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Body orientation contributes to modelling the effects of gravity for target interception in humans

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Key points

- It is known that interception of targets accelerated by gravity involves internal models coupled with visual signals.
- Non-visual signals related to head and body orientation relative to gravity may also contribute, although their role is poorly understood.
- In a novel experiment, we asked pitched observers to hit a virtual target approaching with an acceleration that was either coherent or incoherent with their pitch-tilt.
- Initially, the timing errors were large and independent of the coherence between target acceleration and observer's pitch. With practice, however, the timing errors became substantially smaller in the coherent conditions.
- The results show that information about head and body orientation can contribute to modelling the effects of gravity on a moving target. Orientation cues from vestibular and somatosensory signals might be integrated with visual signals in the vestibular cortex, where the internal model of gravity is assumed to be encoded.

Abstract Interception of moving targets relies on visual signals and internal models. Less is known about the additional contribution of non-visual cues about head and body orientation relative to gravity. We took advantage of Galileo's law of motion along an incline to demonstrate the effects of vestibular and somatosensory cues about head and body orientation on interception timing. Participants were asked to hit a ball rolling in a gutter towards the eyes, resulting in image expansion. The scene was presented in a head-mounted display, without any visual information about gravity direction. In separate blocks of trials participants were pitched backwards by 20° or 60°, whereas ball acceleration was randomized across trials so as to be compatible with rolling down a slope of 20° or 60°. Initially, the timing errors were large, independently of the coherence between ball acceleration and pitch angle, consistent with responses based exclusively on visual information because visual stimuli were identical at both tilts. At the end of the

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experiment, however, the timing errors were systematically smaller in the coherent conditions than the incoherent ones. Moreover, the responses were significantly ($P = 0.007$) earlier when participants were pitched by 60° than when they were pitched by 20°. Therefore, practice with the task led to incorporation of information about head and body orientation relative to gravity for response timing. Instead, posture did not affect response timing in a control experiment in which participants hit a static target in synchrony with the last of a predictable series of stationary audiovisual stimuli.

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Introduction

There is abundant evidence indicating that people can deal with complex dynamic environments even with sparse sensory information (Battaglia *et al.* 2013; Hamrick *et al.* 2016; Lacquaniti and Maioli 1989; Sanborn *et al.* 2013; La Scaleia *et al.* 2015). This indicates that successful interactions with objects in our daily routine imply an underlying model of the physical properties and forces involved, a model that can surrogate missing or ambiguous sensory information (Wolpert & Kawato 1998). Internal models are used also by other animals to intercept a moving target, such as monkeys (Streng *et al.* 2018), cats (Cerminara *et al.* 2009) and dragonflies (Mischiati *et al.* 2015). However, we still have an incomplete understanding of how critical elements of these internal models, such as the reference frame used to decode the effects of environmental forces, are constructed for each given task.

Gravity, as a ubiquitous force, must be a constituent part of the physical model of the environment. An internal model of gravity is required because no single sensor can distinguish between gravitational and inertial accelerations according to Einstein's equivalence principle. Indeed, an internal model of gravity has been shown to contribute to interceptions of falling targets (Lacquaniti *et al.* 1993; Tresilian 1997; McIntyre *et al.* 2001; Zago *et al.* 2004; Indovina *et al.* 2005; La Scaleia *et al.* 2015; Jörges and López-Moliner 2017; Russo *et al.* 2017; Zago *et al.* 2011), optimal control of reaching movements (Gaveau *et al.* 2016), perceived duration of gravitational motion (Moscatelli & Lacquaniti 2011), time-to-passage estimates during visual self-motion (Indovina *et al.* 2013), naturalness judgments of motion under gravity (La Scaleia *et al.* 2014*b*; Ceccarelli *et al.* 2018), interpretation of biological motion (Troje & Chang 2013; Maffei *et al.* 2015) and perception of the visual vertical (Van Pelt *et al.* 2005; De Vrijer *et al.* 2008).

These and other studies showed that internal estimates of both the magnitude and the direction of gravity are available for perception and action (Zago 2018). During dynamic head tilts, gravito-inertial accelerations signalled by the otoliths (Fernandez & Goldberg, 1976) can be disambiguated by filtering the otolith signals (Mayne 1974) and/or combining them with the signals of the semicircular canals (Angelaki *et al.*, 1999; Glasauer, 1992; Merfeld *et al.* 1999). As a result, even with eyes closed, generally, we do not confuse a backward pitch with a forward acceleration of the head, and we perceive the world as stable, despite frequent movements of the eyes, head and body (Snyder 1999; Day & Fitzpatrick 2005).

When the task requires aligning a visual line to the vertical in the dark, the so-called subjective visual vertical (SVV) (Lacquaniti *et al.* 2015; Kheradmand & Winnick 2017), the direction of gravity is estimated by combining retinal cues about the line orientation with vestibular and somatosensory cues about head and body orientation, plus the prior assumption of an upright head orientation (Mittelstaedt 1983; Dyde *et al.* 2006; MacNeilage *et al.* 2007; De Vrijer *et al.* 2008).

Gravitational acceleration of objects is experienced by vision, although the visual system is poorly sensitive to image acceleration (Calderone & Kaiser, 1989; Werkhoven *et al.* 1992; Brouwer *et al.* 2002). Thus, it has been proposed that the visual effects of gravity on a moving target are interpreted by combining information about the rate of change of retinal image with binocular (stereo, vergence) and monocular (familiar size, vertical and horizontal scene contours, perspective, shading, texture gradient, lighting) cues allowing to map from the retinal to the environment frame, plus the prior assumption of Earth gravity (Zago *et al.* 2009).

For target interception, also vestibular and somatosensory cues about head and body orientation can help constructing a gravity reference, as occurs for the SVV task. Thus, a few previous studies have shown that the participant's posture relative to gravity direction contributes to providing a sense of 'up' and 'down' in the interception of targets moving along the vertical (Senot *et al.* 2005; Le Séac'h *et al.* 2010; Baurès & Hecht, 2011). In these studies, participants intercepted a ball approaching from above or below in a virtual scene presented with a head-mounted stereoscopic display. Above (below) was obtained in sitting subjects (Senot *et al.* 2005) who pitched the head backward (forward) so as to look up (down) toward a virtual ceiling (floor), or in lying subjects

(Le Séac'h *et al.* 2010; Baurès & Hecht, 2011) who looked up (down) when supine (prone). The interception responses turned out to be significantly earlier for downward than upward moving targets, consistent with a naïve expectation that downward motion is faster than upward motion under gravity (Senot *et al.* 2005; Le Séac'h *et al.* 2010; Baurès & Hecht, 2011). This expectation is naïve because it violates Newtonian mechanics, in accordance with which downward and upward displacements under gravity along a given vertical path have the same duration.

A role of vestibular inputs was shown with parabolic flight experiments, where the response bias reversed sign between the above and below conditions in parallel with the sign reversal of otolith signals at the transition from the hypergravity to the hypogravity phase of flight (Senot *et al.* 2012). Also, artificial sound-evoked stimulation of the otolith receptors interferes with the anticipation of gravity effects during visually simulated self-motion in the downward direction (Indovina *et al.* 2015) and unloading of the otoliths in the weightless conditions of space flight affects up/down asymmetries in the perception of self-motion (de Saedeleer *et al.* 2013).

These previous studies demonstrated a qualitative contribution of vestibular cues about posture toward establishing a sense of up and down in the interception of targets moving along the vertical. As noted above, response timing complied with naïve rather than Newtonian physics. Therefore, it remains to be determined whether the effects of posture generalize to targets moving along oblique directions, and whether they can contribute to modelling the effects of gravity consistent with Newtonian physics, as occurs for SVV. A stringent test of the effects of head and body posture on interception timing is provided by taking advantage of Galileo's law of motion along an inclined plane (Fig. 1). A ball rolls down an incline with an acceleration a that depends on gravity g and slope β non-linearly ($a = 5/7g \sin\beta$). If the visual scene is devoid of a reference frame, the estimate of the time of ball arrival at the interception point would be difficult because visual accelerations are poorly discriminated and the descent slope cannot be determined from visual cues (La Scaleia *et al.* 2014*a*, 2015; Tresilian & Lonergan 2002). However, in line of principle, the direction of target motion relative to gravity and therefore the slope could be estimated indirectly by combining retinal and gaze signals about the direction of target motion relative to the head with vestibular and somatosensory information about the orientation of the head relative to gravity. Estimates of gravity g and slope β would then allow anticipating the time of ball arrival correctly.

To test this hypothesis, in the main experiments, we asked participants who were tilted backwards at different angles to hit a ball that was rolling in a gutter and approaching at different accelerations along the sightline. The scene was virtual, being presented in a head-mounted stereoscopic display, and lacking any reference to either vertical or horizontal directions. Participants punched the ball with actual arm movements, and were provided with

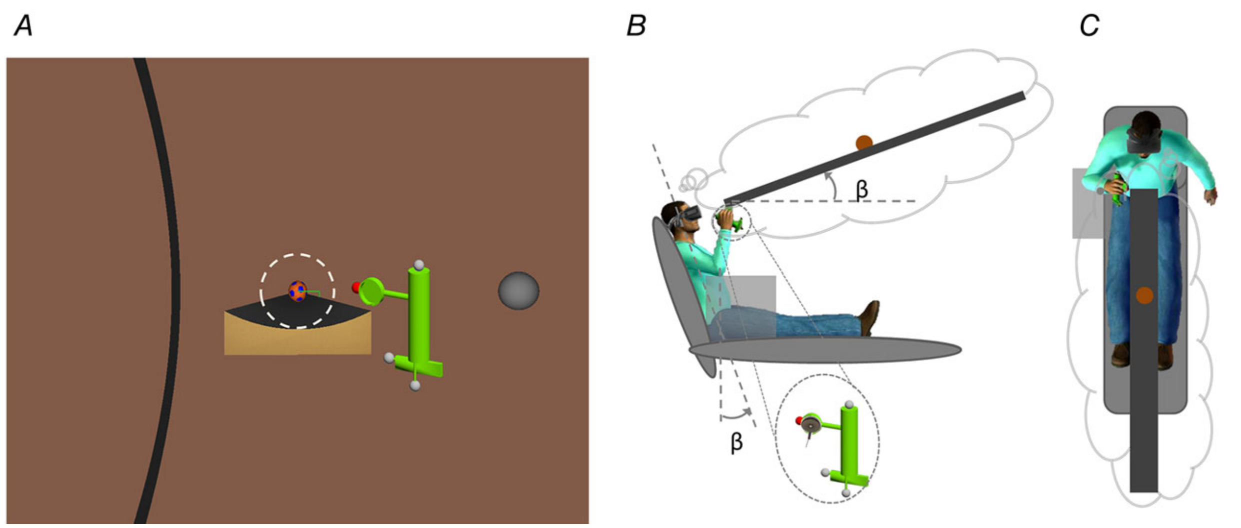

Figure 1. Visual stimuli and schematic view of the set-up
A, visual stimuli as seen by the participants. The target sphere, initially behind a lever arm, rolled forward along the gutter. Participants moved the hand-held hitter (green) from the starting position (grey sphere) attempting to hit the sphere as soon as it arrived at the end of the gutter, so as to deviate it into a circle (arc segment shown in black). The white dashed circle (not shown in the experiments) indicates the ball at the end of the gutter. *B* and *C*, schematic lateral and top view of the set-up. Participants' head and torso were tilted backwards in the sagittal plane. They wore a head-mounted display and kept the right arm on a foam box (grey) with the hand-held hitter (green). In the bubble, the gutter is depicted at the same inclination β as that of the participant, although observers always saw the same image irrespective of their tilt. [Colour figure can be viewed at wileyonlinelibrary.com]

visual and haptic feedback about successful interceptions to increase the sense of presence in the virtual environment (Zago *et al.* 2004).

