



**RODRIGO RIBEIRO
FREITAS**

**ORIENTAÇÃO VISUAL ESPACIAL E GRAVIDADE
REPRESENTACIONAL: A ORIENTAÇÃO DAS
PISTAS VISUAIS MODULA A EXTRAPOLAÇÃO DE
MOVIMENTO**

**VISUAL SPACE ORIENTATION AND
REPRESENTATIONAL GRAVITY: ORIENTATION
POLARIZING VISUAL CUES MODULATE THE
EXTRAPOLATION OF MOTION**



**RODRIGO RIBEIRO
FREITAS**

**ORIENTAÇÃO VISUAL ESPACIAL E GRAVIDADE
REPRESENTACIONAL: A ORIENTAÇÃO DAS
PISTAS VISUAIS MODULA A EXTRAPOLAÇÃO
PERCETUAL DE UM ALVO EM MOVIMENTO**

**VISUAL SPACE ORIENTATION AND
REPRESENTATIONAL GRAVITY: ORIENTATION
POLARIZING VISUAL CUES MODULATE THE
PERCEPTUAL EXTRAPOLATION OF MOTION**

Dissertação apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Psicologia da Saúde e Reabilitação Neuropsicológica, realizada sob a orientação científica do Doutor Nuno Alexandre de Sá Teixeira, Professor Auxiliar Convidado do Departamento de Educação e Psicologia da Universidade de Aveiro

Dedico este trabalho aos meus pais, Orlando e Elsa, pois sem eles nada disso seria possível. Muito obrigado por tudo aquilo que investiram em mim, por acreditarem em mim e por todas palavras de apoio ao longo destes cinco anos. Para sempre louvarei o que fizeram por mim e tenho a certeza de que esta não é uma conquista apenas minha, mas também vossa. Mil obrigados pelo amor e dedicação.

Ao meu irmão, Santiago, obrigado pela sua alegria, companhia e por todos os momentos incríveis que já passamos juntos. Não imagino o meu percurso e a minha vida sem ti.

Ao professor Nuno, pela paciência, apoio incansável, ensinamentos e pela incrível relação de amizade que estabeleceu comigo desde o início deste processo. Obrigado por despertar o interesse numa área nova para mim e acreditar no meu trabalho. Foi sem dúvida o melhor orientador que poderia ter e foi uma peça-chave para o meu sucesso académico.

Aos meus avós, João, Nélia, Orlando e Maria Emília, pois foram um suporte essencial ao longo deste meu percurso académico. Sempre foram e serão uns autênticos pais e não imagino o meu percurso e a minha vida sem eles. Obrigado por todo o amor e carinho.

À minha namorada, Fabiana, por estar sempre lá para mim, nos bons e maus momentos. Foste uma peça fundamental ao longo de todo este processo, pois fizeste-me acreditar mesmo nos momentos em que eu próprio pensava não ser capaz. Desde o início da nossa relação que és e sempre serás uma pessoa essencial na minha vida. Muito obrigado por tudo.

Aos meus Padrinhos e Tios, Jorge, Helena, Francisco e Sofia. Desde o início que estiveram presentes neste meu percurso. Muito obrigado por todo apoio e pelas visitas sempre que voltava a casa para férias. São através de pequenos gestos que se mostra o carinho e amor pelos outros.

Aos meus Primos, Maria Helena, Clara e Diogo. Além de primos, somos como irmãos e sem dúvida que tiveram um papel fulcral para esta conquista. Obrigado por todos os momentos bons e que no futuro estejamos a festejar a vossa vez.

A todos os meus amigos. Sem eles a vida não faz sentido e são através dos momentos que passamos juntos que vou buscar forças para ultrapassar o mais difícil da vida. Sou um sortudo por ter vários e bons amigos. Não vou referir nomes em concreto pois são muitos aqueles que são muito importantes para mim. Eles sabem quem são e na minha perspetiva este reconhecimento é o mais importante.

o júri
Presidente

Professora Doutora Anabela Maria Sousa Pereira
Professora Associada com Agregação da Universidade de Aveiro

Doutor Sergio Delle Monache
Investigador Doutoramento, Unicamillus - International Medical University In Rome

Professor Doutor Nuno Alexandre de Sá Teixeira
Professor Auxiliar Convidado da Universidade de Aveiro

palavras-chave

Orientação Espacial, Percepção do Movimento, Vertical Visual Subjetivo, Percepção Vertical, Momento Representacional, Gravidade Representacional

Resumo

O local de desaparecimento de um objeto em movimento é geralmente percebido como desfasado para diante, na direção do movimento (Momento Representacional), e para baixo, na direção da gravidade (Gravidade Representacional). No que se refere a esse último, o termo “para baixo na direção da gravidade” é ambíguo, pois está estabelecido que a direção percebida da gravidade (“para baixo”) resulta de uma interação entre sinais vestibulares, sensíveis ao vector gravito-inercial, uma tendência *a priori* para assumir que essa se alinha com o eixo principal do corpo (vector idiótrópico) e pistas visuais. Assim, este trabalho procura perceber quais os efeitos que pistas visuais têm sobre a Gravidade Representacional. Os participantes realizaram três tarefas. Uma tarefa de localização espacial, outra de percepção da direção vertical subjetiva (SVV) e ainda uma tarefa de reconhecimento da orientação de caracteres (OCHART). Os estímulos foram apresentados sobre um fundo realista e rico em pistas visuais, alinhado na direção da gravidade ou inclinado para a esquerda/direita. Os resultados indicam que pistas visuais têm um efeito significativo na percepção da localização espacial. A saber, o desfasamento no sentido do movimento do alvo (Desfasamento-M) foi superior para alvos que se deslocaram na direção “horizontal” imposta pelo fundo. Este padrão, adicionalmente, correlacionou-se com a magnitude da vertical visual subjetiva, mas não com a orientação ‘vertical’ percebida (medida pela OCHART). Estes resultados mostram que os juízos de localização espacial são modulados pela orientação espacial induzida visualmente, oferecendo assim uma base teórico-empírica para expandir estudos sobre a orientação espacial, além de clarificar a natureza multissensorial da Gravidade Representacional.

Keywords

Spatial Orientation, Motion Perception, Subjective Visual Vertical, Perceptual Upright, Representational Momentum, Representational Gravity

Abstract

The perceived offset of a moving target is usually displaced forward, in the direction of motion (Representational Momentum), and downwards, in the direction of gravity (Representational Gravity). In what refers to the latter, the meaning of “downward in the direction of gravity” is ill-defined, for it is known that the perceived direction of gravity (“downward”) results from the interaction of vestibular signals, sensitive to the gravito-inertial vector, an aprioristic tendency to assume that it aligns with the body’s main axis (idiotropic vector) and visual cues. The present work aims to disclose what effects visual cues have on Representational Gravity. Participants performed a spatial localization task as well as a Subjective Visual Vertical (SVV) and an Oriented Character Recognition Task (OCHART), with stimuli being presented above a realistic background either aligned with earth’s vertical or tilted rightward or leftward. Outcomes disclosed significant and lawful effects of the orientation of the visual context on spatial localization judgements. Specifically, forward displacement along the target’s motion direction (M-displacement) was bigger for targets moving along the ‘horizontal’ direction implied by the background scene. These trends were furthermore found to be correlated, at an individual level, with the magnitude of SVV, but not of the Perceptual Upright (as measured with OCHART). These findings show that features of the spatial localization judgements specifically index the visually induced spatial orientation, thus offering the prospect to expand available tools for inquiries concerning human spatial orientation, besides clarifying the multisensorial nature and significantly expanding the notion of Representational Gravity.

Index

Introduction.....	1
Representational Momentum and Representational Gravity.....	1
Spatial Orientation, Subjective Visual Vertical, and Perceptual Upright.....	4
Spatial Orientation and Representational Gravity.....	6
The present study.....	6
Methods.....	7
Participants.....	7
Stimuli.....	7
Apparatus, procedure and design.....	8
Calculations, Hypotheses and Statistical Analyses.....	11
Results.....	14
SVV and PU.....	14
M-displacements.....	16
Discussion and conclusions.....	18
References.....	21

Introduction

A prominent tenet in contemporary research on the visual perception of events holds that humans possess internalized representational analogues of physical principles, such as momentum, friction and gravity, in the form of internal models (Tin & Poon, 2005; Grush, 2005; Lacquaniti et al, 2013; Zago & Lacquaniti, 2005) and thought to support the anticipation of seen or experienced dynamics, so as to aid subsequent motor interactions (Tresilian, 2004, 2005; McIntyre et al, 2001; Zago et al, 2008). Among the several perceptual phenomena that have been linked to the functioning of these putative internal models (Lacquaniti et al, 2013) is *Representational Momentum* (for reviews, Hubbard, 2005, 2010, 2014) and the closely related *Representational Gravity* (for a review see Hubbard, 2020), both measurable through a simple spatial localization task.

