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RESEARCH ARTICLE

Egocentric and allocentric reference frames for catching a falling object

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Abstract When programming movement, one must account for gravitational acceleration. This is particularly important when catching a falling object because the task requires a precise estimate of time-to-contact. Knowledge of gravity's effects is intimately linked to our definition of 'up' and 'down'. Both directions can be described in an allocentric reference frame, based on visual and/or gravitational cues, or in an egocentric reference frame in which the body axis is taken as vertical. To test which frame humans use to predict gravity's effect, we asked participants to intercept virtual balls approaching from above or below with artificially controlled acceleration that could be congruent or not with gravity. To dissociate between these frames, subjects were seated upright (trunk parallel to gravity) or lying down (body axis orthogonal to the gravitational axis). We report data in line with the use of an allocentric reference frame and discuss its relevance depending on available gravity-related cues.

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Introduction

When interacting with our environment in everyday life, we have to pay particular attention to moving objects. Such interactions can be as varied as avoiding a car when crossing a street or catching a glass falling from a table. In these situations, our brain has to evaluate the object's trajectory and the time it will take to reach the interception/impact point. In many cases these two parameters have to be precisely predicted because of the tightness of the interception/avoidance temporal window, especially when trying to catch a falling object (c.f. Zago et al. 2009). One has also to take into account limitations of our own bodies (motor command delays, inertia of the limb) to compute a motor command that will achieve the desired action.

In an interceptive task, a human observer can evaluate information from different sensory modalities to estimate the timing of the impact. The best way to predict the impact time of a moving object would be to evaluate its speed, acceleration and even higher time derivatives to calculate time-to-contact (TTC) at every moment. Unfortunately, the human visual system is poorly able to discriminate instantaneous accelerations (Brouwer et al. 2002; Port et al. 1997; Todd 1981; Werkhoven et al. 1992). Accordingly, previous studies have shown that, to intercept a moving object, subjects evaluate impact time based on information about distance and velocity only, without resorting to higher-order derivatives (Benguigui et al. 2003; Senot et al. 2003). But using such a "first-order strategy" (Bootsma and van Wieringen 1990) leads

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to errors because TTC is under-estimated for decelerating objects and over-estimated for accelerating ones. Nevertheless, in an experiment involving the catching of falling objects, Lacquaniti and Maioli (1989a, b) showed that subjects used an estimation of TTC that was more precise than what would be obtained if the downward acceleration was completely ignored. To explain these results, they proposed that subjects anticipate the effect of gravity on the ball's movement and confirmed this hypothesis by a series of subsequent experiments (see review by Zago et al. 2009).

In an experiment using virtual reality, Senot et al. (2005) asked subjects to intercept balls coming either from above or below. The virtual balls accelerated, decelerated or moved at constant velocity, regardless of whether they approached from above or below, independent of the force of gravity. The results showed that, even though the approaching movement of the ball with respect to the subject was the same in both conditions, subjects responded earlier to a downward versus upward moving object, consistent with the use of a (simplified) internal model of gravity's effects. Moreover, although maximum success was achieved for balls approaching at constant velocity, success rate was somewhat greater when balls accelerated or decelerated in a manner congruent with the direction of movement, i.e. success rate was higher for accelerating approaches when the ball came from above and higher for decelerating balls when they came from below. A similar a priori on gravity effects has been observed during perception studies (Hubbard 1990, 1995; Nagai et al. 2002) where subjects estimated the displacement of visual cues. Subject's responses reflected an a priori assumption that the target moved under the influence of gravity.

To anticipate the effects of gravity one needs to have a sense of 'up' and 'down'. Logically, this representation should be defined with respect to the world based on the sensation of gravity's pull on the body, via otolithic, proprioceptive or somatosensory information, or based on visual cues from the environment, such as the orientation of trees and buildings and directional lighting that is presumed to come from above (Ramachandran 1988). Alternatively, since we normally function in an upright posture, 'up' and 'down' could be referenced with respect to our own bodies, i.e. the CNS may have learned through experience to associate gravitational acceleration with objects that move in the head-to-feet direction. While such an egocentric representation of vertical (parallel to the body axis) and horizontal (perpendicular to the body axis) would not always be correct, such a mechanism would be 'good enough' (Gibson 1977) in the most typical cases to improve catching performance.

The experiment reported here was based on the observation that subjects respond earlier to intercept a downward versus upward moving object (Senot et al. 2005). Here, we asked subjects to intercept objects approaching approximately along the sight-line either while seated upright or while lying in a supine or prone position. We thus tested whether subjects anticipate gravity's effects when the object moves along the gravitational axis, independent of the body's orientation in space. In other words, we tested whether the internal model of gravity's effects is implemented with respect to an egocentric or allocentric reference frame.