We used a 2 × 2 factorial design crossing ball acceleration and subject tilt (Fig. 2). The participant and the visual display were tilted backwards in the sagittal plane by 20° or 60°, whereas ball acceleration was compatible with rolling down a slope of 20° or 60°. The visual stimuli were identical at both subject tilts. Thus, for each tilt, there was one target acceleration consistent with the physical laws of a ball rolling down a surface inclined with a corresponding tilt (coherent conditions) and another acceleration inconsistent with physics (incoherent conditions). Acceleration and starting position of the ball were randomized across trials to make ball arrival time unpredictable from trial to trial, whereas the subject's tilt was blocked to provide immersiveness during the entire experimental session.

Figure 3 illustrates schematically the predicted timing errors (TE) of the responses. If the responses were based exclusively on visual information, they should be independent of posture (dashed lines) because the visual stimuli were the same at both subject's tilts. By contrast, if the subject tilt relative to gravity contributed to estimating the direction of target motion, it would be predicted that the responses provided by more tilted participants should be timed earlier (smaller TE values, blue continuous line) than those provided by less tilted participants (red continuous line), for a given target acceleration. This is because a ball rolling down a steeper slope typically would have a higher acceleration and should induce an observer to expect an earlier arrival time. Importantly, if subject tilt contributed quantitatively to modelling the effects of gravity on target motion, it would further be predicted that, in the coherent conditions (i.e. when ball acceleration was consistent with subject tilt), the responses should be timed more accurately (TE closer to zero) than the responses in the incoherent conditions. In the latter conditions, ball accelerations are unexpected because they are inconsistent with subject tilt, and should give rise to responses timed later when the acceleration (and final speed) is higher than the expected value (red) or to responses timed earlier when the acceleration (and final speed) is lower than the expected value (blue).

A main effect of body tilt on response timing would thus be compatible with the hypothesis that head and body orientation contribute to estimating the effects of gravity on a sphere rolling along an incline. However, a main effect of body tilt might also be a result of the effects of gravity on planning and/or executing the arm movement required for interception. Indeed, previous studies showed that kinematic and dynamic features of arm movements depend on movement orientation with respect to gravity during drawing (Papaxanthis *et al.*

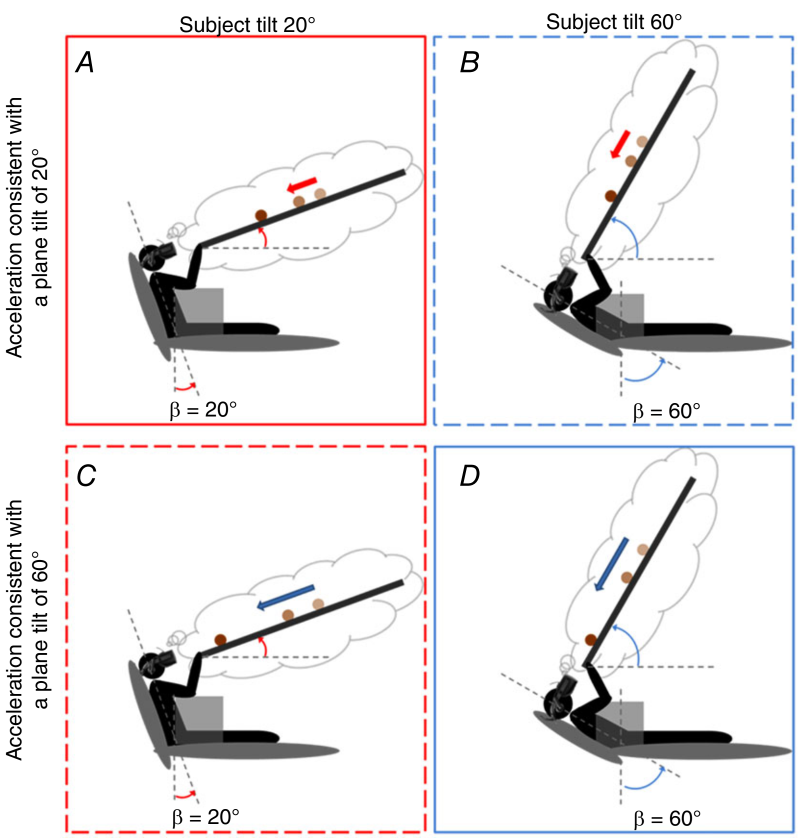

Figure 2. In a factorial design, participant's tilt (β = 20° or 60°, red and blue boxes, respectively) was crossed with ball acceleration (a = 2.397 or 6.068 m s^{-2}, red or blue arrows respectively)
A and *D* (or *B* and *C*) denote conditions coherent (or incoherent) with physics. [Colour figure can be viewed at wileyonlinelibrary.com]

1998), pointing (Gentili *et al.* 2007; Pinter *et al.* 2012; Gaveau *et al.* 2016) and grasping (Verheij *et al.* 2013). To discriminate between the two alternatives, we ran a control experiment in which participants tilted backwards by 20° or 60° (as in the main experiments) were asked to hit a static target in synchrony with the last of a predictable series of beeps and images (Hening *et al.* 1988). The hypothesis that body posture affects interception timing by contributing to the estimate of target kinematics under gravity predicts that response timing should not depend on body posture in the control experiment with a static target. By contrast, the hypothesis that body posture affects interception timing because of the effects of gravity on arm movement planning and/or execution predicts that response timing should depend on body posture also in the control experiment.

Methods

Ethical approval

All participants gave written informed consent to procedures approved by the Institutional Review Board of Santa Lucia Foundation (protocol no. CE/PROG.454), in conformity with the *Declaration of Helsinki* regarding the use of human subjects in research.

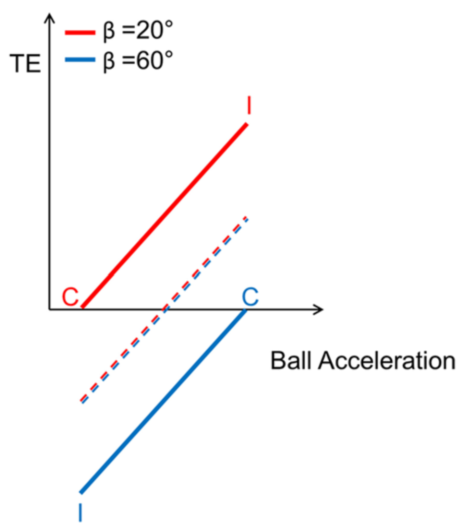

Figure 3. Theoretical TE of the interception responses at subject's tilt of 20° or 60° (red and blue, respectively)
Dashed lines, TE of responses based exclusively on visual information, which was identical at both subject tilts. Continuous lines, TE of responses predicted by the hypothesis that subject tilt relative to gravity contributes to estimating the direction of target motion. When ball acceleration is coherent with subject tilt (C), TE should be closer to zero than when acceleration is incoherent with tilt (I). [Colour figure can be viewed at wileyonlinelibrary.com]

Participants

Participants were recruited for three different sets of experiments. Interception of ball motion along a plane involved two sets of experiments: one with a between-groups design and another one with a within-subject design with respect to subject tilt (see Protocols). For the between-groups protocol, 40 participants were randomly assigned to one of two groups with 20 subjects each (11 females and nine males, mean ± SD age 25 ± 5 years, in one group; 12 females and eight males, 24 ± 4 years, in the other group). The within-subject protocol involved 8 participants (six females and two males, 23 ± 2 years). The control experiment with interception of a static target involved 20 participants (12 females and eight males, 25 ± 6 years). All participants were right-handed (as assessed by a short questionnaire based on the Edinburgh scale), had normal or corrected-to-normal vision, no history of psychiatric or neurological diseases, and were naïve to the specific purpose of the experiments.

Experimental set-up and stimuli

Participants laid on a physiotherapy bed with an adjustable backrest, so that the head and torso were tilted backwards at either 20° or 60° relative to the vertical (measured with a plumb line), whereas the lower part of the body was horizontal. They wore a head-mounted display (HMD) (Oculus Rift DK2; Oculus VR, LLC, Menlo Park, CA, USA), where a virtual scene was rendered three-dimensionally (3D) by XVR software (eXtreme Virtual Reality; VRMedia s.r.l., Pisa, Italy) using a Thinkpad W541 (Lenovo, Quarry Bay, Hong Kong) with a GeForce GTX 970 graphics card (NVIDIA, Santa Clara, CA, USA). Visual stimuli were shown stereoscopically with the HMD. Each screen of the HMD had a resolution of 960 × 1080 pixels, a refresh rate of 75 Hz, and a diagonal field of view of 100°. The time-varying position of the HMD in 3D space was recorded by means of a Vicon system equipped with 10 Bonita cameras (250 Hz sampling frequency) (Oxford Metrics, Oxford, UK). Four reflective passive spherical markers were attached at the HMD front. The 3D position of the midpoint between the eyes was derived from the position of these markers measured in real time by the Vicon system. The time-varying orientation of the HMD was measured in 3D by Oculus inertial sensors. Virtual scene update was based on the position of the midpoint between the eyes and the orientation of the head. As a result of the backrest constraint, head (HMD) tilt generally remained within ± 7° of the preset value (20° or 60°) in each experiment.

The main experiments involved the interception of ball motion along a plane. The virtual scene showed a gutter with the shape of a curved groove (length 2.85 m, width 0.2 m), with the long axis in the sagittal plane of the observer's head, along the sightline (assuming central fixation). The lower end of the gutter was at an apparent distance of 0.4 m from the eyes (Fig. 1). A target sphere (diameter 9 cm), patterned with blue pentagons (side length 1.9 cm; chromaticity co-ordinates: $x = 0.154$, $y = 0.042$ in the CIE System, measured with a J17 LumaColor photometer; Tektronix, Beaverton, OR, USA) and orange hexagons ($x = 0.567$, $y = 0.394$), was placed over the surface and was kept in the starting position by a green lever arm. Once released by the lever rotation, the ball rolled forward along the gutter (without slipping or bouncing) toward the observer's viewpoint at a constant acceleration that depended on the trial (see Protocols), remaining centred horizontally and vertically on the screen throughout the motion on the gutter. Thus, ball rotation, disparity and expansion rate provided information about its approaching motion. In particular, the time of arrival was directly related to image dilation (Fig. 4). After exiting from the gutter, the ball fell in air under virtual gravity (9.81 m s^{-2} vertical acceleration). The scene background was uniformly brown (chromaticity: $x = 0.425$, $y = 0.370$). All objects were drawn with perspective geometry. Lights were non-directional (no shadows).