Representational Momentum and Representational Gravity

Briefly, when observers are shown a moving target which is suddenly and unexpectedly halted, and if further required to indicate its offset location, a systematic displacement forward, in the direction of motion (*Representational Momentum*), and downward, in the direction of gravity (*Representational Gravity*), can be observed. Originally reported by Freyd and Finke (1984), *Representational Momentum* was posed as one instance of a *Dynamic Representation* – mental representations for which time itself was intrinsically, necessarily, and analogically represented (Freyd, 1987). In the seminal experiment, participants were shown a sequence of three rectangles implying a rotational motion (inducing sequence), followed by a static rectangle whose orientation should be judged as ‘same’ or ‘different’ regarding the last one in the sequence (mnestic probe). Results disclosed a systematic tendency to accept as ‘same’ a probe which was actually further rotated in the direction of implied motion. It was hypothesized that, upon a sudden vanishing of the visual input, the accompanying *Dynamic Representation* could not be instantaneously halted and, thus, would continue to unfold for some time, as if it possessed an analogue of physical momentum (and hence the label with which the phenomenon was coined).

Following this report, it was found that the magnitude of *Representational Momentum* increased with implied speed (Freyd & Finke, 1985; Finke, Freyd, & Shyi, 1986), with increasing temporal intervals between the inducing sequence and the onset of the probe (until a maximum at about 300 ms; Freyd & Jonhson, 1987), that its magnitude was modulated by the identity of the target (e.g., a rocket or a weight; Reed & Vinson, 1996), that it was bigger

for implied motions aligned with the gravitational pull (Bertamini, 1993; Nagai, Kazai, & Yagi, 2002), that it emerged even for static pictures where motion was solely implied (Freyd, 1983; Bertamini, 1993), just to name a few of the factors that were found to affect the phenomenon (see Hubbard, 2005).

Research on *Representational Momentum* was significantly expanded following the report of Hubbard and Bharucha (1988; see also Hubbard, 1990, 1995, 1997, 1998). These authors presented to observers a small target moving smoothly across the screen at a constant speed, either following a horizontal or vertical trajectory, which suddenly disappeared. Participants were required to locate the vanishing position of the target by adjusting a cursor with a computer mouse to the desired location. Outcomes disclosed a pattern where the perceived offset of the target was displaced forward, in the direction of motion, and downward, in the direction of gravity, for targets moving horizontally.

These spatial localization errors were coined *M-displacement* (with ‘M’ standing for ‘Motion’) and *O-displacement* (with ‘O’ indexing a measurement made Orthogonal to the motion direction) and taken as empirical measures of the standard *Representational Momentum* and of a similar phenomenon reflecting an internal analogue of physical gravity – *Representational Gravity* – respectively. For targets moving vertically, *M-displacement* (localization error measured along the target’s motion direction) was found to be bigger for descending targets (moving towards the gravitational pull) and smaller for ascending ones (moving contrary to the gravitational pull), suggesting that depending on the relation between target’s trajectory and the direction of gravity, *Representational Momentum* and *Representational Gravity* would jointly determine a spatial localization judgement. As was the case for *Representational Momentum*, a time course was furthermore reported for *Representational Gravity*, where it increased for increasing temporal intervals imposed before a response (De Sá Teixeira, Hecht, & Oliveira, 2013).

Notwithstanding, subsequent research cast some doubts on the degree to which *M-displacement*, at least when measured for smooth continuously moving targets, could be taken unambiguously as a measure of *Representational Momentum*, for it is well established that for that type of stimulus, smooth pursuit eye movements are engaged and continue to move forward after target’s offset (Mitrani & Dimitrov, 1978; Pola & Wyatt, 1997; see also Kerzel, 2006, and Hubbard, 2006, for a response). Accordingly, it has been reported that *M-*

displacement is null or strongly reduced when eye movements are prevented (e.g., Kerzel, 2000; Kerzel, Jordan, & Müsseler, 2001; De Sá Teixeira, Hecht, & Oliveira, 2013; De Sá Teixeira, 2016), albeit not for targets undergoing implied motion (Kerzel, 2003a, 2003b). The relationship between oculomotor behaviour and *M-displacement* for smoothly moving targets is further complicated by the fact that it seems to be mediated by the type of response used to measure spatial localization (mnestic probe, computer mouse, or direct pointing with the finger; Ashida, 2004; Kerzel & Gegenfurtner, 2003; De Sá Teixeira et al, 2019).

Importantly enough, the downward displacement typically found when observers indicate the vanishing location of a moving target (indexed with *O-displacement*, for horizontal trajectories, or with *M-displacement*, for vertically moving targets), thought to reflect *Representational Gravity*, does not seem to depend upon oculomotor behaviour (De Sá Teixeira, Hecht, & Oliveira, 2013; De Sá Teixeira, 2016) or response modality (De Sá Teixeira et al, 2019). For instance, De Sá Teixeira (2016) measured *M-displacement* for targets moving linearly along 16 possible directions in the fronto-parallel plane, encompassing horizontal (leftward and rightward), vertical (upward and downward) and intermediate trajectories. In accordance with previous experiments, *M-displacement* increased progressively as the trajectories approached a downward trajectory and decreased for targets moving for upward directions.

By virtue of its periodicity as a function of target's direction, *M-displacement* could be subjected to a discrete Fourier decomposition (see Sekuler & Armstrong, 1978; see also Figure 2 and equation 2 below) to independently estimate its underlying harmonic terms. It was found that *M-displacement* could be accurately accounted for by a constant c , capturing a constant displacement forward, irrespective of motion direction (i.e., *Representational Momentum*), plus a sine component (first harmonic term), characterized by a negative coefficient b_1 , which resulted in an increase/decrease of *M-displacement* for descending/ascending directions (i.e., *Representational Gravity*), and a significant second harmonic term, defined by a positive coefficient a_2 , reflecting the fact that *M-displacement* was slightly bigger for targets moving close to the horizontal (either leftward or rightward; *Horizontal Bias*). When the same procedure was employed while participants were prevented from moving their eyes, the constant c , but none of the remaining harmonic terms, was reduced to 0, suggesting that eye movements affect *Representational Momentum*, but not *Representational Gravity* or the found *Horizontal Bias*.

Besides adding to the ongoing discussion on the role of eye movements on *Representational Momentum*, this study offered the prospect of disentangling the phenomena involved in spatial localization tasks, via the decomposition of *M-displacement* into its harmonic terms. For example, the same logic was employed in an attempt to clarify the neurophysiological substrates of *Representational Momentum* and *Representational Gravity* (De Sá Teixeira, Bosco, Delle Monache, & Lacquaniti, 2019) and, of relevance to the experiment to be presently discussed, how *Representational Gravity* relates to the literature on spatial orientation (Howard & Templeton, 1966; Howard, 1982; Mittelstaedt, 1986).

Spatial Orientation, Subjective Visual Vertical, and Perceptual Upright

Up until now, we have been referring to *Representational Gravity*, succinctly, as a perceptual displacement of the offset location of a moving target *downward in the direction of gravity*. The latter expression (in italics), is arguably ill-defined, for it has been acknowledged ever since the seminal research conducted by Mittelstaedt (1983; 1986; see also Glasauer & Mittelstaedt, 1992; Zupan, Merfeld, & Darlot, 2002; MacNeilage et al, 2006) that the perceived direction of ‘downward’ results from a complex interaction between vestibular signals in the internal ear (in particular from the otolithic organs; see, e.g., Mars et al, 2001; Volkening et al, 2014), orientation polarizing cues available in the visual scene (e.g., trees, texture gradients in the surfaces, posture of conspecifics, architectural lines, etc; Howard, 1982; MacNeilage et al, 2006), and a tendency to assume *a priori* that the vertical direction aligns with one’s own longitudinal body axis (*idiotropic vector*; Mittelstaedt, 1986; MacNeilage et al, 2006). Importantly, and depending on the relative directions implied by these disparate sources, the perceived vertical direction might diverge significantly from the actual vertical, tantamount to the direction of the gravitational pull, or result in a conflict between different cues, with implications for spatial orientation and navigation (e.g., Oman, 2003). In fact, the perceived and the actual vertical direction seldom coincide, apart from the special case of an upright observer embedded in an environment with rich and congruent visual cues.