Method

Subjects intercepted a virtual ball that moved upward or downward with respect to gravity. We used essentially the same paradigm as the one used by Senot et al. (2005), the major difference being that subjects were now either seated and tilted the head or lay prone or supine and looked straight ahead in order to look up or down.

Experimental apparatus

Virtual reality allowed us to modify easily the parameters of the task, such as the speed, acceleration, flight duration of the ball, and visual cues in the environment. We used an HMD (Virtual Research model V8, visual field 60° diagonally; 640 × 680 pixel resolution) that provided stereoscopic vision. This HMD was fitted with LEDs seen by an optical tracker (SAGEIS Optical Tracker, ±0.1 mm resolution for displacement, ±0.015° resolution for orientation). Measurements of the position and orientation of the subject's head were used to update the virtual scene according to the subject's movements and gaze direction within the virtual room.

Task

Subjects were immersed in a virtual room that measured 4 m × 4 m and 9.5 m high. Walls, floor and ceiling were textured to be distinguishable: brick for walls, a wooden parquet floor, and metallic girders for the ceiling. A 2-m long cannon was fixed on the floor (Below condition) or on the ceiling (Above condition). This cannon launched an 8-cm radius ball that followed an upward (Below condition) or downward (Above condition) vertical trajectory toward the interception point, 50 cm in front of the subject.

In each condition (Above/Below), nine stimuli were used: the ball approached with one of three different accelerations ($-1g$, $0g$, and $+1g$) and the initial velocity was adjusted such that the time to reach the interception point was one of three different flight durations (750, 800, and 850 ms). Each stimulus was presented 5 times in a pseudo-random order. At the end of each block subjects had performed 45 trials, giving a total of 90 trials for the two conditions combined.

Subjects initiated the beginning of each trial by pushing a handheld button. When the button was pressed, the cannon's color changed from green to orange and a ball was ejected from the cannon after a randomized time (200–1,000 ms). Then subjects had to push another button to trigger the racquet's movement in order to intercept the ball.

The racquet (16 cm^2) was placed at a distance of 20 cm to the right of the ball's trajectory (i.e. on the subject's right), 50 cm in front of the subject. Subjects triggered a stereotyped movement of the racquet that followed a linear path from right to left, crossing the vertical path of the ball. The racquet's path was 40-cm long and this distance was covered in 150 ms with its speed calculated according to the minimum jerk law (Flash and Hogan 1985). Since the racquet did not reach the interception point instantaneously, subjects had to take into account the racquet's travel time to trigger their response at the right moment. To hit the ball dead center, the ideal response was to trigger the racquet 57 ms prior to the ball's arrival at the interception point.

For each trial subjects knew if they had touched the ball, thanks to changes of its color and trajectory: a hit ball kept its green color and was deviated to the left. A missed ball turned red and continued its straight-line trajectory. At the end of each condition, a score reporting the number of successful hits was given to subject.

Protocol

Each subject performed the task in two different postures. In the first, as in the previous experiment (Senot et al. 2005), subjects were seated and had to tilt their head up or down (Fig. 1, panels **a** and **b**, respectively) to observe the ball coming from above and below, respectively. In the second, subjects lay in a supine or prone position and looked straight ahead (Fig. 1, panels **c** and **d**, respectively) to see the ball coming from above and below, respectively. Depending on their posture (seated or lying down), the subject's body axis was orthogonal or aligned with gravity. In each position, however, the head orientation relative to the gravity was about the same. Note that the virtual scene was always congruent with the subject's gaze direction with respect to gravity. Subjects had to look up (Above condition) or down (Below condition) to see the cannon when seated. In the lying position, subjects looked straight ahead to see the floor when prone (Below) and the ceiling when supine (Above).

When arriving for a test session, subjects received instructions and performed a set of trials to learn the task. For these practice trials they sat in front of a computer screen showing the same scene that we used in the HMD, but the virtual ball was launched from a wall at a distance of 9.5 m in front of him/her. The main purpose of these trials was to learn the timing of the racquet's movements.