In the control experiments involving the interception of a static target, the virtual scene showed a transparent square box (side 9 cm; chromaticity: $x = 0.388$, $y = 0.307$) instead of the gutter. The centre of the box was placed at an apparent distance of 0.4 m from the eyes along the sagittal axis (i.e. at the same distance as the lower end of the gutter), with the frontal face parallel to the frontal plane of the observer's head. Inside the transparent box, four different 3D objects were presented seamlessly in sequence, first a ring (external diameter 9 cm, internal diameter 4.5 cm, height 1 cm) orthogonal to the sightline (assuming central fixation), then a cone with the base on the lower face of the box (diameter 9 cm, vertical height 9 cm), then a square box (side 9 cm), and finally a target sphere (diameter 9 cm). The first three objects were blue (chromaticity: $x = 0.332$, $y = 0.265$) and were displayed for 317 ms. The target sphere was red (chromaticity: $x = 0.423$, $y = 0.344$) and was displayed for 50 ms. In synchrony with the initial display of each object, 50 ms duration beeps (58 dB, 1000 Hz) were delivered by the computer sound card (Xonar DG; Asus, Taipei, Taiwan). The inter-stimulus interval was 317 ms, so that the total duration of the audio-visual stimuli was 1001 ms (3×317 ms + 50 ms). This sequence of stationary stimuli was designed not to evoke any sensation of target motion.

In all experiments, participants held in their right hand an instrumented plastic hitter, which consisted of a cylinder (diameter 3 cm, height 12 cm) with a rod (diameter 0.6 cm, height 8 cm) perpendicular to the cylinder axis. They grasped the hitter so that the rod protruded between the index and middle finger. The tip of the rod had a red sphere, 0.75 cm radius, and a vibrotactile device (C2 Tactor™; Engineering Acoustics, Casselberry, FL, USA) was attached nearby (Fig. 1, inset). Four retroreflective markers on the hitter were tracked at 250 Hz by means of the Vicon, allowing a visual rendering of the hitter in the virtual scene consistent with its time-varying location in the real world. The Vicon, XVR and Tactor systems were networked via a user datagram protocol protocol.

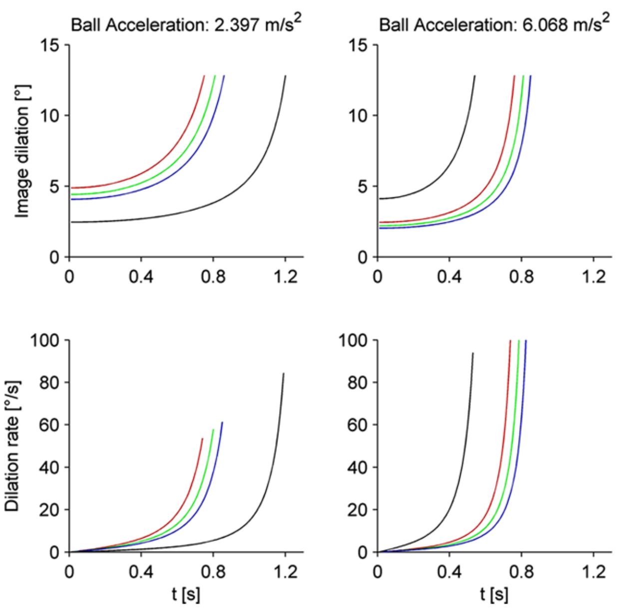

Figure 4. Changes of image dilation and dilation rate
Time course of changes of image dilation (top) and dilation rate (bottom). Red, green and blue curves correspond to target motion durations of 0.75, 0.8 and 0.85 s, respectively. Black curves correspond to durations of 0.534 and 1.193 s for ball acceleration of 6.068 and 2.397 m s^{-2}, respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

Task

In each trial of the main experiments, the ball appeared at the starting position on the gutter (see Protocols). Participants had to place the tip of the hitter (red sphere) in the virtual scene within a grey sphere (diameter 4.5 cm), located in the same plane as the lower end of the gutter, at a distance of ~30 cm to the right and ~4.5 cm above the midpoint (Fig. 1). To reach the grey sphere, participants had to place their right elbow on a (real) foam box, with the result that the adducted upper arm was flexed by ~45° at the shoulder, the forearm in the sagittal plane was flexed by ~90° at the elbow, the wrist mid-pronated, and the hand and fingers clenched around the hitter. When the tip of the hitter was inside the grey sphere, after a pseudo-random delay between 200 and 400 ms (in 50 ms steps), the ball was released by the lever arm, rolled forward and

Table 1. Parameters of ball motion

Case #	Ball acceleration (m s^{-2})	Ball motion duration (s)	Distance (m)	Speed (m s^{-1})
1	2.397	0.750	0.674	1.797
2	2.397	0.800	0.767	1.917
3	2.397	0.850	0.866	2.037
4	2.397	1.193	1.707	2.860
5	6.068	0.750	1.707	4.551
6	6.068	0.800	1.942	4.855
7	6.068	0.850	2.192	5.158
8	6.068	0.534	0.866	3.242

Ball acceleration, motion duration and distance travelled were from the starting position until the end of the gutter. Speed was at the end of the gutter. Case #4 and case #8 were control conditions to match starting positions across target accelerations. Case #4 (#8) and case #5 (#3) had the same starting position but different ball acceleration.

disappeared immediately after reaching the end of the gutter. Participants were asked to hit the ball as soon as it arrived at the end of the gutter with the tip of the hitter, so as to deviate the ball into a virtual circle (diameter 2 m), parallel to the direction of ball motion, 60 cm to the left of the midpoint of the end of the gutter. This required participants to hit the ball with a movement quasi-orthogonal to the direction of ball motion.

The XVR routine computed (at 75 Hz) the instantaneous distance between the tip of the hitter and the centre of the ball. The radius of the ball was subtracted from this distance and the resulting metric was used to indicate whether or not the ball was intercepted. Thus, if this metric became null or negative, the ball was considered intercepted and participants received visual and haptic feedback about the success. For visual feedback, the ball was shown deviated to the left for 1 s. For haptic feedback, the hitter (Tactor) vibrated for 50 ms. If the interception was missed (metric >0), neither visual, nor haptic feedback were given.

In the control experiments, participants were asked to hit the static target sphere (the last object of the sequence) with the tip of the hitter, in synchrony with the last of the predictable series of beeps and images. Starting position of the arm and general procedures were similar to those in the main experiments, although, here, no performance feedback was provided to the participants to better ascertain the influence of gravity on arm movements.

Protocols

In the main experiments, we manipulated the acceleration and duration of ball motion independently of participant's tilt (Table 1). In a 2 × 2 factorial design, the participant's tilt in the sagittal plane was set at $\beta = 20°$ or $60°$, whereas ball acceleration a was set at 2.397 or 6.068 m s^{-2}, corresponding to $a = \frac{5}{7}\,9.81 \sin\beta$ with $\beta = 20°$ or $60°$, respectively (Fig. 2). Therefore, there were two conditions coherent with physics: a participant tilted by 20° watching a ball accelerating at 2.397 m s^{-2}, and a participant tilted by 60° watching a ball accelerating at 6.068 m s^{-2}. The two conditions incoherent with physics, instead, involved a participant tilted by 20° watching a ball accelerating at 6.068 m s^{-2}, and a participant tilted by 60° watching a ball accelerating at 2.397 m s^{-2}. Subject tilt was blocked, whereas ball acceleration was randomized across trials.

We ran two different experimental designs with respect to subject tilt: between-groups and within-subject. The between-groups protocol was designed to confirm the effect of treatment (subject tilt) without the potential contamination of carry-over effects between sessions (related to potential long-term effects of practice with the task). Accordingly, we randomly assigned participants to one of two groups: the first group was exposed to 20° tilt, whereas the second group was exposed to 60° tilt. The within-subject protocol was designed to confirm the effect of tilt within individuals. Accordingly, all participants were exposed to both 20° and 60° tilts, tested in two separate sessions (counterbalanced across subjects), 15 days apart.

In each experimental session at both subject tilts, we set the starting position of the ball at one of six different values, resulting in five different values of ball motion duration from the starting position to the lower end of the gutter (Table 1). Three values of duration (0.75, 0.80 and 0.85 s) were common to both accelerations, whereas two other durations (0.534 and 1.193 s) were added to match two starting positions of the ball across the two accelerations. Overall, the combination of the manipulated variables resulted in eight different experimental conditions, denoted as cases hereafter. Case #8 at the higher acceleration matched the starting position (0.866 m) of case #3 at the lower acceleration, whereas case #5 at the higher acceleration matched the starting position (1.707 m) of case #4 at the lower acceleration. Overall, there were four motion durations (each associated with a given starting position) for each acceleration. In each session, targets were presented in consecutive sequences in which each case (two accelerations × four motion durations) was presented in random order, different from one sequence to the next. There were 15 such sequences (repetitions), resulting in a total of 120 trials.

The control experiments involving the interception of the static target followed a within-subject protocol. Accordingly, participants were tested in two blocked sessions (20° and 60° tilts, counterbalanced across subjects). We presented the same audio-visual stimuli for 100 repetitions at each subject tilt, so as to make the sequence fully predictable.

Before all of the experiments, participants received general instructions and familiarized with the set-up.

Participants were allowed to pause any time they wished during an experimental session, which lasted ~35 min in the main experiments and 25 min in the control experiments.

Data analysis

We excluded a few trials (less than 1% of all trials) from the analysis as a result of the presence of artefacts or lack of subject's attention (as marked in the experiment notebook).

The 3D co-ordinates (x, y, z) of the tip of the hitter recorded by Vicon were numerically low-pass filtered (bidirectional, 20 Hz cut-off, first-order Butterworth filter). These data, as well as the positional data of the ball centre, were interpolated at 1 kHz using a cubic spline interpolation.

Success rate. For each trial, we computed the metric defined above (distance between the tip of the hitter and the centre of the sphere minus the sphere radius). We considered a hit when this metric became null or negative. The success rate was defined as the proportion of successful trials (hits) relative to the total number of trials for each experimental condition of each participant. Thus success rate was cumulated over all repetitions of each condition.

Analysis of timing and spatial errors. For each trial, we computed the hitter intersection point as the position where the trajectory of the hitter tip intercepted, for the first time, the sagittal plane tangent to the ball surface facing the hitter (i.e. the right side of the ball). The ball intersection point was the position of the ball when its surface first reached the minimum distance relative to the hitter intersection point (La Scaleia *et al.* 2015). Hitter and ball intersection times were defined as the time samples when the corresponding intersection points were reached. We then computed the timing error (TE) as the difference between the hitter intersection time and the ball intersection time. Accordingly, a positive (negative) value of TE corresponded to a response later (earlier) than that theoretically expected if the hitter tip arrived at the intersection time at the same time as the ball. We computed the spatial error as the Euclidean distance between the hitter intersection point and the ball intersection point minus the ball radius.

For the control experiments, we computed the arrival time of the hitter as the time when it first reached the minimum distance relative to the surface of the target sphere. TE was defined as the difference between the hitter arrival time and the time when the target first appeared.

