session. This question is related to the issue of how humans interact with multiple environments. Concurrent learning of two conflicting environments, such as opposing force fields or opposing visuomotor rotations, has previously been reported to be difficult or very slow, probably because of interference in working memory (Brashers-Krug *et al* 1996, Gandolfo *et al* 1996, Krakauer *et al* 1999). Osu *et al* (2004) reported that subjects can learn two opposing

force fields when provided with contextual cues and random, frequent switching. However, concurrent learning was slower and more difficult than separate learning. When subjects are exposed to a force field whose amplitude varies randomly from trial to trial, they learn to set their response to the average field experienced over the previous few movements (Scheidt *et al* 2001, Takahashi *et al* 2001). In a bi-manual manipulation task, when the properties of the manipulated object are randomly changed between trials, the anticipatory modulation of grip force depends on the weighted average of the object's properties, as experienced over the previous three trials, with the weighting increasing for the most recent trials (Witney *et al* 2001). These studies indicate that computational mechanisms which average across recent trials are used to learn both predictable and randomly varying tasks (Davidson and Wolpert 2003, Wigmore *et al* 2002). They also suggest that only short-term memory seems to be used for motor adaptation.

A different conclusion, however, was reached by Zago *et al* (2005) when they compared five protocols that differed in the probability of 0g versus 1g trials. Intuitively, one would expect that the higher the probability of 0g trials and the shorter their temporal distance, the greater the adaptation rate. Indeed the studies reviewed above indicate effects that tend to decay beyond three consecutive trials. Surprisingly, it was found that the adaptation rate to 0g was essentially invariant, bearing no significant relation with the probability or the temporal distance. Adaptation even occurred through very few 0g trials sporadically interspersed during immersive practice with 1g trials. Thus fast learning was event-dependent rather than time-dependent, being linked to the serial repetition of each condition within an experiment. This result suggests that the memory store for adapted states of the internal gravity model is triggered by individual events and can be sustained for prolonged periods of time separating sporadic repetitions. This form of event-related learning could depend on multiple-stage memory, with exponential rise and decay in the initial stages followed by a sample-and-hold module.

7. Neural substrates

In section 5, we reviewed evidence that subjects learn to deal with 0g targets on Earth by changing the time margin λ for triggering the interceptive action, rather than by using the more obvious strategy of adapting the internalized estimate of target acceleration \hat{g} . One reason for this might be that the magnitude of the internalized estimate of gravity is kept fixed to 1g because that is the physical variable being shared with other sensori-motor systems. Several sensory systems are sensitive to Earth's gravity, from vestibular otoliths to neck, limb and truncal proprioceptors. Also, gravity effects are taken into account when planning limb movements or sensing limb position. It has been proposed that the internal estimate of gravity is computed by the central nervous system as a Bayesian weighted average of multi-cue information, including optokinetic, vestibular, neck and truncal signals (Zupan *et al* 2003). Therefore, adaptation of \hat{g} for the sake of coping with microgravity visual targets might derange the other systems, unless microgravity was the ubiquitous

condition as during space flight or when living on another planet.

From these considerations, one is led to hypothesize that visual processing of gravitational acceleration shares the representation of gravity with the classical graviceptive systems. Specifically, it has been suggested that the internal model calculating the effects of gravity on seen objects is derived from graviceptive information, is stored in the vestibular cortex, and is activated by visual motion that appears to be coherent with natural gravity (Indovina *et al* 2005, Zago *et al* 2004). The basis for this hypothesis is that: (i) the vestibular system is able to estimate the gravity vector in head coordinates by combining signals from otoliths and semicircular canals (Merfeld *et al* 1999), and (ii) multi-sensory neurons in the vestibular cortex also respond to visual stimuli (Grusser *et al* 1990). Note that the vestibular cortex is involved in processing both vestibular and neck proprioceptive stimuli in man (Bottini *et al* 2001) and monkey (Grusser *et al* 1990). One can surmise that, through experience, the vestibular estimate of Earth's gravity is transformed and stored as an abstract representation of gravity accessible by the visual system. To test the internal model hypothesis, Indovina *et al* (2005) measured motor performance and brain activity during different visual tasks. They predicted that when the acceleration of a visual target is coherent with represented natural gravity, the gravity model will enable subjects to compute TTC accurately, by engaging the vestibular network. Conversely, when target acceleration has the same amplitude but opposite direction to natural gravity, subjects will compute TTC less accurately, relying on visual motion areas that are poorly sensitive to arbitrary accelerations.