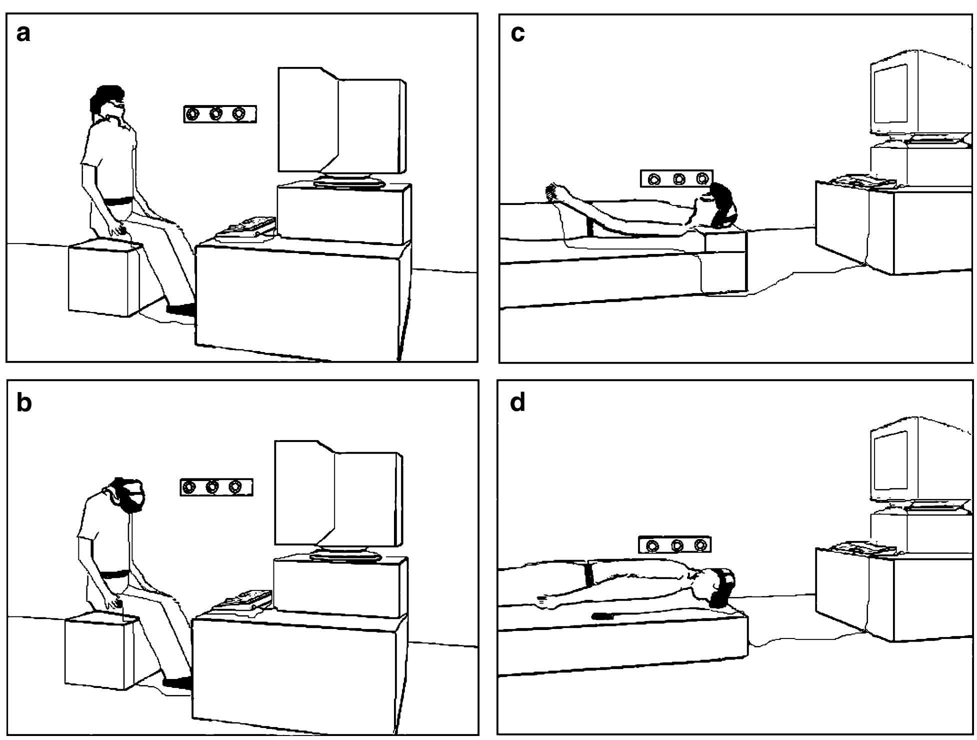

Fig. 1 Experimental setup and postures: **a** and **b** seated; **c** and **d** lying down. For the Above (**a** and **c**) condition subjects directed their gaze toward ceiling, while for the Below condition (**b** and **d**) subject's looked toward the floor

Subjects

Twenty-five healthy volunteers, with normal or corrected vision, performed the experiment (14 women and 11 men, ages 17–33 years old). Twenty-two were right-handed, while 2 were left-handed. All right-handed subjects used their right hand to press the button that triggered movement of the racquet. One left-handed subject usually used a computer mouse with right hand and so performed the task with the right hand. The other left-handed subject used his left hand to trigger the racquet movement. All were naïve to the hypothesis of the experiment.

Subjects were separated into 4 groups: group IA (7 subjects) performed the experiment first lying down and then seated, starting with the Above condition; group IB (6 subjects) performed the experiment first lying down and then seated, starting with the Below condition; group IIA (6 subjects) performed the experiment seated first and then lying down, starting with the Above condition; and finally group IIB (6 subjects) performed the experiment seated first and then lying down, starting with the Below condition.

Data and statistical analysis

We defined the *response delay* as the time between the ball launch and the "click" on the left mouse button. We also studied the *trigger time* defined as the response time relative to the theoretical moment when the ball crossed the ideal interception point. *Success rate* was also evaluated for each experimental condition.

Subjects performed 5 trials for each of the 9 possible ball kinetics (3 accelerations × 3 flight durations) in each posture and for each direction of movement of the ball. Values of *response delay* and *trigger time* were averaged over the 5 repetitions and subjected to a four-factor ANOVA with the following within-subject factors: Posture (Seated/Lying) × Direction (Above/Below) × Flight Duration (750, 800, and 850 ms) × Acceleration ($-1g$, $0g$, and $1g$). *Success rate* was computed for the 15 trials in each condition having the same acceleration (grouping together the 3 flight times for the same acceleration) and a 3-way repeated-measures ANOVA was performed with within-subject factors: Posture (Seated/Lying) × Direction (Above/Below) × Acceleration ($-1g$, $0g$, and $1g$).

Some subjects were surprised by the first trial and so did not trigger the racquet's motion at all. These trials were excluded from the calculation of the average *trigger time*, meaning that the average *response delay* and *trigger time* were in a few cases based on 4 values instead of 5 (12 trials out of 4,500). Nevertheless, these trials were included in the computation of the *success rate*, i.e. such trials were counted as 'misses'.

Results

To ensure that subjects used a timing strategy based on an estimation of TTC, we performed an ANOVA on *response delay* that revealed a main effect of the flight duration ($F_{(2,48)} = 108.31$, $p < 0.01$). Subjects initiated the racquet movement later when the flight time was longer, showing that the subjects were indeed synchronizing their responses to the expected arrival of the ball, and not simply pressing the button after a fixed time delay.

We subsequently analyzed response timing with respect to the arrival time of the ball in the interception zone (i.e. *trigger time*). In accordance with previous experiments, an ANOVA revealed a main effect of the factor Direction on *trigger time* ($F_{(1,24)} = 9.03$, $p < 0.01$): when the ball fell from the ceiling (Above) the subjects initiated the racquet's movement earlier on average with respect to the ideal *trigger time* than when the ball rose from the floor (Below; Fig. 2). There was no cross-effect between the factors Direction and Posture, indicating that the difference in timing between ball's moving upward and downward with respect to gravity was present whether the subject tilted the head while seated or looked straight ahead while lying prone or supine. Indeed, Newman–Keul's post hoc analysis confirmed the difference in *trigger time* between the Above and Below conditions in both the Seated ($p < 0.01$) and the Lying ($p < 0.05$) postures.