Analysis of hand kinematics. For both the main and control experiments, we considered the time-varying position of the tip of the hitter, which was differentiated to compute the tangential velocity as $v_T = \sqrt{(\dot{x}^2 + \dot{y}^2 + \dot{z}^2)}$. Movement onset was computed according to a algorithm described previously (La Scaleia *et al.* 2015). First, we normalized the tangential velocity to the maximum: $v = v_T/v_{max}$; then, going back from the sample at which $v = 1$, we defined the first sample for which $v < 0.08$ is the onset time. Movement duration was defined as the interval between the onset time of hand movement and the arrival time at the hitter intersection point.

Statistical analysis

The main statistical analyses involved the trials at the three motion durations (0.75, 0.80 and 0.85 s) that were common to both accelerations. The trials at the two other durations (0.534 and 1.193 s) were included in a separate analysis, as a control for the effect of starting position.

Repeated measures (RM)-ANOVA was conducted on continuous outcome variables (i.e. timing error, duration and maximum speed of hand movements); instead, for the binary response (i.e. success rate), we used the generalized linear mixed model (GLMM) (Jaeger, 2008).

RM-ANOVA. Results are given as the mean ± SD, and uncertainty is reported using the 95% confidence interval (CI). Statistical differences between conditions were assessed using RM-ANOVA with ball acceleration, motion duration and repetition as within-subjects factors, and subject tilt as a between-subjects factor for the between-groups protocol. For the within-subject protocol, subject tilt was a within-subjects factor (in addition to ball acceleration, motion duration and repetition), whereas session order was the between-subjects factor. For the control experiments, RM-ANOVA had subject tilt and repetition as within-subjects factors, and session order as between-subjects factor. The degrees of freedom for the within-subjects comparisons were corrected (Greenhouse-Geisser) in case of deviance from sphericity. Whenever RM-ANOVA detected a significant difference ($\alpha = 0.05$), we performed post hoc Bonferroni corrections for multiple comparisons. Effect size was assessed as partial eta-squared (η_p^2).

GLMM. Success rate is reported as quartiles (median and interquartile range, IQR). We assessed how success rate depended on the experimental conditions by means of the GLMM (Moscatelli *et al.* 2012), which separates the overall variability into a fixed component and a random component, and assumes that the response variable has a binomial distribution. The fixed component estimates the experimental effects, whereas the random component estimates the heterogeneity between participants. We considered the following model:

$$logit[P(Y_{ij} = 1)] = \delta_0 + u_{j0} + (\delta_1 + u_{j1})A + \delta_2 S + \delta_3 T \times A + \delta_4 A \times S$$

In this model, the logit transform of the probability that participant j hit the ball in trial *i* is equal to a linear combination of fixed and random effect predictors. Specifically, A is the dummy variable for the acceleration ($A = 0$ or 1 for 2.397 or 6.068 m s^{-2}, respectively), S is the dummy variable for the subject tilt ($S = 0$ or 1 for 20° and 60°, respectively), $T \times A$ is the interaction between ball motion duration and acceleration, and $A \times S$ is the interaction between ball acceleration and subject tilt. δ_k are the fixed effects coefficients, u_{jk} are the random effects coefficients. For the within-subjects protocol, the model also included the dummy variable ***O*** for the experimental session order ($O = 0$ or 1 for first session or second session, respectively). The significance of fixed effect parameters was assessed by means of Wald statistics. We selected each GLMM model from a pool of nested models based on the Bayesian information criterion (Schwarz 1978).

We performed data preprocessing with custom software in MATLAB (MathWorks, Natick, MA, USA) and statistical analyses with MATLAB, SPSS (IBM Corp., Armonk, NY, USA) and the R software environment (R Development Core Team, 2011; R Foundation for Statistical Computing, Vienna, Austria) with the lme4, lmerTest and MERpsychophysics packages.

Results

Main experiments: between-groups protocol

In this experimental series, two groups of participants were asked to intercept ball motion along a plane: one group at 20° body tilt, and the other one at 60° tilt.

Success rate. The success rate computed over all repetitions was quite variable, although it was comparable in the two groups of participants, irrespective of their tilt (20° or 60°) (Fig. 5*A*). Instead, success rate was higher in the coherent conditions (when ball acceleration was physically compatible with subject tilt) than in the incoherent conditions (when acceleration was incompatible with tilt) (Fig. 5*B*).

To assess the dependence of success rate on the experimental variables in a statistically robust manner, we used the GLMM (Table 2). This analysis showed that the success rate did not depend significantly on group (or equivalently subject tilt). Instead, the success rate depended significantly on ball acceleration, being greater with the lower (2.397 m s^{-2}) acceleration than with the higher (6.068 m s^{-2}) acceleration (median = 60%, IQR = 27 and median = 13%, IQR = 27 for the two ball accelerations, respectively, two groups × three motion durations × 20 subjects, $n = 120$). It also depended significantly on motion duration, although only for the higher acceleration when success rate was larger for the higher motion duration (0.850 s). In addition, we found a statistically significant interaction between acceleration and subject tilt, with the success rate being higher in the coherent conditions than in the incoherent conditions (median success rate = 41%, IQR = 50 and 27% IQR = 51, respectively, for the coherent and incoherent conditions).

Response timing. Table 3 shows that, according to RM-ANOVA, timing errors TE depended significantly on several experimental variables. In particular, the responses were timed significantly earlier for the lower acceleration than the higher acceleration (by 49 ± 26 ms, mean ± SD, $n = 120$, pooling the results across motion durations

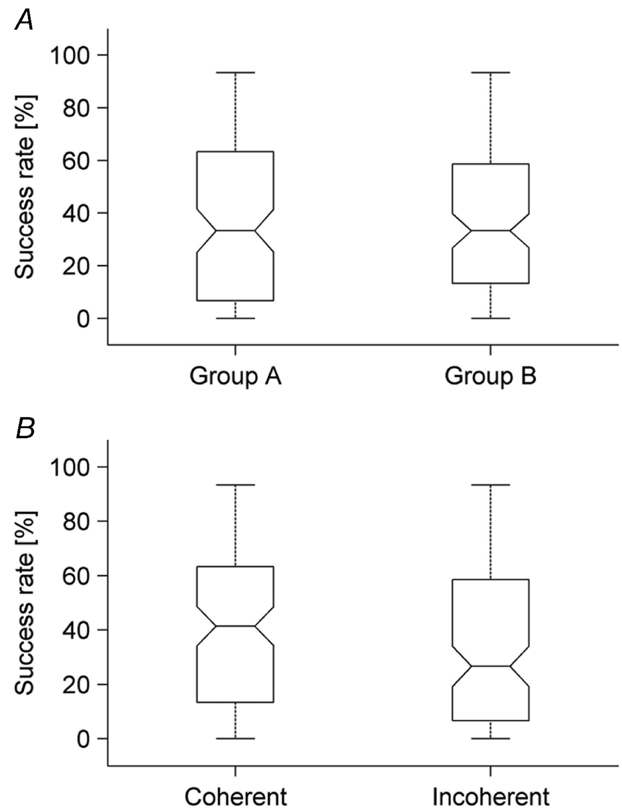

Figure 5. Interception success rate in the between-groups protocol
A, results plotted separately for each group of participants, group A and B tilted by 20° and 60°, respectively (20 participants × three motion durations × two ball accelerations in each group). *B*, results plotted separately for the conditions coherent or incoherent with physics (40 participants × three motion durations in each plot). In the box-and-whisker plots, the bottom and top of the boxes correspond to the lower and upper quartile, respectively, and define the IQR. The notch displays the 95% CI of the median and the whiskers extend to the lowest and highest data points.

Table 2. Success rate for the between-groups protocol

	Intercept	Acceleration	Subject tilt	Acceleration (2.397 m s^{-2}): motion duration	Acceleration (6.068 m s^{-2}): motion duration	Acceleration: subject tilt
Coefficient	0.418	–7.095	-0.268	0.061	5.133	1.102
P value	0.679	3.490×10^{-5}***	0.311	0.961	0.002**	0.005**

All coefficients of the GLMM for the fixed factors in the model used to fit the score reached by participants and the relative *P* value values are shown (subject tilt = 20°, ball acceleration = 2.397 m s^{-2} are the baseline).
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

Table 3. Timing error (matched ball motion durations) for the between-groups protocol

Factors	*F* (d.f.)	*P* value	η_p^2
Acceleration (*A*)	162.700 (1,38)	0.000***	0.811
Motion duration (*T*)	1.186 (1.977,75.107)	0.311	0.030
Repetition (*R*)	5.365 (4.145,157.499)	0.000***	0.124
Subject tilt (*S*)	5.186 (1,38)	0.028*	0.120
$A \times S$	0.136 (1,38)	0.714	0.004
$T \times S$	0.242 (1.977,75.107)	0.783	0.006
$R \times S$	1.537 (4.145,157.499)	0.192	0.039
$A \times T$	23.541 (1.906,72.444)	0.000***	0.383
$A \times T \times S$	4.234 (1.906,72.444)	0.020*	0.100
$A \times R$	19.700 (7.615,289.382)	0.000***	0.341
$A \times R \times S$	1.253 (7.615,289.382)	0.270	0.032
$T \times R$	8.809 (14.688,558.143)	0.000***	0.188
$T \times R \times S$	1.580 (14.688,558.143)	0.076	0.040
$A \times T \times R$	5.484 (14.405,547.386)	0.000***	0.126
$A \times T \times R \times S$	1.238 (14.405,547.386)	0.241	0.032

RM-ANOVA on TE considering two accelerations (*A*) × three motion durations (*T*) × 15 repetitions (*R*) as within-subjects factors and subject tilt (*S*) as a between-subjects factor.
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

and participants). The timing errors were not stationary during an experiment but depended significantly on repetitions, tending to decrease with practice. Figure 6 plots TE values averaged over participants, considering the three matched motion durations in each repetition (see Methods). It can be seen that the effect of practice was different in the coherent conditions *vs.* the incoherent conditions because the mean TE converged toward zero for both subject tilts in the former case, whereas the mean TE remained conspicuous for both tilts in the latter case.

Figure 7 compares the mean TE computed over the first four repetitions with the mean TE computed over the last four repetitions. RM-ANOVA (two accelerations × three motion durations as within-subjects factors, two subject tilts as a between-subjects factor) over the first four repetitions showed that TE at the beginning of the experiment was independent of tilt (Table 4). Moreover, the mean TE values over these repetitions were significantly different from zero for both ball accelerations and both subject tilts (paired *t* tests, $n = 20$ participants, $P < 0.05$, corrected for multiple comparisons). By contrast, RM-ANOVA carried over the last four repetitions showed that TE at the end of the experiment depended significantly on tilt (Table 4), the responses being timed generally earlier when participants were tilted by 60° than when they were tilted by 20°. Moreover, the mean TE values over these repetitions were significantly different from zero in the incoherent conditions ($P < 0.002$, corrected for multiple comparisons), although they did not differ significantly from zero in the coherent conditions ($P < 0.08$, uncorrected for multiple comparisons). Very similar results were obtained by considering the first three repetitions or the last three repetitions, instead of four repetitions.