Classically, the subjective vertical direction is gauged by requiring the participants to adjust a visual rod to match their perceived ‘downward’ direction – *Subjective Visual Vertical* task (SVV). In the absence of visual contextual cues, human observers are considerably accurate in adjusting the rod when in an upright posture. When assuming a posture misaligned with gravity, a conflict between vestibular otolithic signals and the idiotropic vector ensues,

resulting in a bias of up to 40° to 50° towards the head (*Aubert Effect*, first reported by Aubert, 1861; Mittelstaedt, 1986; De Vrijer, Medendorp, & Van Gisbergen, 2008, 2009). On the other hand, even if an observer is upright and aligned with gravity's direction, imposing a visual rectangular frame askew away from the vertical by about 30° results in an adjustment of the visual rod biased by up to 10° or more toward the direction implied by visual cues, albeit varying considerably across observers (*rod-and-frame illusion*; see, e.g., Wenderoth, 1974; Howard & Childerson, 1994; Haji-Khamneh & Harris, 2010).

A related concept, developed from studies on object orientation recognition (e.g., Howard et al, 1990; Jenkin & Howard, 1998; Jenkin et al, 2004), refers to the so called *Perceptual Upright* (PU), measurable with the *Oriented Character Recognition Task* (OCHART; Dyde, Jenkin, & Harris, 2006). In this task, participants are shown the letter 'd' with varying orientations and asked to indicate if they perceive it as a 'd' or a 'p' (notice that, graphically, these letters are distinguishable solely by their orientation). The perceptual thresholds as a function of the character's orientation, where 50% 'd' responses are observed, are used to determine the orientation at which the character is seen as 'upright'. Notice that, unlike the SVV, which reflects the internal perceived direction of gravity, PU reflects a judgement concerning the orientation of an external observed object (the orientation at which it *seems to be upright*; Dyde, Jenkin, & Harris, 2006; Haji-Khaman & Harris, 2010). If the character is embedded in a visual context with orientation cues, the PU is significantly changed accordingly (Dyde, Jenkin, & Harris, 2006; see also Jenkin et al, 2011, for an effect of dynamic visual cues).

PU, like SVV, is also affected by the sensed direction of gravity, as signalled by the otolithic organs, and by the orientation of the participants' bodies, albeit both measures reflect disparate weightings of these cues. Dyde, Jenkin and Harris (2006) systematically varied the orientation of a visual context (background scenes) and the observers' posture, while measuring both SVV and PU. Based upon the obtained results, these authors estimated that the relative weights of vision and bodily cues, normalized to gravity (with a weight = 1) was about 1.2 and 2.6, respectively for the PU, but about 0.1 and 0.2 for SVV. That is, while PU seems to reflect a more or less balanced compromise of visual, bodily and vestibular cues, SVV seems to be mostly dominated by vestibular signals.

Spatial Orientation and Representational Gravity

To the degree that *Representational Gravity* manifests as a perceptual spatial displacement ‘downward’, it might be asked what factors, known to determine spatial orientation, determine its dynamics and direction. Following this reasoning, and taking advantage of the Fourier decomposition referred above, previous research showed that *Representational Gravity* (indexed by the first harmonic term present in a set of *M-displacements*), acts mainly along the body’s longitudinal axis (*idiotropic vector*). That is, if an observer performs a spatial localization task while in a lateral decubitus posture (at an angle of 90° in relation to the direction of gravity), a bigger displacement can be observed for targets moving towards the observers’ feet and a smaller one for targets moving towards the observers’ heads (De Sá Teixeira & Hecht, 2014a; De Sá Teixeira, 2014; but see Nagai, Kazai, & Yagi, 2002). This trend can be observed even if the observers’ posture is not changed, but they experience an artificial gravity vector sideways when accelerated in a centrifuge (*somatogravic illusion*; Gillingham & Previc, 1993; Glasauer, 1995; Clément, Moore, Raphan, & Cohen, 2001).

Of relevance, while the direction of *Representational Gravity* seems to be entirely determined by the idiotropic vector, its time course seems sensitive to the degree of misalignment between the observers bodies and the direction of gravity – when both coincide (for an upright observer), *Representational Gravity* increases with time; when the observers are positioned at an angle in respect to the actual vertical, that time course is constrained, and more so as they are further rotated away from the vertical, being null when the participants body is orthogonal (and sideways) in relation to the vertical (De Sá Teixeira & Hecht, 2014a; De Sá Teixeira, 2014; see also, De Sá Teixeira et al, 2016).

The Present Study

A conspicuous gap in the literature reviewed thus far refers to the effects of visual contextual cues on the direction and/or time course of *Representational Gravity*. Usually, in spatial localization tasks, the target is shown moving against a blank uniform background, with no relevant visual cues (apart from peripheral visible features of the laboratory or the frame of the monitor, dominated by vertical and horizontal lines). The present work aims primarily to offer a first inquiry on the role that orientation polarizing visual cues play in providing a ‘downward’ direction along which *Representational Gravity* presumably unfolds. In order to do so, participants performed a spatial localization task referring to the vanishing position of a

target moving along several possible directions (so as to allow a decomposition of its harmonic terms from the measured *M-displacements*) against a visual background either aligned with the actual vertical or tilted leftward or rightward by 22.5°, and after an interval of 0, 300 or 600 ms.

Furthermore, and to aid the interpretation of the results, as well as to ensure that the chosen visual context was effective in modulating spatial orientation, participants also performed a SVV and an OCHART task. Based on the available literature, we hypothesized that three different scenarios where the visual context affects *Representational Gravity* could be the case, each with a predictable pattern of results: (i) Similarly to what happens when a conflict emerges between the idiotropic vector and the vestibular signals, it could be the case that conflicting visual cues diminish or abolish *Representational Gravity*'s time course, without affecting its direction; (ii) Orientation polarizing visual cues might significantly affect the direction of *Representational Gravity* (with or without simultaneously change its time course), as indexed by the first harmonic term; (iii) Orientation of the visual context might also affect the *Horizontal Bias*, as indexed by the second harmonic term, where targets moving along the perceived 'horizontal' directions result in a bigger *M-displacement*. These scenarios and how they related to specific empirical tests, are further elaborated in the section *Calculations, Hypotheses and Statistical Analyses*, below.

Methods

Participants

Thirty-five students (9 males and 26 females) from the University of Aveiro, with ages between 17 and 28 years ($M = 19.86$; $SD = 2.44$), volunteered for the experiment in exchange for partial course credits. Sample size was estimated based upon previous related studies (De Sá Teixeira, 2016; De Sá Teixeira, Bosco, Delle Monache, & Lacquaniti, 2019). All participants were unaware of the purposes of the experiment and had normal or corrected-to-normal vision, no known vestibular deficits or history of vestibular or neurologic disorders.

Stimuli

A public domain photography of the interior of the Harmony ISS module¹ was used as visual context for all tasks (see below). This photograph was chosen because it provides photo-realistic orientation polarizing visual cues, in the form of a structural frame, which are

nonetheless invariant when the picture is flipped (allowing an experimental control of eventual salient visual features which might serve as a landmark for the spatial localization task; see Hubbard & Ruppel, 1999).

