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ORIGINAL ARTICLE

A novel dissociation between representational momentum and representational gravity through response modality

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Abstract

When people are required to indicate the vanishing location of a moving object, systematic biases forward, in the direction of motion, and downward, in the direction of gravity, are usually found. Both these displacements, called representational momentum and representational gravity, respectively, are thought to reflect anticipatory internal mechanisms aiming to overcome neural delays in the perception of motion. We challenge this view. There may not be such a single mechanism. Although both representational momentum and representational gravity follow a specific time-course, compatible with an anticipation of the object's dynamics, they do not seem to be commensurable with each other, as they are differentially modulated by relevant variables, such as eye movements and strength of motion signals. We found separate response components, one related to overt motor localization behaviour and one limited to purely perceptual judgement. Representational momentum emerged only for the motor localization task, revealing a motor overshoot. In contrast, representational gravity was mostly evident for spatial perceptual judgements. We interpret the results in support of a partial dissociation in the mechanisms that give rise to representational momentum and representational gravity, with the former but not the latter strongly modulated by the enrolment of the motor system.

Introduction

When observers are instructed to identify the last-seen position of a moving object that is suddenly occluded, they indicate a location displaced in the direction of the object's motion. This error has been named representational momentum by Freyd and Finke (1984; Freyd, 1987), who suggested that the spatial displacement results from a representational analogue of physical momentum, that is, a cognitive representation of the object's motion with properties similar to inertia and momentum. This putative representation of the object's dynamics would contribute to the updating of its perceived motion, leading to a discrepancy between the actual and judged vanishing position. By now, a rather large literature has investigated the factors that contribute to this phenomenon. In a sense, these contributing factors can be summed up as pertaining to perceived object properties and the perceiver's motor system (see Hubbard, 2005, 2010, 2014, 2015, for reviews of the findings).

Besides the displacement forward, in the direction of motion, it has also been reported that people judge the position of a visually presented object as displaced downwards, in the direction of gravity, irrespective of the target's motion direction, which emerges even for static stimuli. This error has been named representational gravity, emphasizing its close connection with representational momentum, and thought to result from a mental analogue of physical gravity (Hubbard, 1997). However, and in contrast with representational momentum, a gravity-congruent spatial bias would be neither perceptually given nor derivable from perceived motion per se, except for downward motions. Rather, it would constitute knowledge about the world, where objects are accelerated downwards.

In the present study, we investigate whether knowledge about the effects of gravity is exclusively intrinsic to the

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perceiver's motor system or whether it is a cognitive factor influencing spatial judgements. Before reporting on this experiment, we review classical studies on representational momentum, factors that modulate the effect, as well as recent studies on representational gravity.

Classical studies on representational momentum

The first studies on the topic used implied motion sequences as stimuli and perceptual judgements of a probe stimulus as psychophysical method. In the seminal report by Freyd and Finke (1984), the inducing sequence was composed of three static images of a rectangle implying a rotational motion. Then, a fourth rectangle with varying orientations (i.e., the probe) was presented and observers judged whether the orientation of the probe coincided with the last rectangle of the inducing sequence. In accordance with the predictions of the momentum metaphor, observers were more likely to accept probes as accurate that were rotated too far in the direction of implied motion (Freyd & Finke, 1984). After Freyd and Finke's original observation, a variety of stimuli, motion trajectories and sensory modalities were used to study the phenomenon (for reviews see Hubbard, 2005, 2010, 2014, 2015). For example, representational momentum was found to be modulated by the object's identity and expectations concerning its motion, so that images of a rocket led to bigger upward displacement than images of a building (Reed & Vinson, 1996). Also, the phenomenon emerged even for completely static pictures showing dynamic situations (e.g., a mid-air photograph of a person jumping from a wall; Freyd, 1983; Freyd, Pantzer, & Cheng, 1988).

Importantly, a link was suspected between representational momentum and time. In the standard procedure, the probe was presented after a retention interval of 250 ms. When the retention interval was varied, representational momentum was found to increase steadily until a maximum at about 300 ms (Freyd & Johnson, 1987). Also, when a schematic representation of a ball on an inclined plane is shown and then removed, the spatial location of the ball reported by observers was increasingly displaced downwards along the plane until a maximum at about 300 ms. The displacement increased more rapidly for steeper inclines, suggesting a mental analogue of gravity (Bertamini, 1993).

In subsequent empirical enquiries, mostly lead by Timothy Hubbard and collaborators (e.g., Hubbard & Bharucha, 1988; Hubbard, 1990), the stimuli and psychophysical method changed. Instead of implied motion and perceptual judgments, smoothly moving targets were presented and observers were asked to adjust the cursor of a computer mouse to the last-seen position of the moving target. Arguably, these methods create a more ecological situation as objects in the real world move smoothly and not in successive snapshots. Also, the mouse response bears similarity, to some extent, with interceptive action. Another benefit of the revised methods was that fewer trials were necessary to estimate observers' memory of the final position and, therefore, systematic manipulation of independent variables was facilitated. Notwithstanding, these changes also increased the number of factors involved in the task, such as patterns of smooth pursuit eye movements, variations in stimulus presentation and engagement of motor actions, the effects of which were not always taken into account for the interpretation of the spatial mislocalization phenomena.

Effects of task, eye movements and display type on representational momentum

Over the last few decades, several patterns of spatial displacements, originally thought to reflect mental analogues of physical variables, were shown to depend on perceptual and oculomotor variables. Most important to the present study, spatial displacement was shown to depend on the experimental task employed to evaluate observers' memory for the final position. In perceptual tasks, a probe stimulus is presented after the target disappeared and observers should indicate its relative position (e.g., whether it is left or right of the final target position). In motor tasks, observers adjust a mouse cursor to the last-seen position of the target. Effects of task are modulated by display type and eye movements in complex ways. Target motion in the experimental displays may approach natural motion by frequent updates of its position on the computer screen (i.e., every 17 ms). Alternatively, target motion may be implied when its position is only rarely updated (i.e., every 500 ms) with the target disappearing after each update (i.e., 250 ms visible followed by 250 ms invisible). Forward displacement with implied motion is observed with perceptual (e.g., Freyd & Finke, 1984; Freyd & Johnson, 1987; but see; Kerzel, 2002) and motor tasks (Kerzel, 2003a), and is unaffected by eye movements (Kerzel, 2003b, Exp. 1). That is, representational momentum occurs invariably for implied motion displays.

In contrast, forward displacement with smooth target motion is strongly modulated by eye movements and judgment type. With smooth target motion, observers may engage in ocular pursuit of the target, which tends to overshoot the final position when the target disappears unpredictably (Mitrani & Dimitrov, 1978). That ocular overshoot contributes to representational momentum has been shown by reports that forward displacement is strongly reduced or absent when observers maintain fixation (Kerzel, 2000; Kerzel, Jordan, & Müsseler, 2001; De Sá Teixeira, Hecht, & Oliveira, 2013; De Sá Teixeira, 2016).