Considering individual results, we found that the mean of the absolute values of TE over the last four repetitions was smaller (i.e. smaller timing errors) in the coherent conditions than the corresponding value in the incoherent conditions in 13 of 20 participants tilted by 20° and 15 of 20 participants tilted by 60°.

Matching the initial ball positions. To match the three durations (0.75, 0.80 and 0.85 s) of ball motion between the two conditions of lower and higher acceleration, the corresponding initial positions of the ball and the distance travelled prior to reaching the interception point necessarily differed. However, the protocol also included two cases (durations of 0.534 and 1.193 s), randomly assorted with the other ones, which matched two starting positions across the two accelerations (see Methods). As a control for the effect of starting position, we separately analysed the trials of these two cases along with those at the corresponding starting position for each acceleration (i.e. cases #3 and #8, cases #4 and #5) (Table 1). Table 5 shows the details of RM-ANOVA results. Figure 8 plots mean TE values for these cases as a function of repetition. These plots indicate a trend with practice roughly similar to that shown in Fig. 6, with a better convergence toward zero error for the coherent conditions than the incoherent conditions. Furthermore, considering these experimental conditions, RM-ANOVA computed over the first/last four repetitions confirmed the previous results, in particular showing that TE at the beginning of the experiment was independent of tilt, whereas at the end of the experiment it depended significantly on tilt, the responses being timed generally earlier when participants were tilted by 60° than when they were tilted by 20° (Table 6), similar to the results reported in Table 4.

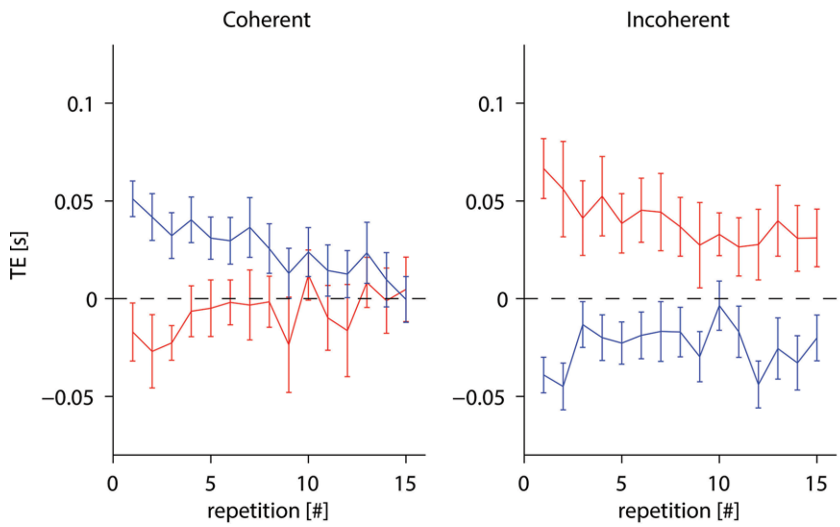

Figure 6. Effect of practice on timing errors in the between-groups protocol
Mean (± 95% confidence interval over all 20 participants) plotted as a function of repetition separately for the coherent conditions (left) and incoherent conditions (right). Results for subjects tilted by 20° and 60° are shown in red and blue, respectively. Only trials with the three motion durations matched across target accelerations are included. [Colour figure can be viewed at wileyonlinelibrary.com]

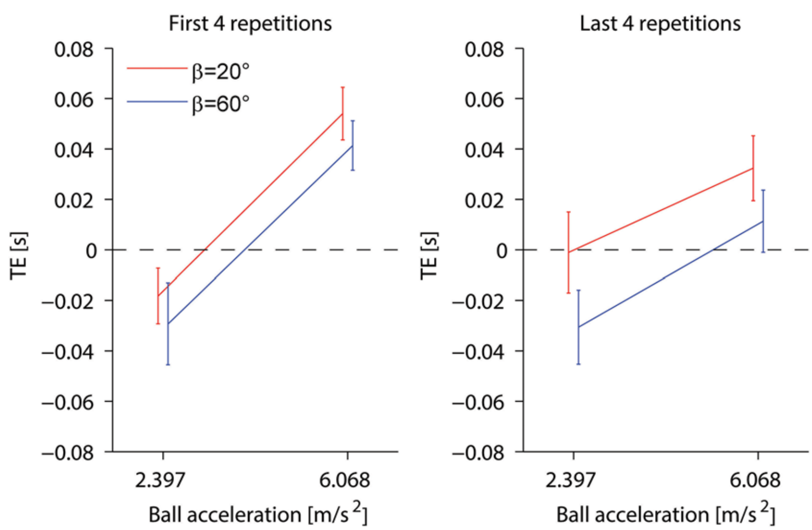

Figure 7. Comparison of TE repetitions
Comparison of TE averaged over the first four repetitions (left) with TE averaged over the last four repetitions (right) in the between-groups protocol. Mean TE (± 95% confidence interval over all 20 participants) for subjects tilted by 20° and 60° are shown in red and blue, respectively. Only trials with the three motion durations matched across target accelerations are included. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 4. Timing error on first and last four repetitions for the between-groups protocol

Factors		Acceleration (*A*)	Motion duration (*T*)	Subject tilt (*S*)	$A \times S$	$A \times T$	$T \times S$	$A \times T \times S$
First four repetitions	*F* (d.f.)	230.323 (1,38)	3.550 (1.98, *75.20*)	2.809 (1,38)	0.031 (1,38)	11.012 (1.95, 73.96)	2.961 (1.98, *75.20*)	3.947 (1.95, 73.96)
	P value	0.000***	0.034*	0.102	0.861	0.000***	0.058	0.024*
	η_p^2	0.858	0.085	0.069	0.001	0.225	0.072	0.094
Last four repetitions	*F*	86.524 (1,38)	0.276 (1.88, *71.44*)	7.986 (1,38)	1.096 (1,38)	5.197 (1.78, 67.76)	1.664 (1.88, *71.44*)	0.831 (1.78, 67.76)
	P value	0.000***	0.746	0.007**	0.302	0.01*	0.198	0.428
	η_p^2	0.695	0.007	0.174	0.028	0.12	0.042	0.021

RM-ANOVA on TE on first or last four repetitions considering two accelerations (*A*) × three motion durations (*T*) as within-subjects factors and subject tilt (*S*) as a between-subjects factor.
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

Table 5. Timing error (matched starting positions) for the between-groups protocol

Factors	*F* (d.f.)	*P* value	η_p^2
Acceleration (*A*)	410.623 (1,38)	0.000***	0.915
Starting position (*SP*)	12.309 (1,38)	0.001**	0.245
Repetition (*R*)	12.148 (5.28,200.74)	0.000***	0.242
Subject tilt (*S*)	3.079 (1,38)	0.087	0.075
$A \times S$	1.522 (1,38)	0.225	0.039
$SP \times S$	1.694 (1,38)	0.201	0.043
$R \times S$	1.107 (5.28,200.74)	0.359	0.028
$A \times SP$	0.084 (1,38)	0.774	0.002
$A \times SP \times S$	0.829 (1,38)	0.368	0.021
$A \times R$	14.804 (8.03,305.03)	0.000***	0.280
$A \times R \times S$	0.939 (8.03,305.03)	0.485	0.024
$SP \times R$	9.885 (8.41,319.76)	0.000***	0.206
$SP \times R \times S$	0.803 (8.41,319.76)	0.606	0.021
$A \times SP \times R$	9.729 (8.98,341.11)	0.000***	0.204
$A \times SP \times R \times S$	0.974 (8.98,341.11)	0.461	0.025

RM-ANOVA on TE considering two accelerations (*A*) × two starting positions (*SP*) × 15 repetitions (*R*) as within-subjects factors and subject tilt (*S*) as a between-subjects factor.
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

Characteristics of hand movements. All participants hit the virtual ball with very small spatial errors [median = 0.09 cm, 0–0.46 cm (25th to 75th percentile), $n = 3575$, pooling the results across all repetitions, motion durations and participants, after exclusion of rejected trials]. Mean ± SD duration of hand movements was 0.157 ± 0.09 s ($n = 1785$) and 0.172 ± 0.09 s ($n = 1790$) for participants tilted by 20° and 60°, respectively. Mean ± SD maximum speed was 4.41 ± 1.41 m s^{-1} and 4.0 ± 1.3 m s^{-1} for participants tilted by 20° and 60°, respectively. Neither movement duration, nor maximum speed differed significantly between the two groups of participants (Table 7). Instead, these movement parameters depended significantly on ball acceleration. On average, hand movements aimed at balls descending with the higher acceleration were faster and lasted less than those aimed at balls with lower acceleration. However, these movement parameters changed with practice, tending to converge to similar values toward the end of the experiment, irrespective of ball acceleration (Fig. 9).

Summary. The results with the between-groups protocol showed that the interception responses at the end of the experiments conformed to the theoretical predictions depicted in Fig. 3, being timed more accurately around ball

Table 6. Timing error on first and last four repetitions (matched starting positions) for the between-groups protocol

Factors		Acceleration (*A*)	Starting position (*SP*)	Subject tilt (*S*)	*A* × *S*	*A* × *SP*	*SP* × *S*	*A* × *SP* × *S*
First four repetitions	*F* (d.f.)	456.458 (1,38)	11.166 (1,38)	1.356 (1,38)	0.875 (1,38)	4.930 (1,38)	0.948 (1,38)	0.514 (1,38)
	P value	0.000***	0.002**	0.251	0.355	0.032*	0.337	0.478
	η_p^2	0.923	0.227	0.034	0.023	0.115	0.024	0.013
Last four repetitions	*F*	161.221 (1,38)	10.157 (1,38)	5.620 (1,38)	1.803 (1,38)	1.613 (1,38)	0.483 (1,38)	3.414 (1,38)
	P value	0.000***	0.003**	0.023*	0.187	0.212	0.491	0.072
	η_p^2	0.809	0.211	0.129	0.045	0.041	0.013	0.082

RM-ANOVA on TE on first or last four repetitions considering two accelerations (*A*) × two starting positions (*SP*) as within-subjects factors and subject tilt (*S*) as a between-subjects factor.
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

arrival in the coherent conditions than in the incoherent conditions.

Several observations further indicate that the effects of coherence on performance were a genuine result of participant's tilt rather than a by-product of group membership. Thus, overall success rate, duration and maximum speed of hand movements, as well as the timing errors over the first few repetitions were comparable between the two groups. Nevertheless, to further corroborate the conclusions, we also carried out a within-subject protocol.

Main experiments: within-subject protocol

In this experimental series, all participants were exposed to both 20° and 60° tilts, tested in two separate sessions (counterbalanced across subjects) 15 days apart. Table 8 reports the results of GLMM on the success rate. As in the case of the between-groups experiments, also the within-subjects experiments revealed a significant effect of ball acceleration, the success rate being higher with the lower ball acceleration than with the higher ball acceleration. We also observed a significant effect of session order, success rate in the second session being higher than in the first one (median = 28%, IQR = 21 and median = 39%, IQR = 25 for the first and second session, respectively, three motion durations × eight subjects, $n = 24$). This global improvement of the interception performance was indicative of a long-term learning process carrying over from the first session onto the second one, and precluded in-depth analyses of the time course of changes in the interception responses, as shown in Fig. 6 for the between-groups experiments.