Furthermore, this scene provides a reasonable analogue of the visual cues available in microgravity environments, supporting tentative links between our results and applied settings for human factors considerations. The image was manipulated in *Adobe Photoshop* so that the back wall was of uniform luminance (a neutral grey, chosen to match the rest of the image; see Figure 1) and to blur all readable writings. Furthermore, the proportion of the image was changed so that the width of the back wall was 1.5 times larger than its height and the image cropped to a central area of 1024×1024 pixels. Finally, four different versions of the photograph were produced by flipping the image both horizontally and vertically (in order to control for the position of salient visual landmarks). For the spatial localization task, a black circle, with a diameter of 20 pixels (0.598° of visual angle), moving linearly at a speed of 150 pixels per second (about $4.49^\circ/\text{s}$), was used as the target. For the subjective visual vertical measurements, an elongated black ellipse, with 300 pixels (8.97°) and 20 pixels (0.59°) for the long and short axes, respectively, was used as the adjustable visual rod. The ellipse was produced with a grating sin pattern which blurred its contours (preventing participants to use vertical disparities of the pixels to perform the task). Finally, and for the OCHART task, the character 'd', shown with an Arial font and a height of about 100 pixels (2.9° of visual angle) was used as the stimulus.

Apparatus, procedure and design

Upon arrival at the laboratory, all participants were briefed on the experimental procedures and asked to sign an informed consent. The study was pre-approved by the local ethics committee (protocol 03-CED/2020). Participants sat comfortably in front of a computer screen (with a refresh rate of 60-Hz, resolution 1080×1026 and physical size of 37.7×30 cm) such that their cyclopean eye was aligned with its centre and at a distance of 56 cm, kept constant with the aid of a chin-rest. Participants view of the screen was restricted to a circular area, centred on the screen and with a diameter of 30 cm (corresponding to the height of the monitor) with a custom-made cardboard cylinder extending from the participants' heads to the screen (thus occluding any peripheral view of the room). All participants performed three tasks, described below, with the order controlled with a Latin-square design. A short break, of a few

minutes, was allowed after each task was completed. All tasks were programmed in python using PsychoPy (Peirce, 2007, 2009) and ran on a personal computer.

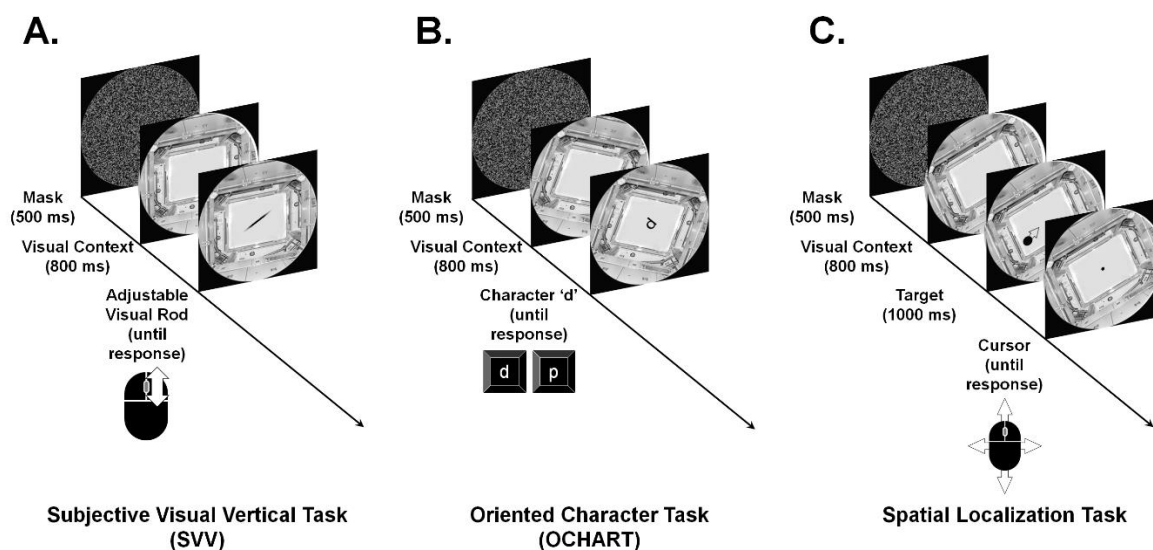


Figure 1 – Trial structure for the Subjective Visual Vertical Task (SVV; Panel A), the Oriented Character Task (OCHART; Panel B) and Spatial Localization Task (Panel C). Notice that stimuli sizes are not to scale.

Subjective Visual Vertical Task (SVV). Each trial started with a rapid sequence of images containing random noise for 500 ms, after which the visual context (4 possible versions) was shown either in an upright orientation (0°) or rotated leftward or rightward by 22.5° (-22.5° or 22.5° , respectively) for 800 ms. Afterwards, the visual rod was shown on the centre of the screen, superimposed on the visual context, and randomly rotated 60° leftwards or rightwards. Participants were instructed to adjust the orientation of the visual rod, using the mouse-wheel, to match the world's vertical (such that if a ball was dropped, its trajectory would be aligned with the rod). Once the visual rod was adjusted to the subjective vertical, participants had to press the 'spacebar' key in a keyboard to confirm their response. A new trial started immediately afterwards (see Figure 1, panel A). The task thus followed a repeated-measures design given by 4 (visual context image) \times 3 (visual context orientation: -22.5° , 0° , or 22.5°) \times 2 (initial orientation of the visual rod: -60° or 60°) \times 2 (replications). Overall, the SVV task took about 10 minutes to complete.

Oriented Character Task (OCHART). As in the SVV task, each trial started with random visual noise for 500 ms followed by the visual context (oriented -22.5° , 0° or 22.5° in

relation to the vertical) for 800 ms. Afterwards, the character ‘d’ was shown superimposed on the visual context and rotated 0° (upright ‘d’), 22.5° , 45° , 67.5° , 90° , 112.5° , 135° , 157.5° , 180° (upright ‘p’), 202.5° , 225° , 247.5° , 270° , 292.5° , 315° , or 337.5° . Participants were instructed to identify the shown character as either a ‘d’ or a ‘p’ by pressing the corresponding key on a standard keyboard, as swiftly and accurately as possible (see Figure 1, panel B). Any response would terminate the trial and a new one started immediately afterwards. The task thus followed a repeated-measures design given by 4 (visual context image) \times 3 (visual context orientation: -22.5° , 0° , or 22.5°) \times 16 (character orientation). Overall, the OCHART took about 10 minutes to complete.

Spatial Localization Task. Similar to the SVV and OCHART tasks, each trial started with random visual noise (500 ms) followed by the visual context for 800 ms, after which the target (black circle) was shown near the limits of the visible window moving toward the centre of the screen at a speed of 150 pixels per second (about $4.49^\circ/\text{s}$). Target’s trajectory was randomly varied across trials between 0° (rightward motion), 22.5° , 45° , 67.5° , 90° (downward motion), 112.5° , 135° , 157.5° , 180° (leftward motion), 202.5° , 225° , 247.5° , 270° (upward motion), 292.5° , 315° , or 337.5° . After covering a total distance of about 600 pixels (17.84°), the target suddenly vanished. The starting location for the target was randomly varied such that it vanished within an area of 50 by 50 pixels beyond the centre of the screen. A black circular cursor (diameter of 5 pixels; 0.15°) appeared on the centre of the screen 0, 300, or 600 ms after target’s offset. Participants were instructed to adjust the location of the cursor, using a computer mouse, to match the judged position where the target disappeared, as precisely as possible and referring to its geometrical centre (see Figure 1, panel C). The judged offset location was confirmed by pressing the left button of the mouse, which also initiated the next trial. The task followed a repeated measures design, given by 4 (visual context image) \times 3 (visual context orientation: -22.5° , 0° , or 22.5°) \times 16 (target’s trajectory) \times 3 (Stimulus-Cursor asynchrony/Retention Interval: 0, 300, or 600ms). Overall, the Spatial localization task took about 40 minutes to complete.

Calculations, Hypotheses and Statistical Analyses

For the SVV task, the deviations in degrees between the adjusted visual rod orientation and the true vertical were calculated for each condition and participant, such that negative numbers depict a leftward orientation and positive numbers a rightward deviation.