Finally, forward displacement is also affected by the way the final target position is judged. In general, motor judgments increase the forward error relative to perceptual judgments when eye fixation is maintained (Kerzel, 2003a), but there are instances where the last-seen position with smooth motion, eye fixation, and motor judgments was slightly, but nonetheless significantly displaced in the direction of motion (Müsseler, Stork, & Kerzel, 2002; Kerzel, 2003a, c) and others where this was not the case (Kerzel, 2000; Kerzel, Jordan, & Müsseler, 2001; De Sá Teixeira et al., 2013; De Sá Teixeira, 2016). An explanation for this discrepancy remains elusive, but it may be sufficient to conclude that suppression of forward displacement when eye movements are not possible is modulated by the engagement of a motor action: employment of a motor task tends to work against the reduction of representational momentum under eye fixation conditions.

Besides mouse adjustments, motor tasks may require observers to directly point to the final position of the target on a touch screen. It was found that forward displacement was stronger with pointing movements than with cursor adjustment (Ashida, 2004) or perceptual probes (Kerzel & Gegenfurtner, 2003). The interpretation of this finding was that there is action-specific extrapolation of the final position of a moving target. To compensate for neuronal processing delays, the visual system may extrapolate the target position into the future for guiding action.

Effects of motion type, eye movements and task naturally lead to the conclusion that even if some spatial mislocalization phenomena do reveal the top-down modulation of cognitive expectations of motion, not all can be interpreted this way. In fact, uncovering a pattern of spatial mislocalization, per se, does not provide enough evidence for a role of high-level cognitive expectations, be it in the form of representational analogues of physical variables, an internalization of physical laws, or a second-order isomorphic mental model of physical invariants. Stated differently, it is likely that widely distinct phenomena have been interpreted under the same label—representational momentum—merely based upon mislocalization patterns. With this in mind, for the remainder of the present article, representational momentum will refer solely to a forward spatial localization judgement of the offset position of a smoothly moving object.

Effects of task on representational gravity and its time course

Similar to representational momentum, the localization bias in the direction of gravity came to be referred as representational gravity, and was interpreted within the same theoretical framework: as a mental analogue of a physical invariant, in this case, earth's gravitational pull (see, e.g., Hubbard, 2005). In striking contrast to representational momentum, however, representational gravity seems to be rather independent of experimental task. It has been reported using perceptual judgements (Bertamini, 1993; Nagai, Kazai, & Yagi, 2002), mouse adjustments (De Sá Teixeira et al., 2013; De Sá Teixeira, 2016; Kerzel, Jordan, & Müsseler, 2001) and direct pointing responses (De Sá Teixeira & Oliveira, 2013). Representational gravity was also found to have an intrinsic time course, increasing in magnitude with time after target offset (see Fig. 1, panel a; Bertamini, 1993; De Sá Teixeira et al., 2013). Finally, both representational gravity and its time course were found to be unrelated to eye movements, emerging equally under conditions of fixation and smooth pursuit (Kerzel, Jordan, & Müsseler, 2001; De Sá Teixeira, 2016).

Notwithstanding, some important dissociations in representational gravity have been noticed, which can be linked to the experimental task. First, spatial displacement was in the direction of gravity irrespective of the orientation of the observer's body when perceptual judgements were used (Nagai, Kazai, & Yagi, 2002), but along the body's main vertical axis when a cursor was adjusted with a mouse or

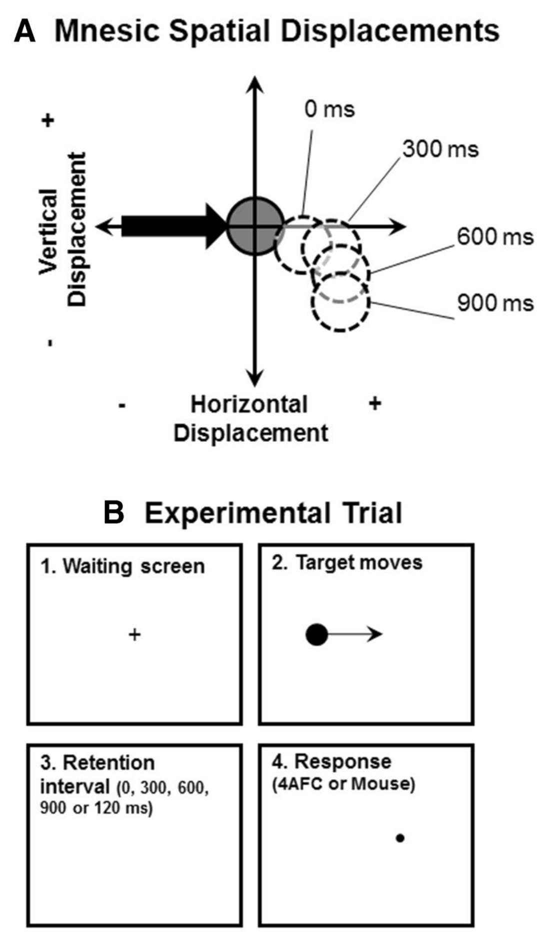

Fig. 1 **a** Coordinate system for the measurement of perceived displacement. The grey disk represents the true vanishing location; open circles represent the typical pattern of mislocalizations as a function of retention interval. **b** Schematic depiction of an experimental trial for the measurement of representational momentum and representational gravity (see text for details)

a trackball (De Sá Teixeira & Hecht, 2014; De Sá Teixeira, 2014; De Sá Teixeira et al., 2016). Second, the downward drift of the target over time was largest when the observers' body orientation and vestibular signals coincided and an adjustment method was used (De Sá Teixeira & Hecht, 2014; De Sá Teixeira, 2014; De Sá Teixeira et al., 2016).

In light of the known role that an internal model of gravity plays in timely motor interception responses (e.g., Bosco, Carrozzo, & Lacquaniti, 2008; La Scaleia, Lacquaniti, & Zago, 2014; La Scaleia, Lacquaniti, & Zago, 2015; Lacquaniti et al. 2014; Zago, McIntyre, Senot, & Lacquaniti, 2008; McIntyre, Zago, Berthoz, & Lacquaniti, 2001), a closer connection between time and representational gravity would be expected for motor judgements that derive, to some extent, from interceptive actions. In contrast, changes in representational gravity may be attenuated or abolished when observers are required to provide a perceptual judgement. Following the logic of previous studies (Ashida, 2004; Kerzel & Gegenfurtner, 2003), the sensorimotor system needs to take into account the future trajectory of moving objects as determined by physical laws, to minimize reaching or grasping errors. Thus, it can be hypothesized that expectations of downward motion of objects without support could have stronger repercussions on motor than on perceptual judgments. In contrast, it can be argued that knowledge about earth's gravity, along with other physical invariants (see, e.g., Amorim et al., 2015), due to its systematic, regular and highly predictable effects, possesses stable predictive value irrespective of any task requirements. If so, there are obvious advantages to factoring in gravity's effects as soon and as widespread as possible when perceiving an event, instead of processing its effects solely when an interceptive action is required (see also Senot, Baillet, Renault & Berthoz, 2008). In this case, one would expect representational gravity and its time course to emerge both with perceptual and motor tasks.