Figure 10 compares the mean TE computed at the start of each session (first four repetitions of session 1 and first four repetitions of session 2) with the mean TE computed at the end of each session (last four repetitions of session 1 and last four repetitions of session 2). RM-ANOVA (two subject tilts × two accelerations × three motion durations as within-subjects factors, two session orders

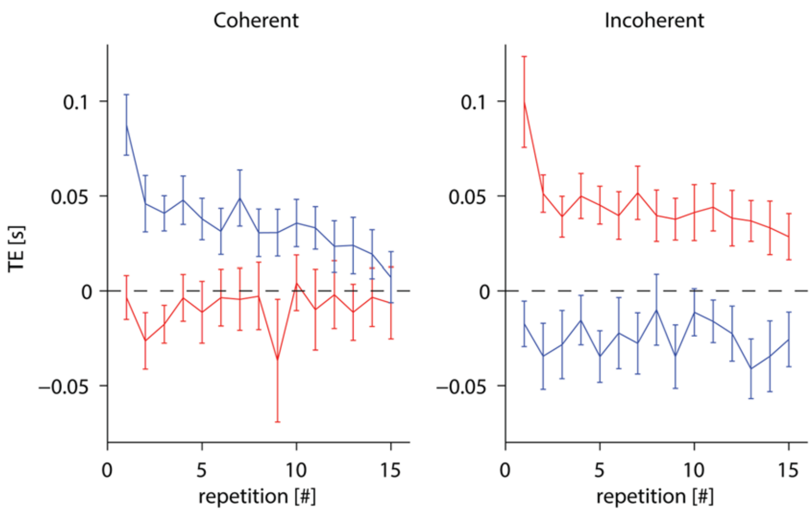

Figure 8. Effect of practice on timing errors
Effect of practice on timing errors, in the between-groups protocol, in the trials with matched initial position of the target across accelerations (cases #3 and #8, cases #4 and #5) (Table 1) (same format as in Fig. 6). [Colour figure can be viewed at wileyonlinelibrary.com]

Table 7. Characteristics of hand movements for the between-groups protocol

	Motion duration			Maximum speed		
Factors	F (d.f.)	P value	η_p^2	F (d.f.)	P value	η_p^2
Acceleration (A)	85.38 (1,38)	0.000***	0.692	78.31 (1,38)	0.000***	0.673
Motion duration (T)	6.87 (1.93,73.24)	0.002**	0.153	1.55 (1.99,75.46)	0.219	0.039
Repetition (R)	2.53 (6.20,235.63)	0.020*	0.063	3.42 (4.16,157.97)	0.009**	0.082
Subject tilt (S)	0.91 (1,38)	0.345	0.023	1.49 (1,38)	0.230	0.038
$A \times S$	0.05 (1,38)	0.827	0.001	3.06 (1,38)	0.088	0.075
$T \times S$	0.76 (1.93,73.24)	0.467	0.020	0.58 (1.99,75.46)	0.564	0.015
$R \times S$	1.04 (6.20,235.63)	0.397	0.027	1.18 (4.16,157.97)	0.322	0.030
$A \times T$	12.13 (1.92,72.83)	0.000***	0.242	5.36 (1.90,72.19)	0.008**	0.124
$A \times T \times S$	0.38 (1.92,72.83)	0.678	0.010	1.82 (1.90,72.19)	0.171	0.046
$A \times R$	2.31 (8.55,324.91)	0.018*	0.057	10.94 (8.96,340.45)	0.000***	0.223
$A \times R \times S$	0.46 (8.55,324.91)	0.894	0.012	1.25 (8.96,340.45)	0.261	0.032
$T \times R$	1.67 (12.16,462.19)	0.070	0.042	2.99 (14.40,547.24)	0.000***	0.073
$T \times R \times S$	0.80 (12.16,462.19)	0.651	0.021	1.24 (14.40,547.24)	0.235	0.032
$A \times T \times R$	1.38 (12.00,453.08)	0.172	0.035	1.14 (13.87,526.90)	0.323	0.029
$A \times T \times R \times S$	1.25 (12.00,453.08)	0.243	0.032	1.32 (13.87,526.90)	0.191	0.034

RM-ANOVA on characteristics of hand movements (motion duration and maximum speed) considering two accelerations (A) × three motion durations (T) × 15 repetitions (R) as within-subjects factors and subject tilt (S) as a between-subjects factor.
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

as between-subjects factor) on the first four repetitions showed that TE was independent of tilt (Table 9), whereas the same statistical analysis carried over the last four repetitions of each session showed that TE at the end of the experiment depended significantly on tilt (Table 9). In particular, we found that, on average, the responses at the end of the experiment were timed later relative to ball arrival when participants were less tilted (20°) than when they were more tilted (60°), when ball acceleration was higher (6.068 m s^{-2}) than when it was lower (2.397 m s^{-2}) and in session order 20° to 60° than session order 60° to 20°.

Figure 10 shows that, on average, the interception responses at the end of the experimental sessions

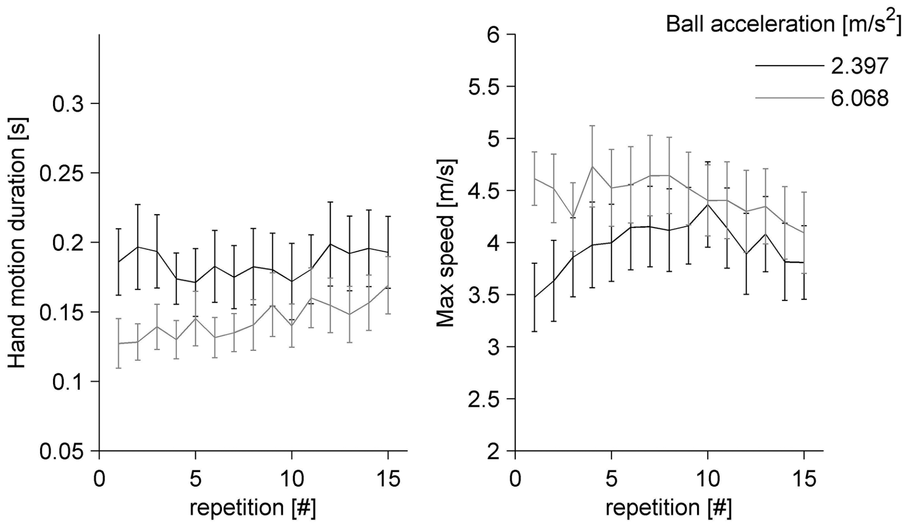

Figure 9. Effect of practice on hand movement
Effect of practice on hand movement duration (left) and maximum speed (right) in the between-groups protocol. Mean TE (± 95% confidence interval over all 40 participants) for target acceleration of 2.397 and 6.068 m s^{-2} are shown in black and grey, respectively. Only trials with the three motion durations matched across target accelerations are included.

Table 8. Success rate for the within-subject protocol

	Intercept	Acceleration	Subject tilt	Motion duration	Experimental session order
Coefficient	1.344	–2.640	–0.254	–1.473	0.570
P value	0.339	1.350×10^{-6}***	0.065	0.372	3.380×10^{-5}***

All coefficients of the GLMM for the fixed factors in the model used to fit the score reached by participants and the relative *P* value are shown [subject tilt = 20°, ball acceleration = 2.397 m s^{-2} and Session Order 'first (I)' are the baseline].

conformed to the theoretical predictions of Fig. 3 also in the within-subjects protocol, being timed more accurately around ball arrival in the coherent conditions than in the incoherent conditions, although the effect was not statistically significant for the 60° tilt.

Considering individual results, we found that the mean of the absolute values of TE over the last four repetitions was smaller (i.e. smaller timing errors) in the coherent conditions than the corresponding value in the incoherent conditions in seven of eight participants.

Control experiments

Here, participants were asked to hit a static target in synchrony with the last of a predictable series of beeps and images. They were exposed to both 20° and 60° tilts, tested in two separate sessions, in a counterbalanced order.

Success rate. The GLMM analysis, using subject tilt and session order as factors, showed that success rate did not depend significantly on any factors or interaction ($P > 0.27$). In particular, median success rate was 20% (IQR = 10) and 19% (IQR = 14), respectively, for the subject tilted by 20° or 60°.

Response timing. Figure 11*B* compares the mean timing errors obtained with the two body tilts. TE did not depend significantly on subject tilt ($F_{1,18} = 0.23$, $P = 0.6$, $\eta_p^2 = 0.01$). In particular, the mean TE was 14 ms [CI = (–12 to 41 ms), $n = 20$ subjects] and 18 ms [CI = (–17 to 52 ms), $n = 20$ subjects] for a subject tilt of 20° or 60°, respectively. Both mean values fall within the theoretical margin of error corresponding to the display interval of the target sphere (0–50 ms). Figure 11*C* plots mean TE values for the two body tilts as a function of repetition. Although a slight trend with practice is noted, this was similar in the two tilt conditions. Moreover, the effect of repetition on TE was not statistically significant ($F_{11.85,213.30} = 1.517$, $P = 0.12$, $\eta_p^2 = 0.08$), nor did TE depend significantly on session order ($F_{1,18} = 0.254$, $P = 0.6$, $\eta_p^2 = 0.01$) or any interactions ($P > 0.05$).

We also evaluated the TE at the beginning or at the end of each session, considering the first or the last four repetitions of session 1 and the first or the last four repetitions of session 2. RM-ANOVA (subject tilt as within-subjects factor and session order as between-subjects factor) showed that TE over the first four repetitions did not depend significantly on subject tilt ($F_{1,18} = 0.23$, $P = 0.64$, $\eta_p^2 = 0.01$), session order

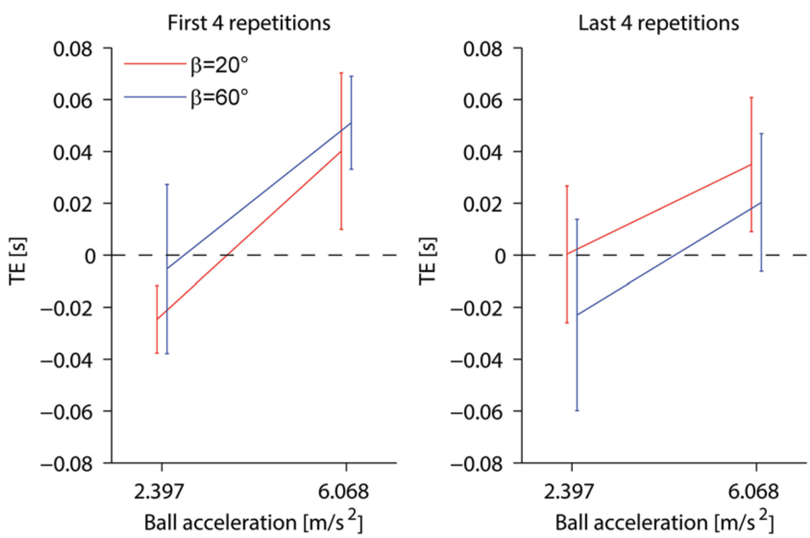

Figure 10. Timing errors in the within-subject protocol
Mean TE over the first four repetitions (left) with TE averaged over the last four repetitions (right) (± 95% confidence interval over all eight participants) for blocks with the subjects tilted by 20° and 60° are shown in red and blue, respectively. Only the trials with the three motion durations matched across target accelerations are included. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 9. Timing error on first and last 4 repetitions for the within-subject protocol