Looking more closely at the different possible kinetics of the ball, we observed a significant effect of the ball's acceleration on the response timing with respect to its arrival in the interception zone (main effect of factor Acceleration on

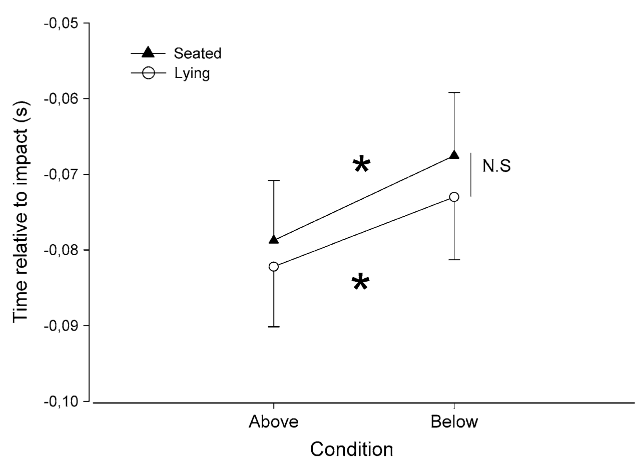

Fig. 2 *Trigger time* as a function of the ball's direction (Above or Below) and the subject's posture (seated—*black triangles*, lying prone or supine—*open circles*). *Trigger time*s differed significantly for Above versus Below in both postures (Newman–Keul's post-hoc test $p = 0.037$ and 0.010, respectively, for the Lying and Seated positions). There was no significant difference between postures and no cross effect. *Bars* indicate the 95% confidence interval of the mean

trigger time; $F_{(2,48)} = 1413.13$, $p < 0.01$): the more the ball accelerated, the later the button was pushed with respect to the ideal trigger time. Subjects appear to have over-estimated TTC for accelerating balls and underestimated TTC for decelerating balls. Furthermore, a significant cross-effect between the factors Flight Duration and Acceleration on *trigger time* was observed ($F_{(4,96)} = 83.13$, $p < 0.005$), i.e. the effect of the duration of the ball's trajectory was different depending on the acceleration of the ball (see Fig. 3). This dependence of *trigger time* on Flight Duration is to be expected if subjects use a fixed, a priori prediction of acceleration, rather than acceleration information acquired in real time during a trial, to trigger their response (McIntyre et al. 2001, 2003; Senot et al. 2005). This dependence of *trigger time* on Flight Duration is consistent with a large number of studies involving similar tasks (Lee et al. 1983; Michaels et al. 2001; Port et al. 1997; Miller et al. 2008).

From Fig. 3 one can see that the racquet was triggered closest to the ideal *trigger time*, on average, when the ball moved at constant velocity. This fact was reflected in the measured *success rate* (see Fig. 4). The ANOVA revealed a main effect of Acceleration ($F_{(2,48)} = 51.12$, $p < 0.01$), and success was highest for 0*g* stimuli (post-hoc Newman–Keul's $p < 0.01$) i.e. for balls that moved with constant velocity. We found a significant difference in *success rate* between −1*g* and +1*g* stimuli (post-hoc Newman–Keul's, $p < 0.02$) with better success for −1*g* than for +1*g* stimuli. This difference is most likely due to differences in the spatio-temporal margin-of-error in the two cases. For a given flight duration, a decelerating ball starts out moving faster and slows down by the time it reaches the interception zone. For an accelerating ball, this relationship is reversed. The slower transit of the interception zone by decelerating balls meant that more temporal variability in *trigger time* could be tolerated for these stimuli (compared to accelerating balls) while still achieving success.

We also observed a main effect of the Posture on *success rate* ($F_{(1,24)} = 4.90$, $p < 0.05$), with slight higher overall success when subjects were seated upright (56.5%) as compared to the prone and supine postures (51%). There was no cross-effect between Posture and Direction. We did not detect any bias in the timing of responses that could explain the higher success in the seated position (i.e. we found no main or cross-effect of Posture on *trigger time*). We therefore hypothesized that variability in the timing of responses could account for this effect on success. With a simple paired *t* test, we compared the average variability of responses (standard deviation of *trigger time* for each stimulus, averaged across all nine possible ball kinetics and across both directions of movement) and found that *trigger time* was, on average, less variable when subjects were seated than when they were lying down. This reduced variability can explain the increase in *success rate* in the seated posture.