The present experiment aims to clarify this issue by measuring the temporal evolution of both representational momentum and representational gravity by juxtaposing a motor task (reproduction of the last seen position) and a perceptual task (comparison of a probe to the last seen position). To obtain independent measures of both phenomena, a target moving smoothly along a horizontal trajectory is employed—in this situation both phenomena are maximally disjointed, with their respective biases orthogonal to each other. In line with previous reports, we expect to find different magnitudes of representational momentum between both tasks: with an increased forward bias for the motor-based responses and a reduced or non-significant spatial displacement for the perceptual task. The degree to which representational gravity and its time course mirror this magnitude difference or dissociation will thus provide an empirical basis to delimit its dependence on perceptual and/or sensorimotor substrates. The two most extreme dissociation scenarios would be (i) for representational gravity to be present only with the motor-based task or (ii) only with the perceptual-based task. If the former obtains, representational gravity, as representational momentum, can be said to be dependent upon the involvement of the motor system, whereas the latter would delimit the phenomenon to the perceptual–cognitive system.

Method

Participants

Sixteen participants (five males; eleven females), with ages between 26 and 42 years ($M = 31.18$; $SD = 4.65$) volunteered to take part in the experiment. All participants had normal or corrected to normal vision and were unaware of the experimental hypotheses. The study was approved by the local ethics committee of the Santa Lucia Foundation, and the experimental protocol was conducted in accordance with the Declaration of Helsinki.

Stimuli

The target was a black circle with a diameter of 30 pixels ($\approx 0.9°$, at 60 cm viewing distance) that moved horizontally, either leftwards or rightwards, at a constant speed of about 597 px/s ($\approx$ 19º/s). The target appeared already in motion and disappeared after covering 597 pixels ($\approx 19°$). Each animation started at a random location such that the target could disappear within a window of 40 by 40 pixels located 80 pixels beyond the centre of the screen (in relation to the motion direction). A smaller black circle, with 6 pixels of diameter ($\approx 0.18°$), was used as a probe for the remembered vanishing location of the target. The probe could appear 0, 300, 600, 900 or 1200 ms after the disappearance of the target (henceforth referred to as retention interval). The location on the screen where the probe appeared depended on the task (see procedure and design below). A fixation cross (+), with a width of 15 pixels, was shown in the centre of the screen after each response and until the participant acknowledged that she/he was ready to start a new trial.

Procedure and design

Participants sat at about 60 cm from the monitor, with their cyclopean eye roughly aligned with the centre of the screen. There were no eye or head constraints, but participants were instructed to keep a steady posture during the experiment. No particular eye movement instructions were provided, but participants were told that they were free to track the target with their gaze. Each participant completed two tasks within the same experimental session, which lasted about one hour including instructions, debriefing and an inter-task resting period of a few minutes. In both tasks, participants were instructed to remember and indicate, after an imposed retention interval, the vanishing location of the target, as precisely as possible, and referring to its geometrical centre (See Fig. 1, Panel b). The tasks varied with respect to the psychophysical procedure employed, with order counterbalanced between participants.

Motor localization

Participants were required to move the probe, which appeared at the centre of the screen after the respective retention interval, to the desired location using a computer mouse. The perceived vanishing location was confirmed by pressing the mouse's left button.

Perceptual judgement

Whereas a motor localization is inherently unconstrained in both vertical and horizontal axes, standard perceptual tasks are limited by the choices made by the experimenter for the location of the probes, usually restricted to the dimension of interest—that is, to representational momentum along the target's motion trajectory. To be able to obtain empirical estimates of both representational momentum and representational gravity, we devised a new procedure in which participants had to provide bi-dimensional judgements, as follows. For each combination of motion direction and retention interval, a probe was placed in a position determined by the participant's previous responses, using an adaptive psychophysical procedure—this ensured that the total number of trials and the time required were kept within reasonable limits. Participants had to press one of four buttons on a custom-made key-pad to indicate whether the probe was to the left and above, to the left and below, to the right and above, or to the right and below the perceived vanishing location (four alternatives forced choice—4AFC). On each trial, the probe was positioned on the screen based on the current values of two staircases, specifying the horizontal and vertical coordinates. A staircase algorithm kept track, for each combination of conditions, of the current values for both staircases. However, on each trial, and unbeknownst to the participant, either the horizontal or the vertical staircase was randomly selected to be active, while the other one was inactive. For example, let us say that on a given trial, a rightward-moving target was shown and, 300 milliseconds later, the probe was presented 70 pixels to the right and 20 pixels below the actual vanishing position. If on this particular trial, the horizontal staircase was active and the participant responded "rightward-below", the value of the horizontal staircase was reduced from 70 to 54 pixels to the right, with the value of the vertical staircase being unchanged. With this procedure, the probe homed in on the perceived vanishing location of the target following a bi-dimensional path (equivalent to the point of subjective equality; see Fig. 2 for an example). On the first trial for each combination of conditions, the probes were located 100 pixels to the right or to the left, and 100 pixels above or below the target's actual vanishing location (starting position of the probes was counterbalanced between participants). The value of each staircase was increased or decreased by 64, 16, 4, 2 or 1 pixels, with the step size decreasing each time the participant reversed his/her response, except for the 1-pixel step size, which required 5 response reversals before the criterion for the termination of the staircase procedure was reached.

Both tasks were programmed in python using PsychoPy routines (Peirce, 2007, 2009) and implemented on a personal computer equipped with a monitor screen with a resolution of 1280 × 1024 (physical size of 40.8 × 30.6 cm), a gaming mouse with report rate set at 1 ms (key switch response time of 3 ms; A4Tech X7 F3 Gaming Mouse 8) and a custom-made response box, controlled with an Arduino board (which recorded response times with an accuracy to the nearest millisecond; synchronization with the experimental stimuli was performed with a USB emulator of a serial port), with five buttons (four arcade buttons arranged as if in the corners of a regular square with cm side length and a middle button).

Each trial, irrespective of the task, started with the presentation of a fixation cross in the middle of the screen until the participant acknowledged that she/he was ready, by pressing either the left button of the mouse (in the motor localization task) or the middle button of the response box (in the perceptual judgement task). The target appeared in motion immediately afterwards and, after the retention interval, the probe was shown on the screen until the participant responded or 6 s had elapsed (in which case no response was recorded).

The experiment thus followed a 2 (task) × 2 (motion direction) × 5 (retention interval) factorial design. For the motor localization, each combination of motion direction and retention interval was presented 30 times per participant. In the case of the perceptual judgement task, for each combination of target direction and retention interval there were two staircases (one for each spatial dimension, horizontal and vertical). Overall, each staircase required an average of 19.9 (SD = 2.9) presentations before reaching the stopping criteria.