	First four repetitions			Last four repetitions		
Factors	*F* (d.f.)	*P* value	η_p^2	*F* (d.f.)	*P* value	η_p^2
Subject tilt (*S*)	1.469 (1,6)	0.271	0.197	8.573 (1,6)	0.026*	0.588
Acceleration (*A*)	26.960 (1,6)	0.002**	0.818	23.090 (1,6)	0.003**	0.794
Motion duration (*T*)	0.891 (1.521,9.124)	0.150	0.136	0.100 (1.75,10.51)	0.883	0.016
Session block order (*B*)	3.662 (1,6)	0.104	0.379	6.673 (1,6)	0.042*	0.527
$S \times B$	0.064 (1,6)	0.809	0.011	0.937 (1,6)	0.371	0.135
$A \times B$	0.238 (1,6)	0.643	0.038	0.001 (1,6)	0.971	0.000
$T \times B$	0.557 (1.521,9.124)	0.545	0.085	1.145 (1.75,10.51)	0.347	0.160
$S \times A$	1.220 (1,6)	0.312	0.169	2.175 (1,6)	0.191	0.266
$S \times A \times B$	19.941 (1,6)	0.004**	0.769	3.349 (1,6)	0.117	0.358
$S \times T$	1.516 (1.97,11.85)	0.259	0.202	0.043 (1.26,7.58)	0.891	0.007
$S \times T \times B$	1.214 (1.97,11.85)	0.331	0.168	2.064 (1.26,7.58)	0.193	0.256
$A \times T$	1.866 (1.23,10.37)	0.216	0.237	3.441 (1.85,11.13)	0.071	0.364
$A \times T \times B$	0.079 (1.23,10.37)	0.836	0.013	1.732 (1.85,11.13)	0.222	0.224
$S \times A \times T$	0.189 (1.73, 10.37)	0.801	0.031	0.095 (1.37,8.25)	0.840	0.016
$S \times A \times T \times B$	1.268 (1.73, 10.37)	0.316	0.174	0.209 (1.37,8.25)	0.735	0.034

RM-ANOVA on TE considering two subject tilts (*S*) × two accelerations (*A*) × three motion durations (*T*) as within-subjects factors and Session Block Order (*B*) as between-subjects factor.
$^{*}P < 0.05$.
$^{**}P < 0.01$.
$^{***}P < 0.001$.

($F_{1,18} = 0.003$, $P = 0.96$, $\eta_p^2 = 0.0001$) and their interaction ($F_{1,18} = 0.89$, $P = 0.36$, $\eta_p^2 = 0.05$). Similarly, TE of the last four repetitions did not depend significantly on subject tilt ($F_{1,18} = 0.40$, $P = 0.53$, $\eta_p^2 = 0.02$), session order ($F_{1,18} = 0.098$, $P = 0.76$, $\eta_p^2 = 0.005$) and their interaction ($F_{1,18} = 0.540$, $P = 0.47$, $\eta_p^2 = 0.03$).

By contrast, the hand motion duration depended significantly on subject tilt ($F_{1,18} = 11.078$, $P = 0.0037$, $\eta_p^2 = 0.002$); in particular, it was 209 ms [CI = (184–234 ms)] and 231 ms [CI = [205–258 ms)] at 20° and 60°, respectively. Hand motion duration did not depend significantly on any other factors or interactions ($P > 0.10$). Also maximum speed depended significantly on subject tilt ($F_{1,18} = 11.078$, $P = 0.0037$, $\eta_p^2 = 0.38$); in particular, it was 2.22 m s^{-1} [CI = (1.91–2.53 m s^{-1})] and 1.96 m s^{-1} [CI = (1.73–2.19 m s^{-1})] at 20° and 60°, respectively. Maximum speed did not depend significantly on any other factors or interactions ($P > 0.18$).

In sum, body posture affected significantly arm kinematics but not interception timing when hitting a static target.

Discussion

The hypothesis and the findings

In the main experiments, participants were asked to hit a ball rolling on a surface viewed stereoscopically in a head-mounted display. Because the ball approached along the sightline and the scene did not include any reference about either vertical or horizontal directions, the surface slope could not be estimated from visual information. However, participants were tilted in the sagittal plane by 20° or 60°, whereas ball acceleration (2.397 or 6.068 m s^{-1}) was compatible with rolling down a slope of 20° or 60°. In theory, therefore, vestibular and somatosensory information about the orientation of the head relative to gravity could help estimating the visual direction of ball motion relative to gravity and therefore the descent slope because the direction of ball motion was head-fixed. This hypothesis predicts that the interception performance should be more accurate when ball acceleration is coherent with subject tilt than when it is incoherent (Fig. 3).

Consistent with this hypothesis, we found that the global success rate computed over all repetitions was significantly higher in the coherent conditions than in the incoherent conditions. However, the performance measured in terms of timing errors was not stationary throughout the experiment, although it tended to improve with practice, significantly more so for the coherent conditions than the incoherent conditions. Initially, the timing errors were large and independent of the coherence between acceleration and subject tilt. This is what would be expected if the responses were based exclusively on visual information because the visual stimuli were identical at both subject tilts. At the end of the experimental session, however, the timing errors were substantially smaller in the coherent conditions than the incoherent ones. This was true for the average of the responses in the last four repetitions over all participants, as well as for the same average parameter computed in individual participants in the majority of them. Moreover, the results did not depend on the distance travelled by the ball prior to interception, as shown by the trials where the starting position was matched between the lower and the higher acceleration.

The results also conformed to another important prediction stemming from the hypothesis. In particular, if subject tilt relative to gravity contributed to estimating the direction of target motion relative to gravity, the responses provided by more tilted participants should be timed earlier than those provided by less tilted participants, for a given target acceleration. This is because a ball rolling down a steeper slope typically is more strongly accelerated, inducing an observer to expect an earlier arrival time. Indeed, although, at the beginning of the experiment, we found that the response timing was independent of posture, at the end, the responses were timed significantly earlier when participants were tilted by 60° than when they were tilted by 20°. Therefore, practice with the task led to incorporation of postural information about head and body tilt relative to gravity for response timing.

The hypothesis that body posture affects interception timing by contributing to the estimate of target kinematics under gravity predicts that response timing should not depend on body posture when the target to be intercepted is motionless. To test this prediction, we ran a control experiment in which participants tilted backwards by 20° or 60° were asked to hit a static target in synchrony with the last of a predictable series of stationary audio-visual stimuli. We found that body posture affected significantly arm kinematics, consistent with previous studies on the effects of gravity on arm movements (Papaxanthis *et al.* 1998, Pinter *et al.* 2012; Gentili *et al.* 2007; Verheij *et al.* 2013; Gaveau *et al.* 2016), although it did not affect interception timing even after extensive practice.

In the main experiments, we also found a robust effect of ball acceleration on the responses. Thus, overall success rate was much lower when ball acceleration was higher than when it was lower. This result is consistent with the

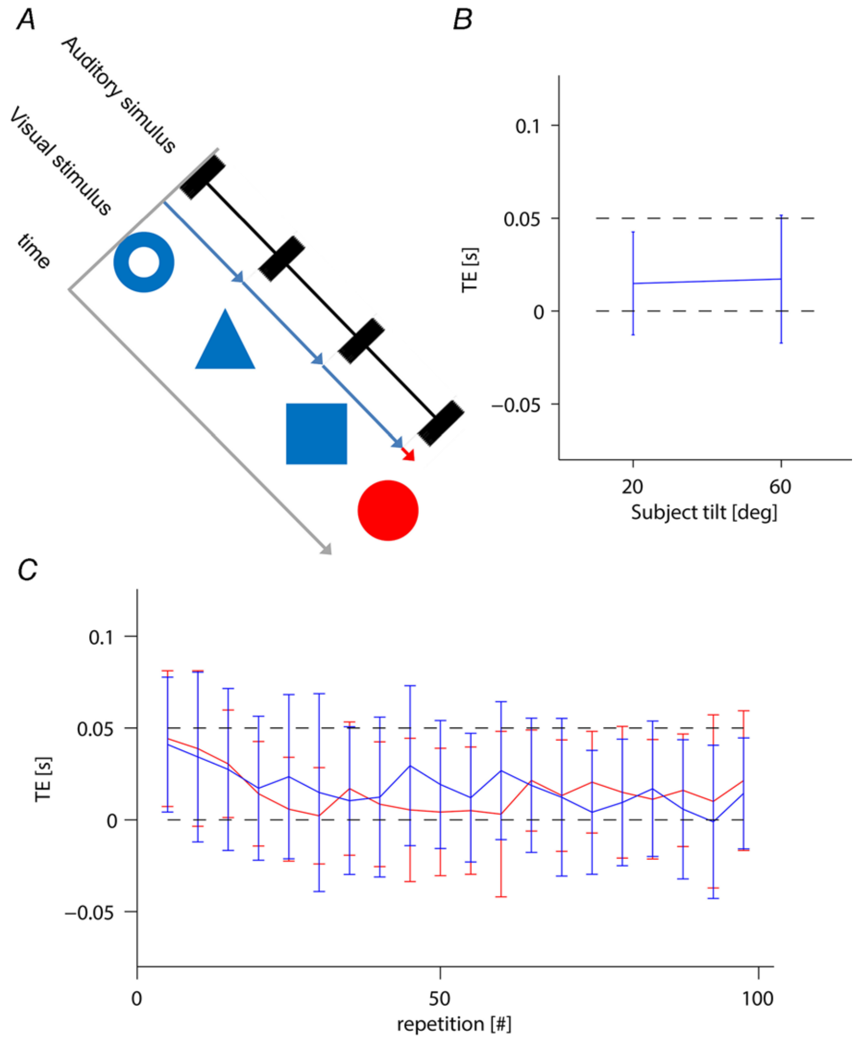

Figure 11. Control experiment
A, stimuli. The predictable series of stationary images (visual stimulus) and beeps (auditory stimulus) presented to participants. The blue and red arrows indicate the display duration of corresponding object. Participants were asked to hit the static target sphere (the last object of the sequence) in synchrony with the last of the predictable series of beeps. *B*, mean TE (± 95% confidence interval over all 20 participants) for subjects tilted by 20° and 60°. *C*, mean TE as a function of repetition for subjects tilted by 20° and 60° (red and blue, respectively). For clarity, each data point represents the average (± 95% confidence interval over all 20 participants) of five consecutive trials. In (*B*) and (*C*), black dashed lines represent the theoretical margin of error corresponding to the duration of the target sphere (0–50 ms). [Colour figure can be viewed at wileyonlinelibrary.com]

well-established notion that fast targets are more difficult to intercept than slow ones (Port *et al.* 1997; Tresilian & Lonergan 2002). Moreover, the responses were timed significantly later for the higher acceleration than the lower acceleration, also consistent with previous results (Bosco *et al.* 2012).