In a first fMRI experiment, subjects were presented with the picture of a woman standing in front of a building, and were asked to maintain fixation on a dot placed just above the woman's head. A ball moved upward from the fixation point at a constant acceleration, bounced on the building cornice and returned downward. Initial ball speed was randomized to make flight duration unpredictable from trial to trial. Additionally, the fixation point expanded transiently after a random delay from the end of ball motion. The ball underwent the same average speed changes in all trials, but gravity was directed either toward the ground of the picture (1g trials: natural gravity) or away from it (−1g trials: reversed gravity). No cue was given to identify either trial type, and perceptually overt differences between them were subtle. Note that, in contrast with the visual stimuli used in the punching experiments described above (Zago *et al* 2004, 2005), here the visual scene included realistic cues to judge familiar size and perspective of critical objects such as the falling ball. Thus, the magnitude of gravitational acceleration of the ball could be gauged based on perceived extent and/or distance of the picture.

In different blocks, subjects were asked either to press a button so as to intercept the descending ball at the time of arrival at the fixation point (proactive task), or to press the button as fast as possible after the Go signal corresponding to the expansion of the fixation point (reactive task). By design, response timing was coupled to the law of motion in proactive tasks, but decoupled in reactive tasks (because of

the random delay intervening between the end of ball motion and the Go signal). We used these two tasks to verify that differences in brain activity between 1g and -1g trials would not merely reflect the nature of the motor task or motor errors. Analysis of the response times in the proactive task showed that the direction of visual gravity significantly affected the subject's ability to intercept the ball. Thus, all subjects correctly estimated TTC in 1g trials only, and in these trials the response times were explained by the internal model that incorporates gravity effects on target motion (see equation (1)). The response times for -1g trials were explained by the τ model that incorporates information about target position and velocity, but ignores acceleration (see equation (6), Lee (1976), Lee *et al* (1983), Port *et al* (1997)). As expected, the direction of gravity had little effect on response times during the reactive task. Analysis of fMRI data showed that 1g trials were associated with significantly larger activity than -1g trials in a network involving the insular cortex, temporo-parietal junction, premotor and supplementary motor areas (SMA), middle cingulate cortex, post-central gyrus, posterior thalamus, putamen, and medial cerebellum. In agreement with the internal model hypothesis, the network processing 1g visual motion included the insulae and temporo-parietal junctions that are generally considered the core regions of the vestibular cortex (Bense *et al* 2001, Bottini *et al* 2001, Guldin and Grusser 1998). Activation of the vestibular network was observed during both proactive and reactive tasks, suggesting that it depends on the presence of natural gravity in the visual stimuli, rather than on the specific motor task (anticipatory ball interception versus reaction-time response). Anatomical localization of the vestibular cortex was carried out by means of a second experiment. Standard caloric vestibular stimulations (alternating cold irrigations of the left and right ear) were performed blindfolded, resulting in vestibular sensations and nystagmus that are known to depend on canal-otolith interactions performed by vestibular internal models (Peterka *et al* 2004). We then statistically assessed what brain regions were activated by both 1g visual motion and vestibular stimulation. This analysis revealed a common network that comprises insular cortex (posterior insula and retro-insula), temporo-parietal junction, ventral premotor area, SMA, middle cingulate cortex, post-central gyrus, as well as posterior thalamus and putamen (figure 4). The findings demonstrate that the vestibular network is involved in processing visual motion when this is coherent with natural gravity, supporting the hypothesis of an internal 1g model. As for target motion unrelated to natural gravity, the hypothesis predicts that there should be less involvement of the internal gravity model and hence less activation of the vestibular network. Indeed, fMRI analysis showed that -1g trials were associated with significantly less activation of the vestibular network and significantly greater activity than 1g trials in a region located around the lateral occipital sulcus in the middle and inferior occipital gyri, a region previously identified as motion-sensitive (Orban *et al* 2003). As expected, vestibular stimulation did not activate this area, emphasizing the segregation between neural representations of natural visual gravity and those of visual motion unrelated to gravity.