Data analysis

Horizontal and vertical coordinates of the localization responses in the motor localization task were taken as the point of subjective equality (PSE) for the target's vanishing

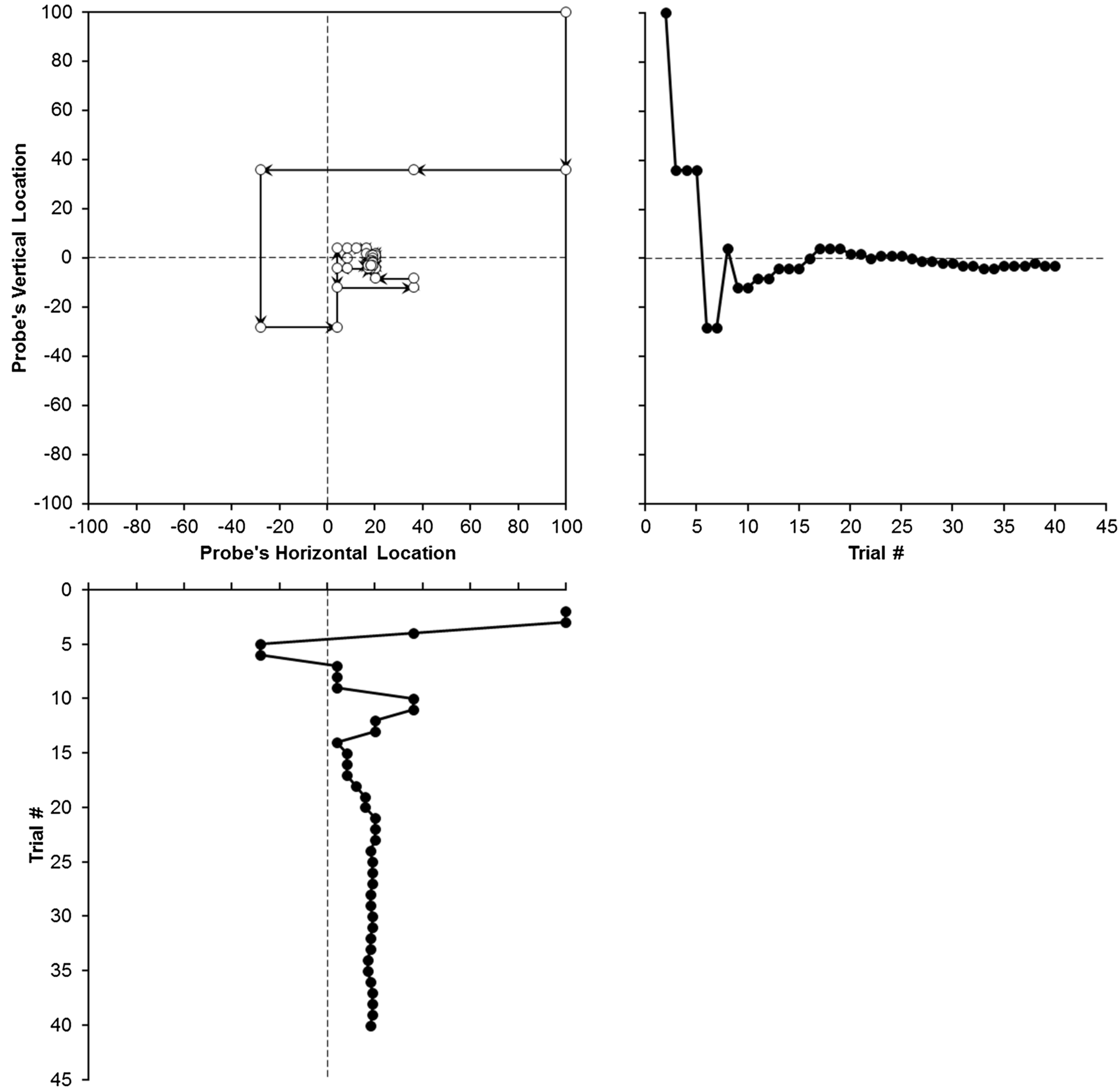

Fig. 2 Illustration of the staircase procedure for the measurement of both the horizontal and vertical remembered vanishing location in relation to the actual offset position (0, 0 coordinates; dashed lines)

location. The arithmetic difference between the horizontal and vertical PSEs and the corresponding coordinates of the actual vanishing location (constant errors) were calculated to obtain a measure of representational momentum (horizontal coordinates, with positive values signalling a displacement forward in the direction of motion) and representational gravity (vertical coordinates, with negative values signalling a displacement downward in the direction of gravity). Also, standard deviations of the spatial localizations obtained for each retention interval were calculated on an individual basis and taken as a measure of the mean just-noticeable difference (JND; that is, the distance in pixels from the point of subjective equality required for a judgement that the probe did not coincide with the perceived vanishing location).

As for the perceptual judgement task, individual upper and lower limens were calculated for both the horizontal and vertical dimensions, and for each retention interval and motion direction, by averaging the corresponding probe coordinates that triggered a reversal of the participant's response when its position was changed in 1-pixel steps (i.e., between "beyond" and "behind", for the horizontal stairs, and between "above" and "below", for the vertical stairs). The individual JNDs for each retention interval and dimension were then calculated, by halving the difference between the upper and lower limens. PSEs were determined by averaging both limens and representational momentum and representational gravity calculated as in the motor localization task.

Representational momentum, representational gravity, mean horizontal and vertical JNDs and mean response times were subjected, as dependent variables, to repeated measures ANOVAs with retention interval and task as factors and, when appropriate, to *t* tests. Whenever the sphericity assumption was not met, the Huynh–Feldt correction for the degrees of freedom was used.

Results

Preliminary analysis

No evidence was found that motion direction had either significant main effects or that it interacted with retention interval or task for all dependent variables. Therefore, this variable was taken as a replication. Figure 3 depicts the bidimensional points of subjective equality for all participants (2 points per participant, corresponding to the two motion directions) in the motor localization (left column) and perceptual judgement (right column) tasks for each retention interval (rows). In both tasks, the data points seem to cluster around a point displaced forward (representational momentum) and downward (representational gravity) in relation to the actual vanishing location. Depicted in grey are the 95% confidence ellipses for all data points in each task, calculated in Matlab with a script adapted from Duarte (2015) and based upon a principal components analysis. For both tasks there seems to be little or no variation in the ellipses' parameters with retention interval. Overall, the dispersion of the data points seems to be well captured by horizontally elongated ellipses, with the axes fairly parallel to the main axes of the screen (frontoparallel plane).

A similar fit was performed on an individual basis for the responses obtained in the motor localization task (for which there were enough data points for individual dispersion analyses—30 localization responses for each combination of motion direction and retention interval) and the area, angle of rotation, major axis length and axes ratio of the 95% confidence ellipse for each retention interval calculated and subjected to a one-way ANOVA. Retention interval had no significant effects on the mean area of the ellipses, $F(1.86, 27.88) = 1.91$, $p = 0.121$, or on the ratio of the lengths of the axes, $F(4, 60) = 1.63$, $p = 0.179$. The angles of rotation of the ellipses were also not affected by retention interval, $F(4, 60) < 1$, but they were significantly different from 0 (t between 3.79 and 4.49, all $p < 0.01$), averaging to about 4.85° downwards. Finally, the length of the major axis, on the other hand, was modulated by retention interval, $F(4, 60) = 2.7$, $p = 0.039$, partial $\eta^2 = 0.153$, decreasing with time until a minimum at 600 ms, slightly increasing for longer times.