We did, on the other hand, see an effect of the shift in timing between upward and downward movement on the pattern of success for different kinetics of the ball. We observed a significant cross-effect between Acceleration and Direction on *success rate* ($F_{(2,48)} = 5.25$, $p < 0.01$) while there was no cross-effect between the factors Posture, Direction, and Acceleration. We hypothesized that the cross effect could be due to variations in *success rate* depending on the coherence or not of the ball's acceleration

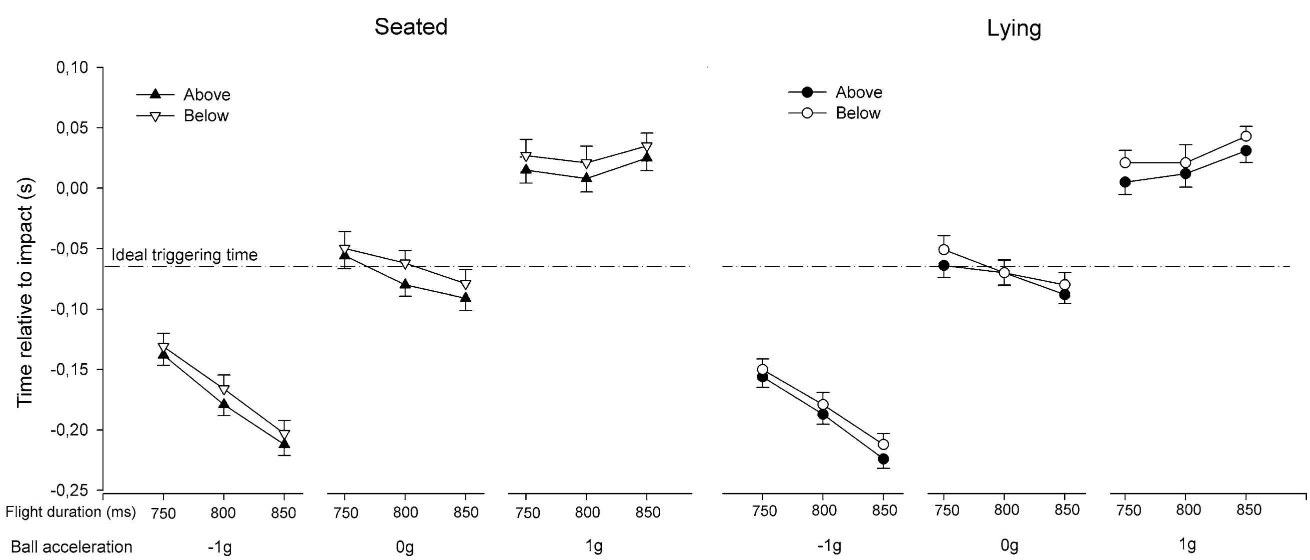

Fig. 3 Effect of Acceleration, Flight Duration, and Direction on *trigger time*. *Trigger time* varied significantly according to the acceleration of the ball. For each Acceleration, *trigger time* also depends on Flight Duration. Whatever the ball's direction and real acceleration, subjects triggered the racquet's motion earlier for balls moving downward. *Bars* indicate the 95% confidence interval of the mean

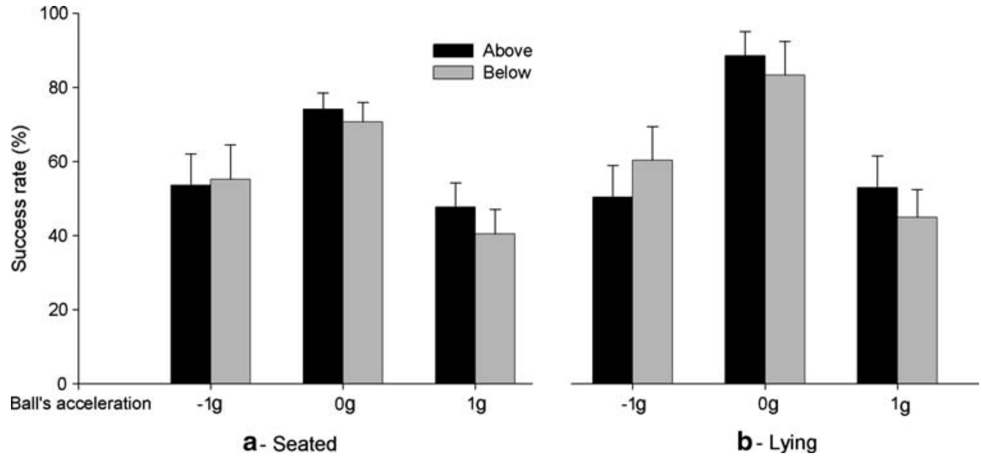

Fig. 4 *Success rate* in Seated (**a**) and Lying (**b**) positions: success rate was higher for constant velocity stimuli in both positions. More interestingly, when the ball accelerated, success rate was higher when the ball came from above and conversely, for decelerating balls, success rate was higher when balls came from below. *Bars* indicate the 95% confidence interval of the mean

with the direction of gravity. To test this specific hypothesis, we performed a two-factor ANOVA on *success rate* for accelerating and decelerating balls with only Acceleration and Direction as within-subject factors. Again, a significant cross-effect was observed between the acceleration of the ball and movement direction, and this difference was maintained when the ANOVA was applied only to trials in the Lying posture ($p < 0.05$) and marginally significant ($p = 0.0605$) in the Seated position. A non-parametric χ^2 test also showed a significant difference in the distribution of successful trials between upward and downward trajectories as a function of the ball's acceleration ($p < 0.05$). These analyses appear to confirm the observation that subjects are more successful at hitting accelerating balls when they come from above and more successful at hitting decelerating balls when they approach from below.