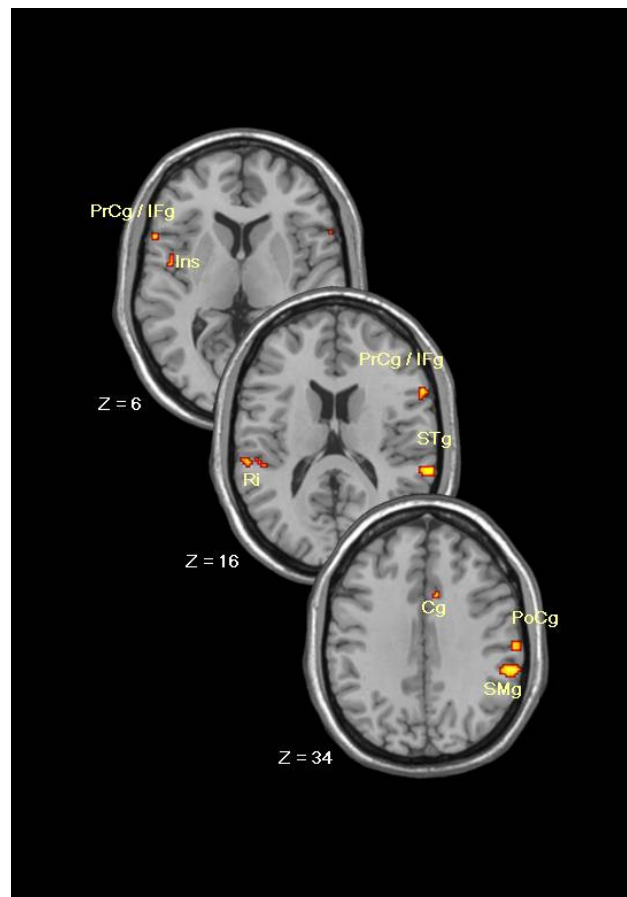


Figure 4. Cortical network of common activations for visual 1g motion and caloric vestibular stimulation, overlaid on three different axial sections from MNI-template in stereotactic space. Cg: middle cingulate gyrus. IFg: inferior frontal gyrus. Ins: insula. PoCg: post-central gyrus. PrCg: pre-central gyrus. Ri: retro-insula. SMA: supplementary motor area. SMg: supramarginal gyrus. STg: superior temporal gyrus.

In summary, we showed that brain regions overlapping with those activated by direct vestibular stimuli are activated when the internal 1g model is called into play by visual exomotion coherent with natural gravity, even if there is no time-varying stimulation of the vestibular sensors. In monkeys, the parieto-insular vestibular cortex (PIVC) at the posterior end of the insula is the core region of the vestibular cortex, as it contains the greatest number of vestibular-driven neurons (Grusser *et al* 1990, Guldin and Grusser 1998). Most PIVC neurons respond jointly to head accelerations, optokinetic and neck somatosensory stimuli. PIVC is reciprocally connected (via the ventro-posterior thalamus) with the vestibular nuclei, as well as with the other vestibular cortical regions (in the temporo-parietal junction, post-central gyrus, ventral premotor and cingulate cortices, Guldin and Grusser (1998)). In addition, PIVC receives anatomical projections from the pulvinar, inferior parietal and superior temporal areas, thus providing possible routes for visual inputs to the vestibular cortex, as implied by the visual responses reported by Indovina *et al* (2005). In man, lesions of posterior insula and retro-insula (probable homologues of monkey PIVC) lead to a tilt of the

perceived visual vertical and rotational vertigo (Brandt and Dieterich 1999). Focal electrical stimulation elicits sensations of altered gravity or body tilt (Blanke *et al* 2002). On the whole, it has been suggested that the cortical vestibular network is involved in the perception of our spatial orientation relative to the gravitational vertical (Guldin and Grusser 1998). Indovina *et al* (2005) proposed a new function for this network, namely a representation of the physical laws of motion. Different forms of sensori-motor coordination might share an internal gravity model permanently stored in the distributed vestibular network. In this network, sensory processing may not be determined by modality but by the nature of the input, i.e. gravitational acceleration. Thus, the vestibular estimate of gravity helps discriminating tilt from translation of the head (Merfeld *et al* 1999), and the gravity model disambiguates visual information in TTC estimates (Indovina *et al* 2005). Furthermore, the areas of somatosensory cortex and ventral premotor cortex activated by visual 1g motion overlap with sensory and motor arm/hand representations, suggesting that the internal 1g model is also used to account for gravity effects on arm position when planning arm movements or sensing arm position (kinaesthesia), in agreement with the notion of multi-modal processing in the cortical vestibular system (Guldin and Grusser 1998).

8. Conclusion

The idea that organisms' perception and action are tuned to environmental constraints by means of their internalization has long been around in psychology (Shepard 1994). The studies reviewed here are beginning to unravel how the fundamental physical constraint of Earth's gravity is internalized in the human brain for visual perception and interception of falling objects.

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