Based upon the responses collected in the OCHART task, the proportion of ‘d’ responses was calculated for each condition on an individual basis (taking the 4 different visual context images as repetitions). The data thus obtained was used to estimate the parameters of two psychometric functions, relating the proportion of ‘d’ responses as a function of character orientation: a p-to-d (character orientations between 0° and 180°) and a d-to-p function (character orientations between 180° and 0°). In order to estimate the points of subjective indifference between a ‘d’ and a ‘p’ response, all individual psychometric functions were estimated with the following equation:

(1)

$$P_{Or} = \frac{1}{1 + e^{-\frac{Or - X_0}{b}}}$$

Equation 1 specifies the p-to-d (180° to 0°) psychometric function (the d-to-p function was simply the same equation subtracted from 1), with P referring to the estimated proportion of ‘d’ responses as a function of character orientation Or , X_0 to the estimated point of subjective indifference (a proportion of 0.5 ‘d’ responses) and b to the slope of the function. Parameters X_0 and b were estimated by minimizing the sum of the squares of the errors between the psychometric function and the observed proportions of ‘d’ responses, using *Microsoft Excel’s Solver* add-in. The obtained p-to-d and d-to-p points of subjective indifference were averaged together for each visual context orientation resulting in the estimated *Perceptual Upright* (PU; cf. Dyde, Jenkin, & Harris, 2006), in degrees of deviation from the actual vertical (as in the SVV measures, with negative numbers referring to a leftward deviation and positive numbers to a rightward deviation).

As for the spatial localization task, the arithmetic difference between the horizontal and vertical coordinates of the actual offset and the position indicated in each trial was calculated and used to determine the deviation in pixels of each response, measured along the target’s motion trajectory – *M-displacement*, with positive numbers indicating a forward displacement and negative numbers a backward displacement, in relation to motion direction. The set of *M-displacements* (M), with the orientation of the target’s trajectory as a parameter (θ), was subjected to a discrete Fourier decomposition procedure (for details see Sekuler & Armstrong, 1978; see also De Sá Teixeira, 2014, 2016) to estimate the harmonic coefficients a_i and b_i (up to $i = 4$ – the fourth harmonic term) in accordance with:

$$(2) \quad M_\theta = c + \sum_{i=1}^n \left(a_i \cos i \frac{\theta}{2\pi} + b_i \sin i \frac{\theta}{2\pi} \right)$$

Given that the targets' trajectories varied within the frontoparallel plane in a periodic fashion, the obtained coefficients allow one to specify, in terms of harmonic components, any pattern of increase/decrease of *M-displacements* for preferential directions and to relate those components to the orientation of the visual context. Figure 2 depicts, in polar plots, examples of harmonic terms. Notice that, depending on the signal of the corresponding coefficients, these shapes can be flipped (for instance, a negative b_1 , panel G, would result in that same shape flipped vertically).

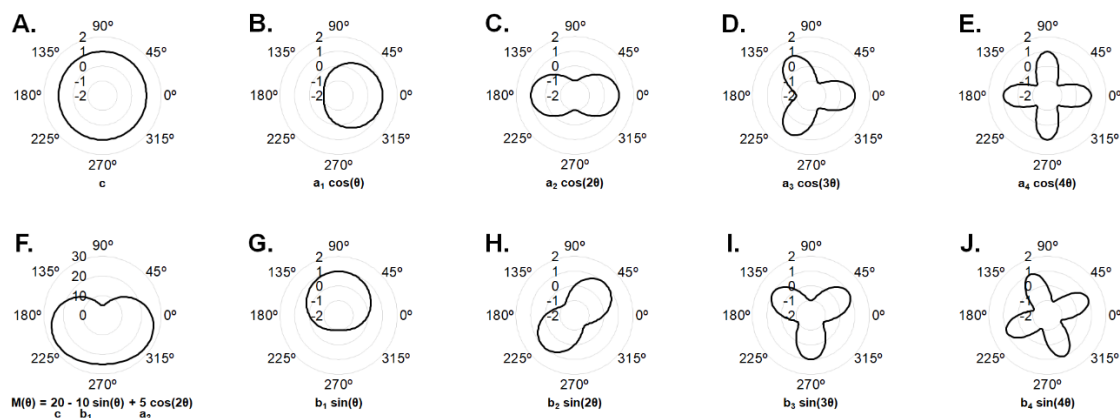


Figure 2 – Catalogue of “shapes”, depicted on polar plots, corresponding to the harmonic terms (up to the fourth). Panel F depicts the sum of terms usually found for spatial localization tasks.

Particular combinations of a and b coefficients can produce any specific orientation of these shapes. Panel F depicts the outcomes usually obtained for spatial localization tasks (cf. De Sá Teixeira, 2014, 2016; De Sá Teixeira et al, 2016; De Sá Teixeira, Bosco, Delle Monache, & Lacquaniti, 2019): a positive c constant, reflecting a spatial displacement forward in the direction of motion – *Representational Momentum* –, a negative b_1 term, accounting for a bigger displacement for descending targets, as compared with ascending ones – *Representational Gravity* –, and a positive a_2 term, capturing a systematic tendency for a bigger forward displacement for targets moving horizontally – *Horizontality Bias*. Importantly, the latter two coefficients can be hypothesized to be affected by the orientation of the visual context, resulting in disparate predictions regarding the patterns of spatial localizations. Figure 3 depicts two possible scenarios where the orientation of the visual context modulates the first (coefficients a_1 and b_1 ; panels A, B, and C) or the second harmonic terms (coefficients a_2 and b_2 ; panels D, E, and F). The first scenario would imply a bigger forward displacement for

targets “descending” along the contextual visual vertical axis; the second scenario would reflect a bigger forward displacement for targets moving along the contextual visual horizontal axis.

Additionally, one further hypothesis can be put forth: previous experiments, as reviewed above, reported that *Representational Gravity* (as indexed with coefficient b_I) increases with time elapsed between target’s offset and the localization response; this temporal course has been found to disappear when the observer’s body axis is misaligned with the direction of gravitational acceleration (De Sá Teixeira & Hecht, 2014a; De Sá Teixeira, 2014; or the gravito-inertial vector in contexts of artificial gravity; De Sá Teixeira et al, 2016). It might be the case that a misalignment between the sensed direction of gravity and the orientation of the visual context would result in a similar reduction or elimination of *Representational Gravity*’s time course. Finally, and it goes without saying, a null effect of the orientation of the visual context on spatial localization responses might arguably be the case, which would imply that phenomena of mislocalization of moving targets is impervious to visual cues of orientation.

In what refers to data analyses, and to test these different scenarios, the obtained values of SVV, PU and all the estimated harmonic coefficients obtained from the localization responses were subjected to repeated measures (M)ANOVAs with visual context orientation as the main independent factor (the different versions of the visual context image, for the SVV, and the target-cursor asynchrony – retention interval – in the spatial localization task, were considered as additional factors when appropriate). Whenever the sphericity assumption was not met, the Greenhouse-Geisser correction for the degrees of freedom was performed.

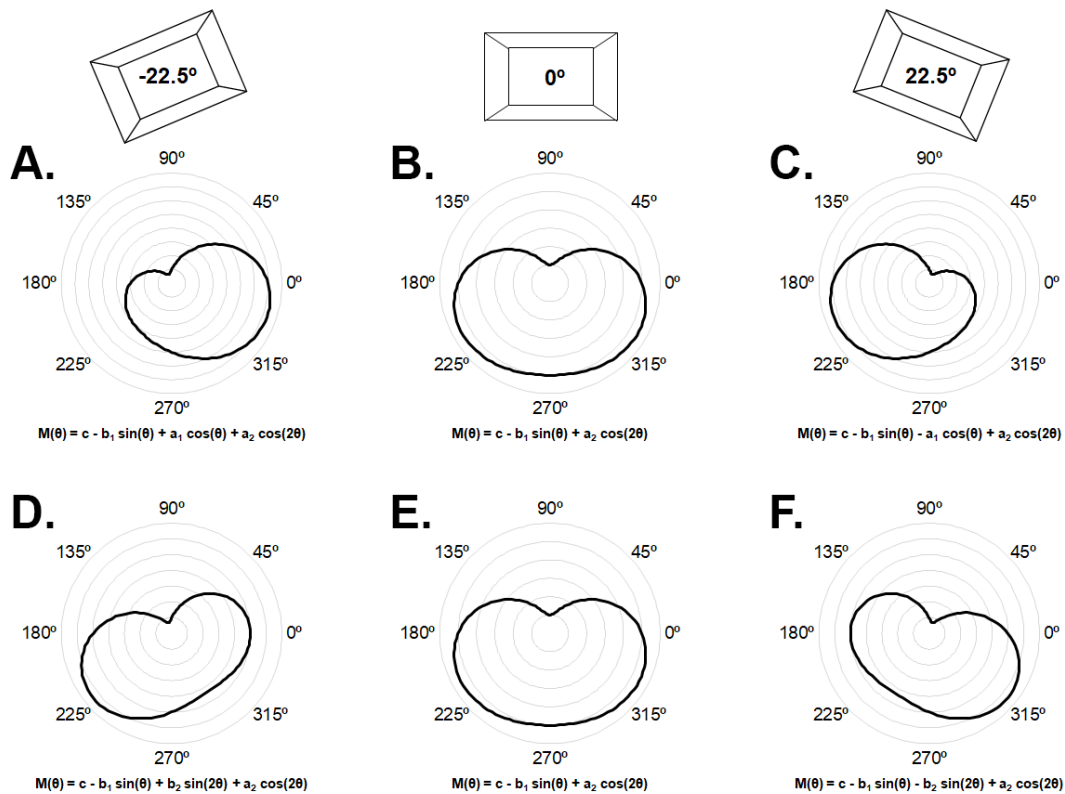


Figure 3 – Hypothesised scenarios where the orientation of the visual context significantly alters the direction of *Representational Gravity* (indexed by the coefficients of the first harmonic term; panels A, B, and C) or the orientation of the *Horizontality Bias* (indexed by the coefficients of the second harmonic term; panels D, E, and F).