Discussion

In this study we looked at the timing of interceptive responses as a function of the target's direction of movement with respect to gravity, as a function of the ball's acceleration, as a function of the time to reach the interception point, and as a function of the ball's direction of movement with respect to the body axis. We found significant effects of the ball's acceleration and direction of movement with respect to gravity, and these effects were the same whether the subject was seated upright or lying down. In the following, we first reiterate how the observed differences in timing for ball's approaching from above or below argue for a simplified internal model of gravity's effects to anticipate future movements of the target (Senot et al. 2005; Zago et al. 2008). We then address the main question of this article: What is the reference frame (egocentric or allocentric) used to define 'up' and 'down' when applying this simplified model of gravity's effects?

Anticipating the effects of gravity

The results of this experiment are consistent with the hypothesis that human observers apply a simplified model of gravity when predicting the vertical movements of an object (McIntyre et al. 2001; Senot et al. 2005; Zago and Lacquaniti 2005; Zago et al. 2004, 2005, 2008, 2009). Response timing varied systematically as a function of the ball's acceleration and flight duration (Fig. 3), as would be predicted if the observer was unable to take into account in real time the acceleration of the ball during the course of a single trial. Indeed, it has been proposed that acceleration can often safely be ignored when estimating the TTC of objects falling over a long distance under gravity (Tresilian 1995). Nevertheless, for a given set of stimulus parameters (ball size, distance, and velocity), interceptive responses were triggered earlier for downward versus upward moving targets, whatever their actual acceleration and flight duration might be. Since the approaching movement was the same in both cases, the observed differences in timing between the two movement directions reflect an a priori expectation that a falling object will accelerate or that a rising object will decelerate under gravity's influence (Hubbard 1990, 1995; Lacquaniti and Maioli 1989b; Nagai et al. 2002; Zago et al. 2005; Zago and Lacquaniti 2005).

Note that the racquet was nevertheless not triggered at the precise time that would be predicted by a veridical estimate of gravitational acceleration. The most accurate trigger times, and thus the highest success rates, were obtained for balls moving at a constant velocity, whether they moved upward or downward, as reported previously (Senot et al. 2005). This optimization may reflect a rapid adaptation of the timing strategy to maximize success rate over the ensemble of all trials (McIntyre et al. 2003; Zago et al. 2004). Since subjects appear unable to measure the ball's acceleration in real time, and since constant velocity lies midway in the range of possible accelerations, overall success will be maximized if the timing delays are adjusted to fit the most likely expected arrival time over all trials (Baures et al. 2007). This could be achieved by adding more or less delay to the minimal sensorimotor response time (McIntyre et al. 2003). Adjustment of the sensorimotor delay of just this type was demonstrated by Zago et al. (2004) who, in an initial experiment, showed that success in intercepting downward-moving balls was greatest when the ball accelerated, as compared to balls descending at constant velocity. But when presented downward moving balls that consistently moved at constant velocity in blocks of trials, the timing of responses was adjusted in just a few trials within the block to increase success rate. Catch trials showed that responses to downward accelerating balls were shifted in this context, reducing success for these rare trials to the benefit of the overall success rate. Subjects could rapidly adjust the latency of their responses to increase success. This rapid adaptation does not, however, mask the effects of an a priori prediction of the effects of gravity on the ball; here and elsewhere we have detected a modification in the timing of responses when changing from balls falling from above to balls rising from below (Senot et al. 2005). In fact, simply changing the sensorimotor delay might also provide the mechanism for a simplified model of gravity's effect; changing from above to below would engender a small adjustment to the sensorimotor delay to reflect the expectation that a ball moving downward will accelerate and therefore arrive a bit earlier than a ball that moves upwards (Senot et al. 2005; Zago and Lacquaniti 2005b). This amounts to what we have called a "pretty good" internal model of gravity (McIntyre et al. 2003).

An allocentric reference frame

In the above paragraphs and elsewhere (Senot et al. 2005), we have argued for the existence of a (vastly simplified) internal model of the effects of gravity, based on the difference in timing between upward and downward moving balls. The main purpose of the experiment reported here was to identify the reference frames underlying this a priori expectation. In Table 1 we compare our results to current knowledge obtained over the last few years about what sensory information evokes a sense of 'up' and 'down' as it pertains to the interception of moving objects. In particular, we show which experiments provide evidence for an anticipation of the effects of gravity on the interceptive behavior and we describe the reference frame that the subjects may have used in each of these studies.