Overall these analyses show that spatial localization responses were less precise along the dimension of motion, with the ellipses only slightly rotated away from the physical horizontal. What is more, the geometrical centres of the ellipses reflect the standard constant errors associated with representational momentum and representational gravity, displaced forward, in the direction of motion, and downward, in the direction of gravity, respectively. Of relevance, a bigger forward displacement seems to be the case for the motor localizations, in comparison with perceptual judgements, while both seem to exhibit a downward bias. To further explore these trends, two-way ANOVAs (retention time and task) were performed separately for representational momentum and representational gravity. Additionally, one-way ANONAs (retention time) were also performed separately for each task as a follow-up analysis.

Representational momentum

Mean representational momentum (See Fig. 4, panels a and c) was found to be significantly larger, that is, displaced forward in the direction of motion by a larger distance, for the motor localizations than for the perceptual judgements, $F(1, 15) = 8.15$, $p = 0.012$, partial $\eta^2 = 0.35$. Retention interval also had a significant main effect on mean representational momentum, $F(4, 60) = 2.7$, $p = 0.039$, partial$\eta^2 = 0.15$. The displacement in the direction of motion increased from 0 ms to a maximum at about 300 ms. For longer retention intervals (600, 900 and 1200 ms), representational momentum seemed to stabilize at its maximum in the motor localization task but to decrease for perceptual judgements, but this pattern was not reliable, $F(1, 15) = 1.87$, $p = 0.127$. In previous reports, however, task had an effect on the time course of representational momentum.

Therefore, we tentatively explored the effects of retention interval for each task separately by one-way repeated-measures ANOVAs. In the motor localization task, representational momentum was found to be significantly affected by retention interval, $F(4, 60) = 20.66$, $p < 0.001$, partial $\eta^2 = 0.58$, showing that it increased until about 300 ms. In contrast, retention interval had no significant effect in the perceptual judgement task, $F(4, 60) < 1$. Moreover, one-sample *t* tests performed for each retention interval revealed that for perceptual judgements, representational momentum was indistinguishable from 0 for all retention intervals: 0 ms, $t(15) = 1$, $p = 0.329$; 300 ms,

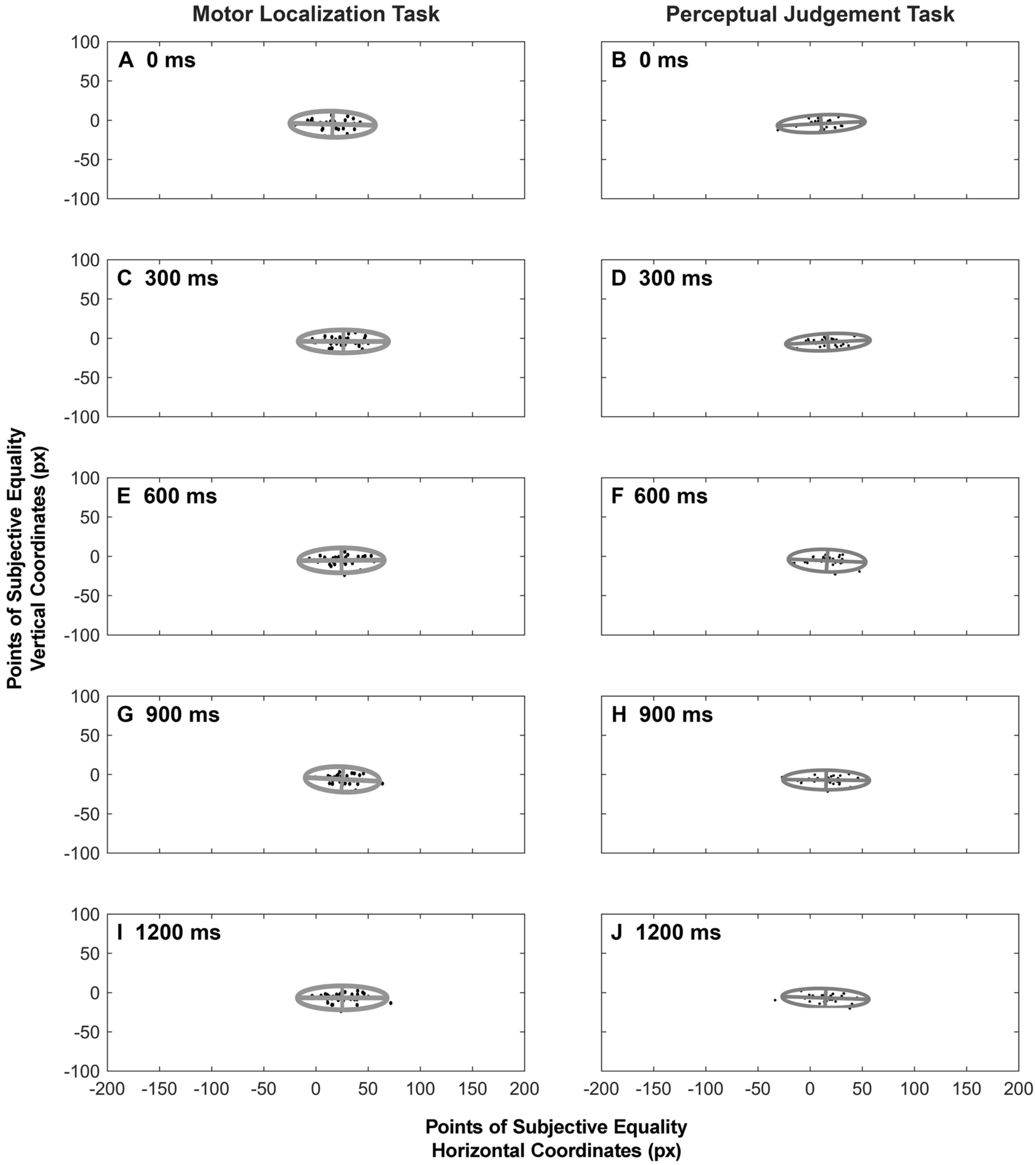

Fig. 3 Horizontal and vertical PSEs for each trial and participant in the motor localization task (left column) and for each motion direction and participant in the perceptual judgement task (right column) for each retention interval (panels) and with respect to the actual vanishing location (plots' origins). The grey curves represent the 95% confidence ellipses, with the respective axes, around the data centroids

$t(15) = 1.7$, $p = 0.12$; 600 ms, $t(15) = 1.3$, $p = 0.21$; 900 ms, $t(15) < 1$; 1200 ms, $t(15) < 1$. For the motor localization task, however, mean representational momentum was significantly greater than 0 for all retention intervals: 0 ms, $t(15) = 4.73$, $p < 0.001$; 300 ms, $t(15) = 6.89$, $p < 0.001$; 600 ms, $t(15) = 6.55$, $p < 0.001$; 900 ms, $t(15) = 8.18$, $p < 0.001$; 1200 ms, $t(15) = 6.78$, $p < 0.001$.