Results

SVV and PU

The orientation of the visual context significantly determined the orientation of the subjective visual vertical, $F(1.104, 37.523) = 23.552$, $p < 0.001$, $partial \eta^2 = 0.409$. No significant effects were found for the different versions of the visual context, $F(2.32, 78.89) = 1.754$, $p = 0.175$, $partial \eta^2 = 0.049$, or the interaction between the latter and its orientation, $F(3,826, 130.09) = 1.793$, $p = 0.137$, $partial \eta^2 = 0.05$. Figure 4, panel A, depicts the mean deviations of the subjective visual vertical in relation to the actual vertical as a function of the orientation of the visual context. It can be seen that the mean SVV values significantly vary

with the orientation of the visual context, amounting to about 4° of deviation in relation to the actual vertical.

As for the perceptual upright, statistical analysis revealed that it too was significantly affected by the orientation of the visual context, $F(2, 68) = 22.793$, $p < 0.001$, $partial \eta^2 = 0.401$. This outcome is shown in panel B of Figure 4. Notice that, although the mean PU covaries with the orientation of the visual context, it seems to be biased leftwards – that is, even for an upright visual context, the orientation of the character ‘d’ which resulted in it being perceived in an upright position was deviated by about 5° counter clockwise.

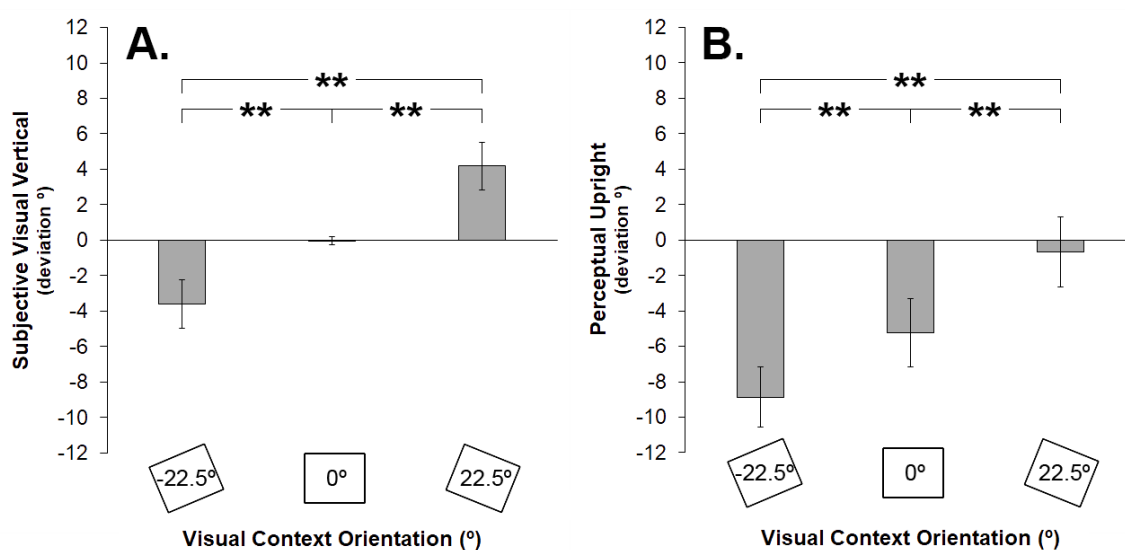


Figure 4 – Empirically found Subjective Visual Vertical (SVV; in terms of deviation in degrees from the actual vertical; Panel A) and Perceptual Upright (PU; panel B), as a function of the visual context orientation (abscissas). Insets () depict the results of post-hoc pairwise comparisons ($p < 0.01$). Error bars represent the standard error of the means.**

For both SVV and PU, all pairwise post-hoc comparisons for the different orientations of the visual context were found to be statistically significant ($p < 0.01$). To further explore these trends, the slopes of the best linear fits between the orientation of the visual context and both the individual SVVs and PUs were calculated and the obtained values subjected to a bivariate Pearson correlation. The obtained slopes for the SVV and PU were found to have no significant correlation, $r(33) = -0.044$, $p = 0.803$ (two-tailed), implying that albeit both were

affected by the orientation of the visual context, these measures tackle disparate perceptual phenomena (see also Dyde, Jenkin, & Harris, 2006; Dyde et al, 2009; Jenkin et al, 2011).

M-displacements

Figure 5, top row, depicts the polar plots for the mean *M-displacements* as a function of target's motion direction (radial lines) and retention interval (line parameters) for the -22.5° (left panel), 0° (middle panel) and 22.5° (right panel) visual context orientations. Preliminary analyses (one sample *t*-tests) showed that for the upright visual context (0°), *M-displacements* could be well described by a significant *c* parameter ($p < 0.001$ for all retention intervals), reflecting a forward displacement for all directions (*Representational Momentum*), a significant b_2 coefficient ($p < 0.001$ for all retention intervals), accounting for a bigger displacement for descending as opposed to ascending targets (*Representational Gravity*), and a significant a_2 coefficient ($p < 0.01$ for all retention intervals), revealing a systematic tendency for an increased forward displacement for targets moving horizontally (either leftward or rightward). All these trends were also present in the remaining visual context orientations and conform to what has been previously reported in similar experiments (cf. De Sá Teixeira, 2014, 2016; De Sá Teixeira, Bosco, Delle Monache, & Lacquaniti, 2019).

These patterns are also clearly visible in the polar plots depicted in Figure 5, along with obvious distortions, contingent with the orientation of the visual context – specifically, *M-displacement* seems to increase for targets moving “downward” leftward/rightward when the visual context is tilted leftward/rightward. In order to disentangle the periodic terms which account for these deviations, the estimated individual values of *c* and a_1 - a_4 and b_1 - b_4 coefficients of equation 2 were subjected to a repeated measures MANOVA with visual context orientation and retention interval as factors. The univariate tests revealed that visual context orientation significantly modulated coefficients b_2 , $F(1.41, 47.928) = 9.017$, $p = 0.002$, *partial* $\eta^2 = 0.21$, a_4 , $F(1.648, 56.034) = 5.522$, $p = 0.01$, *partial* $\eta^2 = 0.14$, and b_4 , $F(2, 68) = 24.655$, $p < 0.001$, *partial* $\eta^2 = 0.42$. The b_2 coefficient (together with a_2) reflects on the fact that the increased forward displacement for “horizontally” moving targets follows the horizontal axis of the visual context (albeit slightly more for the -22.5° condition). On the other hand, coefficients a_4 and b_4 reveal a tendency for bigger forward displacements when the target moves along the main diagonals of the visual context. All the relevant harmonic terms found are depicted below the polar plots in Figure 5.