In the early experiments conducted by Lacquaniti et al. (Table 1, line a), subjects caught a real ball that dropped into the outstretched hand in normal Earth gravity. Subjects were seated and tilted the head upward to observe the ball dropping from above. The ball moved downward with respect to all three potential reference frames (gravity, visual scene, and body axis). Evidence for an anticipation of the effects of gravity was given by the precision in timing of the responses. Since the visual system is insensitive to acceleration on short-time scales, it was proposed that subjects incorporated an a priori expectation of gravitational acceleration to predict the arrival time of the ball. Systematic variations in the timing of the motor response would have occurred if the acceleration of gravity had been ignored.

In McIntyre et al. (2001) subjects also caught a real ball projected downward from above their head, both on Earth and in the weightless environment of Earth orbit. On Earth, subjects were in the same position as described above (Lacquaniti and Maioli 1989a, b). On orbit, the visual environment and the movement with respect to the body axis were the same as on Earth, however, there was no longer a defined gravitational axis in these conditions (Table 1, line b). Evidence for an anticipation of the effects of gravity was given by the earlier responses elicited in the absence of

Table 1 Comparison of directional cues used in different catching studies

	Study	Experimental condition	Gravity	Visual scene	Subject's body axis	Ball	Anticipation of gravity's effects
a	Lacquaniti and Maioli (1989a, b)	Real ball and environment on Earth	↓	↓	↓	↓	Yes
b	McIntyre et al. (2001)	Real ball and environment, weightlessness		↓	↓	↓	Yes
c	Indovina et al. (2005)	Virtual reality on Earth, rich visual scene	↓	→	→	→	Yes
d	Senot et al. (2005)	Virtual reality on Earth, "poor" visual scene—*main experiment*	↓	↓	↓	↓	Yes
e	Senot et al. (2005)	Virtual reality on Earth, "poor" visual scene—*control experiment*	↓	→	↓	→	No
f	This study	Virtual reality on Earth, "poor" visual scene	↓	↓	→	↓	Yes

Arrows indicate 'down' as defined by gravity, the visual environment, or the body axis (in the latter case, down = feet), and the direction of the ball's trajectory. The last column indicates whether an anticipation of the effects of gravity was observed, either by a better tuning for balls that accelerate downward or by a differential effect on timing for balls that approached the subject from above or below (see text) gravity and the specific effect of the initial velocity of the ball in 0 g, consistent with an a priori assumption that the ball would accelerate downward. Here, 'downward' was defined by the visual scene and the posture of the subject.

In Indovina et al. (2005) subjects lay supine in an MRI scanner to perform the task. Virtual targets were projected on a mirror placed in front of the eyes. Balls moved downward with respect to a rich visual scene and with respect to the body axis (i.e. in the head-to-feet direction). The ball's movement was perpendicular, however, to the direction of gravity (Table 1, line c). Here, evidence for an anticipation of the effects of gravity was given by the better timing for balls that accelerated 'downward' with respect to the visual scene and body axis at $1g$ than for balls that decelerated in the same direction at $-1g$.

Senot et al. (2005) performed a test of interception in an immersive virtual environment with two postural conditions. In the main experiment (Table 1, line d) subjects were seated and tilted the head upward or downward to see the ball approaching from above or below, respectively. In this case the ball moved parallel to gravity, to the body axis and to the up/down axis defined by directional cues in the visual environment. Here evidence for an anticipation of the effects of gravity on the ball was given by the earlier responses for balls coming from above than for balls coming from below, regardless of the ball's actual acceleration ($-1g$, $0g$, and $+1g$). In a control experiment described in the same article (Table 1, line e), the virtual scene was rotated 90° such that the subject looked straight ahead to look 'above' and 'below', the latter directions being defined only by the visual cues. In this case, the ball moved parallel to the vertical axis of the visual scene, but perpendicular to the gravitational and body axes. In this situation, there was no difference in time for balls coming from 'above' and from 'below' and thus no evidence for an anticipation of the effects of gravity.

The current experiment (Table 1, line f) completes the table by testing whether gravity itself is sufficient to evoke the anticipatory shift in timing. Here the ball moved parallel to the gravitational axis and to the visually defined vertical, but perpendicular to the body axis. Subjects looked straight ahead in a prone position to see balls arriving from below and looked straight ahead while lying supine to intercept balls coming from above. As it was the case in Senot et al. (2005), responses occurred earlier with respect to the arrival of the ball for balls coming from above versus below. Since the shift in timing occurred independent of the orientation of the body axis in space, this experiment shows that subjects can use an internal model implemented in a gravicentric reference frame to anticipate the effects of gravity on the ball. This is not to say that gravity provides the only pertinent cue; other egocentric and allocentric references may also have come into play (see below). Nevertheless, gravity appears to have dominated over body axis in defining the vertical direction in these conditions.