Representational gravity

As for representational gravity (See Fig. 4, panels a and b), the two-way ANOVA (retention interval × task) revealed an effect of retention interval, $F(2.53, 37.95) = 4.6$, $p = 0.011$, partial $\eta^2 = 0.24$, with the perceived vanishing location drifting downward with time. This trend was evident in

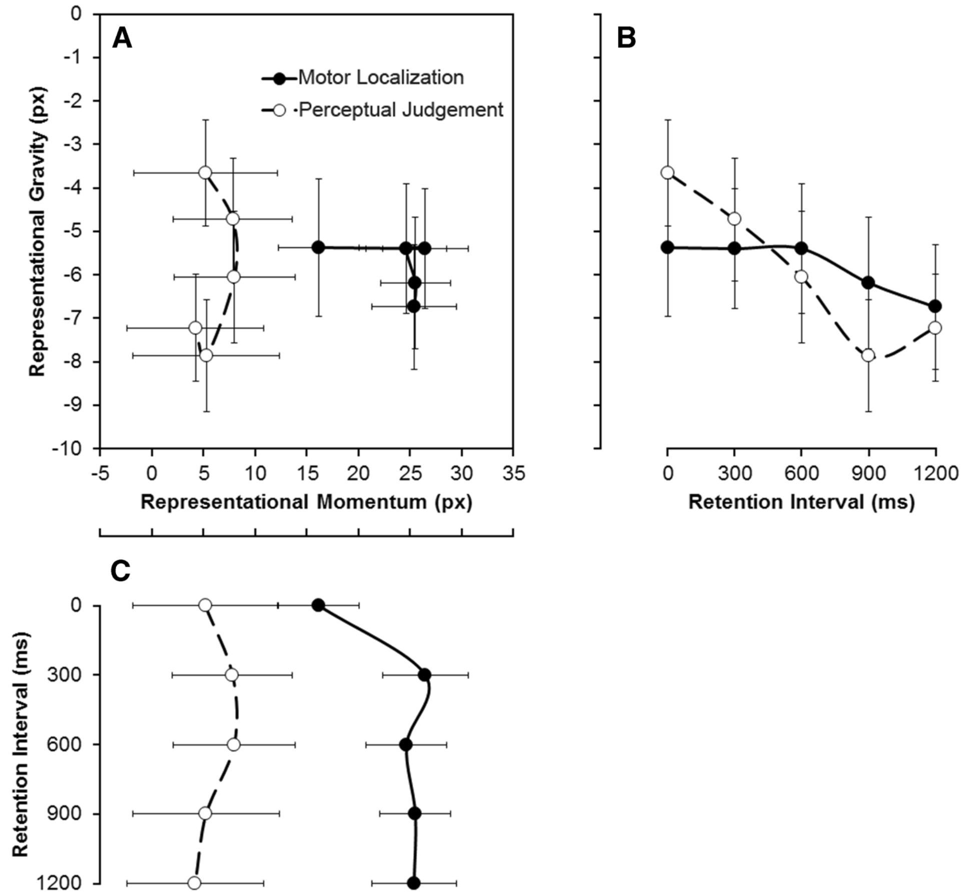

Fig. 4 Points of subjective equality found for the motor localizations (filled circles and continuous lines) and the perceptual judgements (open circles and dashed lines). Error bars refer to the standard error of the means. **a** Representational gravity as a function of representational momentum for each retention interval condition. **b, c** Representational gravity and representational momentum as a function of retention interval, respectively

the perceptual judgements for all retention intervals but the longest (1200 ms), for which the perceived vanishing location seemed to stabilize. In the motor localizations, there was a noticeable downward drift only for retention intervals longer than 600 ms. Accordingly, the interaction between retention interval and task was significant, $F(2.79, 41.79) = 2.99$, $p = 0.045$, partial $\eta^2 = 0.17$. No main effect of task was found, $F < 1$.

Separate ANOVAs conducted for each task revealed that for perceptual judgements, there was an effect of retention interval, $F(2.33, 34.91) = 4.53$, $p = 0.014$, partial $\eta^2 = 0.23$, that only approached significance in the motor localization task, $F(4, 60) = 2.23$, $p = 0.077$, partial $\eta^2 = 0.13$. For both tasks, only the linear component of the main effect of retention interval was found to be significant: motor localizations, $F(1, 15) = 4.6$, $p = 0.049$, partial $\eta^2 = 0.24$; perceptual judgements, $F(1, 15) = 9.5$, $p = 0.008$, partial $\eta^2 = 0.38$. For both tasks and all retention interval levels, mean representational gravity was found to be significantly different from 0, as revealed with one-sample t tests: motor localizations: 0 ms, $t(15) = -3.56$, $p = 0.003$; 300 ms, $t(15) = -3.95$, $p = 0.001$; 600 ms, $t(15) = -3.68$, $p = 0.002$; 900 ms, $t(15) = -4.19$, $p = 0.001$; 1200 ms, $t(15) = -4.92$, $p < 0.001$; perceptual judgements: 0 ms, $t(15) = -3.25$, $p = 0.005$; 300 ms, $t(15) = -3.63$, $p = 0.002$; 600 ms, $t(15) = -4.2$, $p = 0.001$; 900 ms, $t(15) = -6.98$, $p < 0.001$; 1200 ms, $t(15) = -6.55$, $p < 0.001$.

Downward drift rate

Figure 5 depicts individual values (separate lines) of representational gravity for each retention interval (abscissas) and task (motor localization: panel A; perceptual judgement: panel B). Mean values of representational gravity for motor localizations are fairly dispersed albeit generally below 0. For all but four participants, mean representational gravity increases or keeps a constant value with increasing retention times. With perceptual judgements, individual representational gravity values seem to be less dispersed and more packed around a negative value. For all but one single participant, representational gravity increases downwards with longer retention intervals. While the increase of representational gravity with retention interval is similar for both tasks, it seems to occur at a greater rate in the staircase task. to further explore the rate at which the perceived vanishing location drifted downwards, the individual slopes of the best linear fit between retention interval and representational