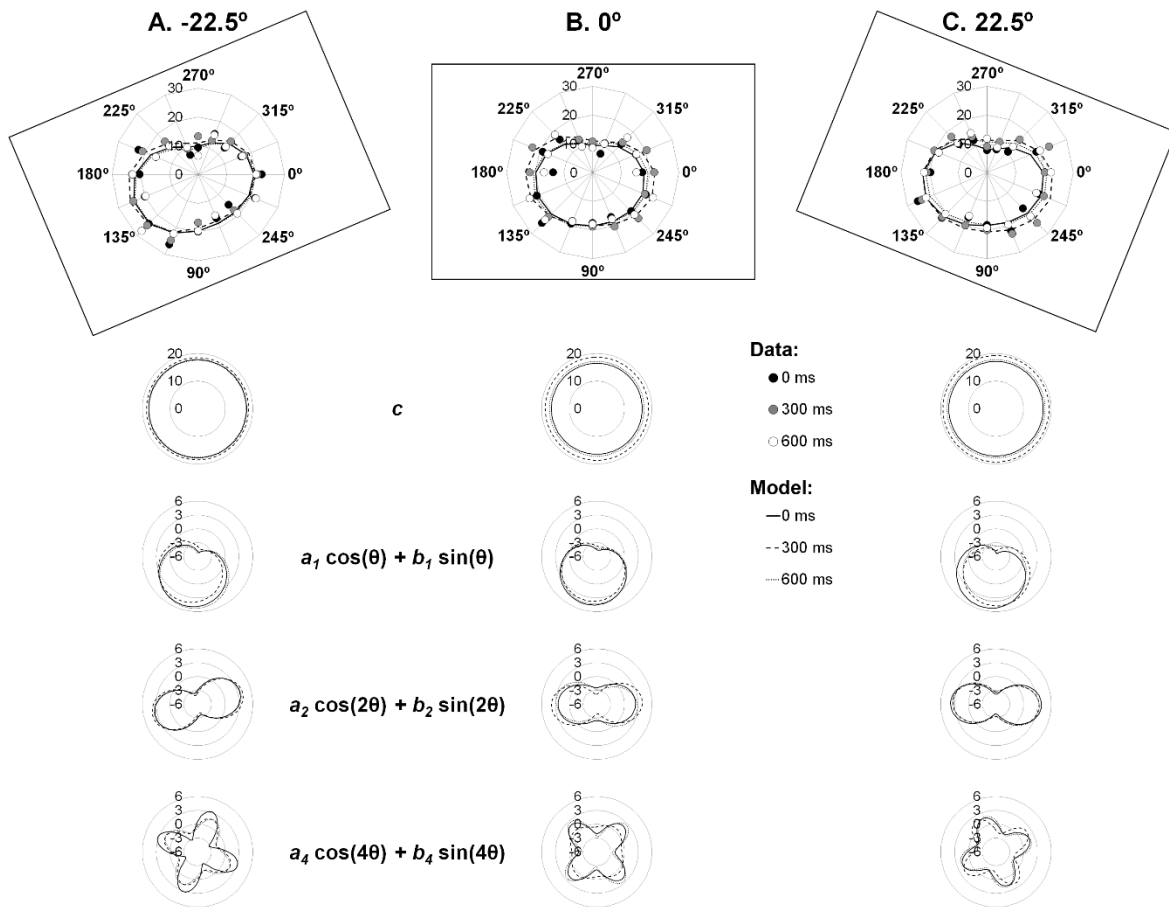


Figure 5 – Polar plots of the found mean *M*-displacements (data points) as a function of target’s motion direction (radial axes) and retention interval (colour of data points) for each visual context orientation (columns). The lines depict the best fit models resulting from the sum of the harmonic terms depicted below each plot and specified algebraically by the accompanying insets.

Retention interval was found to significantly modulate the *c* constant, $F(1.437, 48.851) = 7.435, p = 0.004, \text{partial } \eta^2 = 0.179$, and equally for all visual context orientations, as revealed by a null interaction, $F(3.171, 107.822) = 1.063, p = 0.377, \text{partial } \eta^2 = 0.03$. Across visual context conditions, the constant *c* was found to peak at 300 ms, being significantly smaller for the 0 and 600 ms conditions. No other main effects or interactions reached the statistical significance threshold.

Finally, the slopes of the best linear functions relating the individual b_2 and b_4 coefficients (which account for the “tilt” of *M-displacements* as the visual context is rotated leftward or rightward) as a function of the orientation of the visual context were calculated and the bivariate Pearson correlations with the same indexes obtained for the SVV and PU determined. No significant correlations were found between the spatial localization coefficients and PU: $b_2 - r(33) = 0.065$, $p = 0.847$, bi-caudal; $b_4 - r(33) = -0.27$, $p = 0.117$, bi-caudal. However, the slopes of SVV were marginally correlated with those for b_2 , $r(33) = -0.316$, $p = 0.065$, bi-caudalⁱⁱ, and significantly correlated with those for b_4 , $r(33) = 0.515$, $p = 0.002$, bi-caudal.

Discussion and Conclusions

The main finding of the present experiment is that the spatial localization of the offset position of a moving target, thought to reflect an internalized representation of implied dynamics (e.g., Hubbard, 2014; De Sá Teixeira, 2016; Lacquaniti et al, 2013), is significantly and lawfully modulated by the orientation of the visual context. This outcome bears particularly on the conceptualization of *Representational Gravity*, commonly referred to as a perceptual displacement “downward” in the direction of gravity (Hubbard, 2020), amplifying/attenuating *Representational Momentum* for ascending/descending targets. In line with the extant literature on spatial orientation (e.g., Howard, 1982; Mittelstaedt, 1986; MacNeilage et al, 2008; Dyde, Jenkin, & Harris, 2006; De Vrijer, Medendorp, & Van Gisbergen, 2008, 2009), the ‘downward’ direction underlying *Representational Gravity* possesses a multifactorial nature, determined in part by the gravito-inertial vector, as sensed by the vestibular system (De Sá Teixeira et al, 2016), the body’s main axis orientation (idiotropic vector; De Sá Teixeira & Hecht, 2014a; De Sá Teixeira, 2014) and, based upon the presently reported findings, orientation polarizing visual cues.

Interestingly, when one considers a set of *M-displacements* for targets with varying motion directions, and so as to allow a discrete Fourier decomposition, those spatial orientation factors impact differently on different harmonic terms: the direction of the first harmonic term (coefficient b_1 , resulting in a unidirectional “bulge” in the polar plots) seems to be chiefly determined by the idiotropic vector, with the time course of that same term modulated by the misalignment between the body’s orientation and the vestibular signals (De Sá Teixeira, 2014); conversely, the perceived context orientation, as inferred from visual cues, seems to impact on

the orientation of the second (b_2 ; accounting for an elongation of the polar plots along the “horizontal” axes of the visual scene) and fourth (b_4 ; toward the corners of the visual frame) harmonic terms. Of relevance, these latter trends were also found to significantly correlate with the *Subjective Visual Vertical*, the golden standard for the measurement of the internal “downward” orientation (Howard, 1982; Mittelstaedt, 1986; MacNeilage et al, 2008), but not with the *Perceptual Upright*, thought to reflect a judgement regarding the orientation of an external scene or object, albeit modulated by body, vestibular cues, and visual cues (Dyde, Jenkin, & Harris, 2006; Haji-Khamed & Harris, 2010). These outcomes offer the prospect to empirically disentangle the varying factors that differentially affect spatial orientation, as it impacts on *Representational Momentum* and *Representational Gravity*.

Notwithstanding, a few caveats should be noticed, in particular as they relate to previous research and raise relevant questions and directions for future research. In the present experiment only one single scene was used as the visual context. Although this choice was purposefully made, in order to carefully keep visual features constant across trials and to ensure that no salient landmarks were present in the vicinity of target’s offset, it prevents us from confidently generalize the observed trends. The fact that the same scene significantly affected our measurements of SVV and PU, provides an important internal validation for our results. However, it might be the case that the disclosed patterns are found solely for the type of structural and architectonic cues present in these scenes, with dominant vertical and horizontal lines and a clear rectangular frame. This issue will be scrutinized in the near future with an experiment employing various visual contexts, with interior and exterior scenes.