Gravity itself therefore appears to be sufficient to define up and down vis-à-vis interception responses, based on the results reported here. But is alignment with gravity a necessary condition? In two MRI studies (Indovina et al. 2005; Miller et al. 2008), as well as in an experiment conducted in microgravity (McIntyre et al 2001), subjects tuned their interception timing as if the ball accelerated 'downward' even if this direction was either perpendicular to gravity (lying in the MRI machine) or irrelevant (weightlessness). In both situations, visual cues and the body axis could define 'up' and 'down'. Coupled with the results reported here, this demonstrates that gravity may be sufficient, but is not a necessary condition, to evoke a sense of verticality.

It remains to be determined whether visual cues alone are sufficient to define 'up' and 'down'. In the MRI studies cited above, the visual scene and the body axis were aligned, making it impossible to determine which of these two factors gives rise to the asymmetric response to accelerating and decelerating targets. In the study by Senot et al. (2005), visual cues were explicitly decoupled from the body axis and gravity by turning the visual virtual room by 90°. Here, no differences in interceptive response timing were observed between the visually defined 'upward' and 'downward', suggesting that body axis might be the determining factor. Note, however, that Miller et al. (2008) compared responses made within a detailed visual scene to responses obtained when the target moved against a plain background. Again subjects were lying on their backs and the visual vertical was aligned with the body axis. For balls that moved 'downward' with respect to this visual/egocentric axis that was nevertheless perpendicular to gravity, response timing was better for accelerating versus decelerating balls only when presented within the rich visual scene. Oriented visual cues might therefore push the a priori adjustment of response timing closer to that predicted for a ball undergoing gravitational acceleration. It is possible, therefore, that a visual scene containing more polarized objects than that used by Senot et al. (2005) could evoke an up–down differential in responses to stimuli that move perpendicular to both the gravitational and the egocentric (body) reference frame.

Finally, even if gravity itself is sufficient to evoke a differential in up/down responses, one might also ask whether the body axis could reinforce the construction of an up/down axis. Our analysis demonstrated no effect of posture on *trigger time;* the difference in timing between Above and Below was present in both cases and not demonstrably different (i.e. no cross effect between the factors Direction and Posture). Nevertheless, there was a significant effect on *success rate*. Subjects had higher success overall in the upright position as compared to lying prone or supine and we attributed this difference to a greater variability of responses in the reclined position. This lower performance while lying down suggests that body axis might indeed contribute cues defining the reference frame normally used to apply one's internal model of gravity's effect. The reference frame would therefore be mixed, implying a combination of both allocentric and egocentric cues. Such mixed reference frames have been postulated to explain how humans perceive verticality (Lipshits et al. 2005; Luyat and Gentaz 2002; Luyat et al. 2005). Furthermore, subjects have been observed to tune kinematic parameters of arm movements to the movement's direction that were vertical and horizontal in one reference frame or the other depending on the available information (Le Seac'h and McIntyre 2007). In the experiment described here, the dissociation of strong references, such as vision and body axis could evoke to a misrepresentation of the vertical reference when subjects were lying down, leading to an increase in variability of the interception response due to the use of incongruent information.

The ensemble of results on this type of interception task indicates that the definition of 'up' and 'down' is a multimodal process that can involve both allocentric and egocentric information. Gravity appears to be a sufficient, but not necessary factor, to determine whether a target is coming from 'above' or 'below'. If gravitational cues are sufficient, however, why resort to another reference frame? As proposed in Sect. "Introduction", self-organizing neural networks in the brain may learn to associate ball acceleration with downward movements defined in both allocentric (gravitational and visual) and egocentric (head-to-feet) reference frames. Alternatively, effects of up and down in an egocentric reference frame could stem from processes required to distinguish vestibular signals that arise from gravitational acceleration from those induced by linear movement of the body. According to at least one model (Bortolami et al. 2006), an egocentric representation of 'up' and 'down' may be essential to the disambiguation of vestibular signals. Finally, the reference frame used by subjects could also depend on the task (Carriot et al. 2008). For example, subjects might be more inclined to employ an egocentric reference frame to estimate TTC of an approaching object and an allocentric reference frame to estimate the time of contact between two colliding bodies. In any case, it is clear that the observed anticipation of gravity's acceleration can occur in either an egocentric or an allocentric reference frame, depending on the available sensory information and environmental factors. Vestibular cortex is a likely locus for the neural processes involved in the selection of orientation cues and the definition of an egocentric or allocentric up and down, as these brain regions receive the multisensory information necessary to perform this task (Indovina et al. 2005; Miller et al. 2008).

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