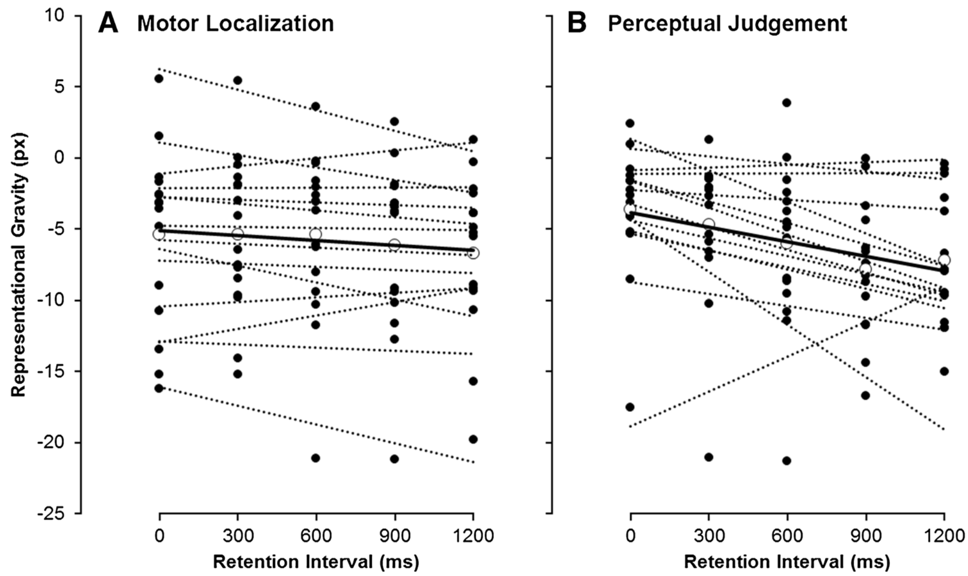

Fig. 5 Mean representational gravity as a function of retention interval (abscissas) for each individual participant (filled circles and dotted lines) and for the whole sample (white circles and continuous line) found with motor localizations (**a**) and with perceptual judgements (**b**). Lines depict the best linear fits

gravity were calculated for each task (resulting in a value expressed in pixels per second) and a R^2 value of at least 0.1 adopted as a cut-off criterion for a relation between retention interval and representational gravity. Four participants in the motor localization but only 2 in the perceptual judgement task showed no discernible trend in representational gravity as a function of retention interval ($R^2 < 0.1$). Three other participants in the motor localization and one in the perceptual judgement task showed a trend where representational gravity decreased with longer retention intervals. For the remaining participants, the R^2 values of the linear fits ranged from 0.17 to 0.92 with motor localizations ($n = 9$; $M = 0.55$, SD = 0.27) and from 0.21 to 0.98 with perceptual judgements ($n = 13$; $M = 0.6$; SD = 0.26).

A paired t test applied to the whole sample ($n = 16$) with task as factor revealed a larger downward drift rate for the perceptual judgements than for the motor localizations, $t(15) = 2.22$, $p = 0.043$, Cohen's $d = 0.55$. This finding did not change when merely looking at the 9 subjects for whom the downward drift rate was both negative and had an associated $R^2 > 0.1$ in both tasks: $t(8) = 3.2$, $p = 0.013$, Cohen's $d = 1.1$. For both tasks, the mean drift rate was found to be significantly different from zero. This was true when considering the whole sample—motor localizations, $M = -1.18$ px/s, SD = 2.2, $t(15) = -2.14$, $p = 0.049$, Cohen's $d = 0.54$; perceptual judgements, $M = -3.42$ px/s, SD = 4.44, $t(15) = -3.08$, $p = 0.008$, Cohen's $d = 0.77$—and when only considering those participants for whom the drift rate was both negative and with $R^2 > 0.1$—motor localizations, $M = -2.6$ px/s, SD = 1.5, $t(8) = -4.9$, $p = 0.001$, Cohen's $d = 1.66$; perceptual judgements, $M = -4.9$ px/s, SD = 2.9, $t(12) = -5.9$, $p < 0.001$, Cohen's $d = 1.65$.

Just-noticeable differences (JNDs)

Mean JNDs, which provide an indication of the precision of judgements, were found to be much higher for the motor localization (horizontally: $M = 21.23$, SD = 9.32; vertically: $M = 8.95$, SD = 4.47) in comparison with the perceptual judgement task (horizontally: $M = 1.56$, SD = 0.86; vertically: $M = 1.5$, SD = 0.83). Separate ANOVAs were conducted on the mean JNDs for each task with retention time and dimension (horizontal versus vertical) as main factors. For perceptual judgements, mean JNDs differed neither among retention interval levels, $F(4, 60) = 1.48$, $p = 0.221$, nor between horizontal and vertical dimensions, $F(1, 15) < 1$. In contrast, for the motor localization task, horizontal JNDs were significantly higher than vertical JNDs, $F(1, 15) = 78.57$, $p < 0.001$, partial $\eta^2 = 0.84$. Retention interval had a slight and marginally significant effect on mean JNDs, $F(2.63, 39.5) = 2.68$, $p = 0.067$, partial $\eta^2 = 0.15$, as well as a marginally significant interaction with dimension, $F(4, 60) = 2.39$, $p = 0.061$, partial $\eta^2 = 0.14$. These trends were mostly due to an observed slightly increased mean JND for the shortest retention intervals that differed between vertical and horizontal.

Response times

Finally, an ANOVA conducted on mean response times with task and retention interval as main factors (see Fig. 6) uncovered, unsurprisingly, significantly higher response times for the adjustment task, $F(1, 15) = 18.53$, $p = 0.001$, partial $\eta^2 = 0.55$, and a significant effect of retention interval, $F(1.96, 29.4) = 27.36$, $p < 0.001$, partial $\eta^2 = 0.65$, with response times decreasing for longer intervals, albeit at a

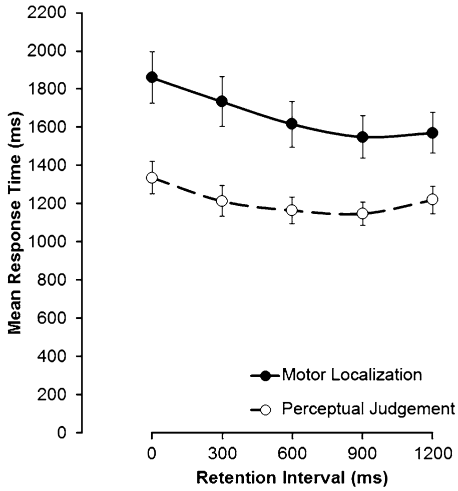

Fig. 6 Mean response times for the motor localization (filled circles and continuous line) and the perceptual judgement (open circles and dashed line) tasks as a function of retention interval

slower rate for the staircase task, as evidenced by a significant interaction between task and retention interval, $F(2.69, 40.39) = 4.56$, $p = 0.01$, partial $\eta^2 = 0.23$.

Discussion and conclusion

The present experiment aimed to assess how representational momentum and representational gravity, as well as their respective time courses, were modulated by the response modality by juxtaposing a behavioural localization task, with a considerable degree of motor engagement, and a purely perceptual judgment. Participants saw a horizontally moving object which suddenly disappeared and were instructed to indicate the perceived vanishing location either by displacing a visual probe with a computer mouse or by emitting a judgement concerning the relative position of the visual probe (4AFC).