The observed bias of the responses as a function of target acceleration confirms that participants were unable to rely on online visual measurements of acceleration in order to time the interceptions. Indeed, it is well known that the visual system poorly estimates image accelerations (Werkhoven *et al.* 1992; Perrone and Thiele 2001; Brouwer *et al.* 2002). Motor timing generally does not take into account arbitrary accelerations, being based on first-order optical parameters such as the dilation rate or the tau-variable (Bootsma *et al.* 1997; Port *et al.* 1997; Engel and Soechting 2000; Senot *et al.* 2003; Brenner and Smeets, 2015; Zago *et al.* 2009). Instead, the present results are consistent with the idea that the interception responses were timed based on a model of the effects of gravity on a ball rolling down a descent, whose slope was estimated indirectly from postural orientation.

Comparison with previous work

As detailed in the Introduction, a few previous studies investigated the effects of posture on target interception (Senot *et al.* 2005; Le Séac'h *et al.* 2010; Baurès & Hecht, 2011). In these previous studies, the virtual scene included visually polarized cues that helped defining Up and Down directions relative to physical gravity. Nevertheless, the results showed that subject posture relative to gravity direction provided a major contribution to the sense of up and down in timing interception of targets moving along the vertical, although the effects were more consistent with naïve physics than with Newtonian physics. In Baurès & Hecht (2011), the effect of posture became apparent only when the last segment of target trajectory was occluded for a prolonged time (2.5 s), consistent with a dominant cognitive influence. In these previous studies, there was no appreciable effect of practice on interception timing, even when visual feedback about the performance was provided to the participants (Senot *et al.* 2005; Le Séac'h *et al.* 2010). However, repetitions of the same condition were limited to five in the latter studies. Moreover, the responses were provided by means of a button press and there was no haptic feedback.

In the present experiments, the visual scene lacked any polarized cues, and the only cues about target motion direction could be derived indirectly from the tilted posture of the participants. There were 15 repetitions of each experimental case, which allowed for practice effects to come to light. Moreover, the participants hit the target by means of actual arm movements and received haptic feedback, in addition to visual feedback. Therefore, during the experiment, the punching movement and the haptic feedback could have created a unitary reference frame between the real and the virtual world, thus reinforcing the coherent conditions. In this regard, it has previously been shown that the interception of targets accelerated by gravity is much better in the presence of real punching movements and haptic feedback from contact with the target than when interception is obtained by clicking a mouse-button and without haptic feedback (Zago *et al.* 2004).

One may wonder why the influence of a prior about gravity direction became most evident at the end of the experiment rather than at the outset. We consider that, in the absence of direct visual cues about gravity direction as in the present experiments, a gravitational reference for the visual stimuli could only be built and refined progressively with practice with the task. Accordingly, the effects on response timing built up progressively and were seen best at the end of the experiment.

Our findings show that the effects of posture extend beyond a mere sense of up and down directions, and involve targets moving along oblique directions. Moreover, the results are compatible with the hypothesis that posture contributes quantitatively to modelling the effects of gravity, giving rise to interception responses that are consistent with Newtonian dynamics. Indeed, in the coherent trials where target acceleration coincided with that of a ball rolling down a slope with the same inclination as the participant's tilt, performance feedback and practice with the task led to fairly accurate responses (Brenner *et al.* 2016; Leow *et al.* 2016). In the incoherent trials, instead, the discrepancy between predicted and actual target kinematics led to significant timing errors, which were only partially corrected with practice. Therefore, performance errors were more salient in the coherent than the incoherent conditions (Jiang *et al.* 2018).

Effects of body posture relative to gravity have been previously shown also for arm pointing movements. Thus, Le Seac'h & McIntyre (2007) reported that arm kinematics changed as a function of body roll (i.e. vertical posture *vs.* reclined on the side). Scotto di Cesare *et al.* (2014) showed that, when subjects point toward a visual target during slow pitch of the body and/or visual scene, the pattern of spatial errors was compatible with a gravity-centred reference frame. In our experiments, the general characteristics (duration, speed) of arm movements directed to hit the ball did not depend on body posture, although they showed a trend with practice.

Sloped trajectories have been previously used in various interception tasks (La Scaleia *et al.* 2014*a*, 2015; Tresilian & Lonergan 2002). In particular, de Rugy *et al.* (2012) studied the interception of balls rolling down paths with variable slope and showed that internal models predict the effects of complex, varying accelerations when they result from lawful interactions with the environment.

Estimates of body and gravity directions

The good performance after practice in the coherent conditions demonstrates that postural cues about the orientation of the subject in space effectively contributed to constructing a gravity reference for the control of target interception. Although our experimental manipulations were insufficient to determine their relative weight, egocentric cues also contributed in addition to gravicentric cues. This was shown by the statistically significant main effect of subject tilt on timing errors, independently of target acceleration (and therefore coherence), in both the between-groups and the within-subject protocols.

Different sensory organs can signal the orientation of the head and body with respect to gravity. Thus, static tilt of the head changes the component of the gravitational shear force acting in the plane of the maculae, and affects background activity and dynamic sensitivity of otolith afferents with regular discharge (Fernandez & Goldberg, 1976). In addition, somatosensory receptors (in the skin, muscles and tendons) and visceral receptors (in the kidneys, vena cava) can contribute to a sense of body orientation by monitoring contact forces between the body and the environment. Finally, the efference copy of the motor commands for reaching the target also may have contributed to a gravity reference in our experiments. Indeed, the muscle effort required to support the outstretched limb against gravity differed when participants were tilted by 20° or 60°.

We argued that postural cues helped estimating the visual direction of ball motion relative to gravity and therefore the descent slope. In this regard, previous studies about the SVV are pertinent. Most such studies assessed SVV in the roll plane. Although the estimates of the visual vertical are very accurate with the participant in the upright position (<2° errors), small roll tilts of the body (<30°) may result in limited overshoots (so called E-effect) and large tilts (>60°) generally result in more appreciable undershoots (A-effect) (e.g. Kaptein and Van Gisbergen, 2004; Tarnutzer *et al.* 2009; Vingerhoets *et al.* 2009). When a peripheral visual frame is added when testing SVV, A-effects at large body tilts tend to decrease relative to when SVV is tested without the frame (Vingerhoets *et al.* 2009).

A few studies assessed SVV in the pitch plane, thus being comparable to the situation of the present experiments. Ebenholtz (1970) tested SVV in the anteroposterior direction with the subject pitched backwards in 15° steps, up to 90° tilt. Small (<5°) overshoots were reported at 15°, 30° and 45° pitch, with small undershoots (<5°) at 60° and slightly larger undershoots (6–12°) for greater tilts. Bortolami *et al.* (2006) assessed the subjective vertical using haptic matches, and their regression parameters indicate that the vertical was undershot by <1° at 20° backward pitch and <2° at 60°. Bringoux *et al.* (2004) studied the perceived gravity-referenced eye level, which corresponds to the subjective Earth-referenced horizon. For participants pitched backwards by 20–30°, the errors remained within 4°, similarly to the previous results of Schöne (1964). In sum, the constant errors in assessing the direction of gravity or the horizontal with a visual or haptic match are small at body tilts comparable to those of the present experiments.

Furthermore, the estimates of the direction of visual motion follow a pattern very similar to that of SVV. De Vrijer *et al.* (2008) asked laterally tilted subjects to align the direction of random dots motion (30% coherence) with the direction of gravity in darkness. They found that, at ≤60° tilts, the errors in both SVV and motion estimate were small (<10°), although the errors became substantial at >60° tilts, indicative of incomplete compensation for large body tilts. Claassen *et al.* (2016) reported that the coherence threshold for detecting the direction of random dots motion was significantly lower when both subject position and motion direction were congruent with gravity.

According to current views, the direction of gravity is estimated by combining retinal cues about the line orientation with static vestibular and somatosensory cues about body orientation, plus the prior assumption of an upright body orientation (Mittelstaedt 1983; Dyde *et al.* 2006; MacNeilage *et al.* 2007; De Vrijer *et al.* 2008; Lacquaniti *et al.* 2015; Alberts *et al.* 2016; Kheradmand & Winnick 2017). Also, the perception of static body tilt results from multisensory fusion, vestibular inputs being integrated with proprioceptive inputs (Bringoux *et al.* 2016), although the perception of body orientation is considered to be independent of the perception of vertical direction, with systematic errors smaller than those in SVV (Kaptein & Van Gisbergen, 2004; Kheradmand & Winnick 2017).

Putative neural substrates

Neuroimaging (Indovina *et al.* 2005; Ferri *et al.* 2016, 2013; Maffei *et al.* 2010, 2015; Miller *et al.* 2008), transcranial magnetic stimulation (Bosco *et al.* 2008; Delle Monache *et al.* 2017) and lesion studies (Maffei *et al.* 2016) in humans have shown that the effects of gravity on a visual target motion elicit neural responses in a distributed cortical-subcortical network, including the vestibular cortex, putamen, thalamus, cerebellum and vestibular nuclei (Lacquaniti *et al.* 2013). In particular, the vestibular cortex integrates visual, vestibular and somatosensory signals in a widely distributed network, mainly localized in the temporal, parietal and insular cortices (Lopez & Blanke 2011). Also, SVV tasks engage temporo-parietal-insular cortices (Fiori *et al.* 2015; Kheradmand & Winnick 2017), although temporal and spatial processing of gravity may not necessarily co-localize in the same regions (Maffei *et al.* 2016).

Detailed electrophysiological studies in monkeys have shown that neurons carrying signals of head and body orientation relative to gravity, independent of visual landmarks, can be found in several brain regions, including the brainstem, cerebellum, thalamus, temporal, parietal and insular cortices (Angelaki *et al.* 2004; Chen *et al.* 2011; Laurens *et al.* 2013, 2016). Several of these neurons use internal models of physics to disentangle gravitoinertial cues (Angelaki *et al.* 2004) or visual motion cues for target interception (Cerminara *et al.* 2009; Streng *et al.* 2018).

Conclusions

We have shown that vestibular and somatosensory cues about head and body orientation in space contribute to model the effects of gravity on a target moving with different accelerations, in the absence of visual landmarks. This work adds to the existing knowledge about the fusion of multisensory cues with internal models of physics. This fusion affords reliable estimates of orientation of ourselves and external objects in space, as well as successful interactions with the environment, even in the presence of ambiguous sensory information.

The protocols that we used in the present study may have translational relevance to test the role of visual–vestibular integration in patients with peripheral or central vestibular dysfunctions. Thus, Maffei *et al.* (2016) showed that some such patients have a reduced ability to discriminate natural from unnatural gravitational acceleration for the interception of targets moving along the vertical. However, the diagnostic power would be enhanced considerably by assessing the patients with targets moving along variable slopes (de Rugy *et al.* 2012) and by tilting the patient relative to gravity to test visual–vestibular integration directly.

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Additional information

Competing interests

The authors declare that they have no competing interests.

Author contributions

The work was performed at the Laboratory of Neuromotor Physiology, IRCCS Fondazione Santa Lucia. BLS conceived the research, performed the experiments and analysed the data. MZ contributed to the methodology. All authors contributed to the design of the work, interpretation of the data and the drafting of the work. All authors approved the final version of the manuscript submitted for publication, agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved, and that all persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

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