The indicated vanishing location of the target was significantly displaced forward (representational momentum) when the visual probe was adjusted with a motor action but not when a perceptual judgement was provided. This outcome suggests that while the visual evaluation of the last seen position occupied by a moving object seems to be fairly accurate (albeit subject to variability), engagement of motor components in the response leads to a spatial overshoot. It might be argued that the perceptual judgements required simultaneous attention to two separate spatial judgements (i.e., vertical and horizontal) and, therefore, increased cognitive load as compared with motor localizations, where the cursor was adjusted to a single location. Thus, the increased cognitive load with perceptual judgments could account for the differences between tasks. We can safely dismiss this possibility for several reasons. First, informal reports from the participants during debriefing suggest that perceptual judgements were no more difficult than motor localizations. Second, increases in attentional load (e.g., with a concurrent task or two targets) have been reported to increase (Hayes & Freyd, 2002) or to have no effect (Kerzel, 2004) on representational momentum. Finally, if mean JNDs are taken as an index of task difficulty, then motor judgments along the motion direction were more difficult than perceptual judgments, even though perceptual judgments require a separate estimation of vertical and horizontal position.

Overall, the indicated vanishing location of the target was displaced downwards, in the direction of gravity, for both tasks. Representational gravity increased with time elapsed after target's offset, but with differences in the time course between the two tasks. For the mouse localization responses, representational gravity was found to be fairly stable until about 600 ms after target offset, but increased for longer retention intervals. The mean overall downward drift rate was found to be between 1 and 3 pixels per second. In contrast, when a perceptual judgement was provided, representational gravity was found to steadily increase immediately after the target vanished at a rate between 3 and 5 pixels per second. These findings suggest that representational gravity is not solely restricted to the sensorimotor mechanisms. If anything, effects of the anticipation of gravity are decreased in motor-guided localization responses, in comparison with perceptual judgments. The fact that motor engagement diminishes the dynamics of the downward displacement seems likewise to corroborate previous findings: representational gravity was found to remain stable until at least 300 ms after target appearance, except when eye movements are constrained (De Sá Teixeira et al., 2013; see also; De Sá Teixeira, 2016). When observers were required to directly touch the screen location where a moving target disappeared, representational gravity was found to be constant and no time-dependent drift was seen (De Sá Teixeira & Oliveira, 2013).

Taking the available evidence together, a case can be made that the downward drift reflects mainly a cognitive mechanism which dynamically updates the representation of the vanishing location by considering expectations based upon a representational analogue of gravity. In general, visually guided motor actions seem to be less susceptible to this phenomenon, either because (i) the timely outputs of the spatial updating mechanisms are not fed into the motor system to guide the localization response or (ii) the involvement of motor components mask the gravity-related downward drift. Supporting the latter, motor localizations resulted in an increased spatial variability (as revealed by mean JNDs) that might have masked, rather than prevented, systematic spatial biases. Notwithstanding, the former cannot be excluded as a direct pointing task, with no associated increase in variability, fails to result in a time-dependent downward drift (De Sá Teixeira & Oliveira, 2013). In any case, the occurrence of the (less pronounced) time course of representational momentum with mouse localizations in the present and previous experiments (e.g., De Sá Teixeira et al. 2013) suggests that the representational update might "leak" into motor responses under certain conditions. In fact, mouse localizations may be an intermediate step between purely perceptual judgements (in the sense that a visual marker needs to be made to coincide with the target's perceived offset location) and a motor response (being mostly based on a motor action directly mapped onto the stimulus plane). If this account is correct, mouse-based spatial localizations would reflect a mixed contribution of cognitive representations of gravity and motor phenomena.

A relevant consequence of this interpretation is that it leaves little room for a direct connection between the time course of representational gravity and visual gravitational motion cues known to guide interceptive actions (Lacquaniti et al., 2013; La Scaleia, Zago, & Lacquaniti, 2015; McIntyre et al. 2001; Séac'h, Senot, & MacIntyre, 2010; Senot et al. 2005, 2012; Zago, Bosco, Maffei, Iosa, Ivanenko & Lacquaniti, 2004, 2008), besides the hypothesis that both reflect an internalization of earth's gravity. It is important, however, not to overlook some crucial differences between studies of spatial displacements and findings on interceptive actions. On the one hand, in spatial localization studies, such as the present one, accelerating stimuli are only rarely shown and constant velocity is usually favoured. This situation is very different from studies on the role of internal models of gravity for interceptive behaviours where the opposite is true (e.g., Bosco et al. 2008; Bosco, Delle Monache, & Lacquaniti, 2012; Delle Monache, Lacquaniti, & Bosco, 2014; La Scaleia et al. 2015; but see; Senot, Zago, Lacquaniti & McIntyre, 2005; Senot, Zago, Séac'h, Zaoui, Berthoz, Lacquantiti & McIntyre, 2012; Zago et al. 2004). This difference alone suggests that any direct comparison between these two research lines should be taken carefully—an object undergoing an explicit downward acceleration provides a powerful visual cue that it is under the influence of a gravitational force, which should be taken into account if an interception is to be successful. There is no such strict constraint for a judgement concerning the spatial location of an object moving horizontally at a smooth and constant velocity. This question should be empirically addressed in the future by measuring representational momentum and representational gravity, with motor localization and visual judgements, for targets with dynamics conforming or violating gravitational acceleration. Even though some evidence suggests that, overall, the human visual system is not efficient in the discrimination of arbitrary accelerations (e.g. Hecht & Bertamini, 2000), it seems to play a role when in congruence with earth's gravity (Moscatelli & Lacquaniti, 2011; Zago et al. 2004). On the other hand, and perhaps more relevant, the nature of the tasks is dramatically different and even, all things considered, opposed: there is little reason to expect commensurate performances when an observer is required to intercept a moving object as opposed to being told to accurately locate its offset position. Interception can hardly be accomplished with reference to where the object was instead of where it will be. Locating the offset position would likely be impaired if made in reference to where the object would have been instead of where it actually was when it disappeared. It goes without saying that the retrospective focus, emphasizing accuracy, as demanded by the localization task, greatly accounts for why representational gravity leads to relatively small spatial biases, of only about 0.2° of visual angle—hardly enough to be useful for a timely interceptive action. Instead, it seems to be the case that representational gravity reflects the best compromise between knowledge about the world's dynamics, gravity in particular, and its instantiation within perceptual mechanisms, and the demands of the localization task, favouring accuracy.

In conclusion, the present outcomes provide evidence in favour of the claim that gravity is internally modelled throughout the visual system and not confined to the motor system. By virtue of gravity's pervasiveness and its role in shaping the behaviour of physical systems at the human scale, gravity might be taken as one of the most paramount invariants to which we have to conform, across virtually all conceivable activity. That gravity effects are modelled and represented for a wide range of seen motions, task requirements and triggered for motor and perceptual judgements alike, even if ultimately leading to localization errors, speaks favourably to the idea that it is to be taken as a critical factor in structuring our spatial apprehension.

Compliance with ethical standards

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Conflict of interest The authors declare no conflict of interests.

Ethical approval All procedures performed in this study were approved by the local ethics committee of the Santa Lucia Foundation, and the experimental protocol was conducted in accordance with the 1964 Declaration of Helsinki and its later amendments.

Informed consent Written informed consent was obtained from all individual participants included in this study.

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