One other relevant issue refers to retention interval. Previous studies consistently report that *Representational Gravity* increases with increasing retention intervals, both with mouse localization responses (De Sá Teixeira, Hecht, & Oliveira, 2013; De Sá Teixeira & Hecht, 2014b; De Sá Teixeira, 2016) and discrete judgements concerning the location of a visual probe (De Sá Teixeira et al, 2019), and as long as the observer is in an upright position aligned with the gravitational pull (De Sá Teixeira & Hecht, 2014a; De Sá Teixeira, 2014; De Sá Teixeira et al, 2016). This effect was not replicated in the present experiment, notwithstanding the fact that the related time course for *Representational Momentum* (e.g., Freyd & Jonhson, 1987; Kerzel, 2003b; De Sá Teixeira, Hecht, & Oliveira, 2013) was found. Since only three levels for the retention interval were used in the present experiment, it is difficult to fully account for this null effect. This said, an interesting hypothesis can be put forth – it might be the case that the mere presence of a visual context abolishes *Representational Gravity*’s time course, similarly

to what happens when vestibular cues are made to conflict with the body's orientation (De Sá Teixeira, 2014; De Sá Teixeira et al, 2016). A future experiment, designed to test this hypothesis by systematically varying the presence/absence of a visual context while imposing several retention intervals, is currently being planned.

As a concluding remark, albeit further research would be required to fully realize this point, the present findings might be extended beyond fundamental research on dynamic representations and internal models and to applied settings, either as a Human Factors tool, for validation of visual cues to aid spatial orientation and navigation in varying environments (such as microgravity; cf., e.g., Glasauer & Mittelstaedt, 1992; Clément & Reschke, 2008; Clément, 2011), or for the development of assessment tools in clinical settings (cf. e.g., Tesio, Longo, & Rota, 2011; Ashish et al, 2017; Piscicelli & Pérennou, 2017; Michelson et al, 2018).

References

- Ashida, H. (2004). Action-specific extrapolation of target motion in human visual system. *Neuropsychologia*, *42*, 1515-1524.
- Ashish, G., Augustine, A. M., Tyagi, A. K., Lepcha, A., & Balraj, A. (2017). Subjective Visual Vertical and Horizontal in Vestibular Migraine. *The Journal of International Advanced Otolaryngology*, *13*(2), 254-258.
- Aubert, H. (1861). Eine scheinbare Drehung von Objekten bei Neigung des Kopfes nach rechts oder links. *Virchows Archiven*, *20*, 381–393.
- Clément, G. (2011). *Fundamentals of space medicine*. El Segundo, CA: Microcosm Press. New York: Springer.
- Clément, G., & Reschke, M. F. (2008). *Neuroscience in Space*. New York, USA: Springer.
- Clément, G., Moore, S. T., Raphan, T., & Cohen, B. (2001). Perception of tilt (somatogravic illusion) in response to sustained linear acceleration during space flight. *Experimental Brain Research*, *138*, 410-418.
- De Sá Teixeira, N. A. (2016). The visual representations of motion and of gravity are functionally independent: Evidence of a differential effect of smooth pursuit eye movements. *Experimental Brain Research*, *234*(9), 2491-2504.
- De Sá Teixeira, N. A., Hecht, H., Artiles, A. D., Seyedmadani, K., Sherwood, D. P., & Young, L. R. (2016). Vestibular stimulation interferes with the dynamics of an internal representation of gravity. *Quarterly Journal of Experimental Psychology*, *70*, 2290–2305.
- De Sá Teixeira, N. A., Kerzel, D., Hecht, H., & Lacquaniti, F. (2019). A novel dissociation between representational momentum and representational gravity through response modality. *Psychological Research*, *83*(4), 1223-1236.
- De Sá Teixeira, N. A., Bosco, G., Delle Monache, S., & Lacquaniti, S. (2019). The role of cortical areas hMT/V5+ and TPJ on the magnitude of representational momentum and

- representational gravity: a transcranial magnetic stimulation study. *Experimental Brain Research*, 237(3), 3375-3390.
- De Sá Teixeira, N. (2014). Fourier decomposition of spatial localization errors reveals an idiotropic dominance of an internal model of gravity. *Vision Research*, 105, 177-188.
- De Sá Teixeira, N. A., & Hecht, H. (2014a). The dynamic representation of gravity is suspended when the idiotropic vector is misaligned with gravity. *Journal of Vestibular Research*, 24, 267-279.
- De Sá Teixeira, N. A., & Hecht, H. (2014b). Can representational trajectory reveal the nature of an internal model of gravity? *Attention, Perception, & Psychophysics*, 76, 1106-1120.
- De Sá Teixeira, N. A., Hecht, H., & Oliveira, A. M. (2013). The representational dynamics of remembered projectile locations. *Journal of Experimental Psychology: Human Perception and Performance*, 39, 1690-1699.
- De Vrijer, M., Medendorp, W. P., & Van Gisbergen, J. A. M. (2008). Shared Computational Mechanism for Tilt Compensation Accounts for Biased Verticality Percepts in Motion and Pattern Vision. *Journal of Neurophysiology*, 99, 915-930.
- De Vrijer, M., Medendorp, W. P., & Van Gisbergen, J. A. M. (2009). Accuracy-precision trade-off in visual orientation constancy. *Journal of Vision*, 9(2), 1-15.
- Dyde, R. T., Jenkin, M. R., Jenkin, H. L., Zacher, J. E., & Harris, L. (2009). The effect of altered gravity states on the perception of orientation. *Experimental Brain Research*, 194, 647-660.
- Dyde, R. T., Jenkin, M. R., Harris, L.R. (2006). The subjective visual vertical and the perceptual upright. *Experimental Brain Research*, 173(4), 612-622.
- Finke, R. A., Freyd, J. J., & Shyi, G. C. (1986). Implied velocity and acceleration induce transformations of visual memory. *Journal of Experimental Psychology: General*, 115(2), 175-188.

- Freyd, J. J. (1983). The mental representation of movement when static stimuli are viewed. *Perception & Psychophysics*, *33*, 575-581.
- Bertamini, M. (1993). Memory for position and dynamic representation. *Memory & Cognition*, *21*, 449-457.
- Freyd, J. J. (1987). Dynamic mental representations. *Psychological Review*, *94*, 427-438.
- Freyd, J. J., & Finke, R. A. (1984). Representational momentum. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *10*, 126-132.
- Freyd, J. J., & Finke, R. A. (1985). A velocity effect for representational momentum. *Bulletin of the Psychonomic Society*, *23*, 443-446.
- Freyd, J. J., & Johnson, J. Q. (1987). Probing the time course of representational momentum. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *13*, 259-269.
- Gillingham, K. K., & Previc, F. H. (1993). *Spatial orientation in flight* (AL-TR-1993-0022). Brooks Air Force Base, TX, Air Force Materiel Command.
- Glasauer, S., & Mittelstaedt, H. (1992). Determinants of orientation in microgravity. *Acta Astronautica*, *27*, 1-9.
- Glasauer, S. (1995). Linear acceleration perception: frequency dependence of the Hilltop illusion. *Acta Oto-Laryngologica*, *520*, 37-40.
- Grush, R. (2005). Internal models and the construction of time: Generalizing from state estimation to trajectory estimation to address temporal features of perception, including temporal illusions. *Journal of Neural Engineering*, *2*, S209-S218.
- Haji-Khamneh, B., & Harris, L. R. (2010). How different types of scenes affect the Subjective Visual Vertical (SVV) and the Perceptual Upright (PU). *Vision Research*, *50(17)*, 1720-1727.
- Howard, I. P., Childerson, L. (1994). The contribution of motion, the visual frame, and visual polarity to sensations of body tilt. *Perception*, *23*, 753-762.
- Howard, I. P., Bergstrom, S. S., Ohmi, M. (1990). Shape from shading in different frames of reference. *Perception*, *19*, 523-530.

- Howard, I. P. (1982). *Human visual orientation*. New York: Wiley.
- Howard, I. P., & Templeton, W. B. (1966). *Human spatial orientation*. New York, USA: Wiley.
- Hubbard, T. L. (2010). Approaches to representational momentum: Theories and models. In R. Nijhawan & B. Khurana (Eds.), *Space and time in perception and action* (pp. 338-365). Cambridge, UK: Cambridge University Press.
- Hubbard, T. L. (2020). Representational gravity: Empirical findings and theoretical implications. *Psychonomic Bulletin and Review*, *27*(1), 36-55.
- Hubbard, T. L. (1990). Cognitive representation of linear motion: Possible direction and gravity effects in judged displacement. *Memory & Cognition*, *18*, 299-309.
- Hubbard, T. L. (1995). Cognitive representation of motion: Evidence for friction and gravity analogues. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 241-254.
- Hubbard, T. L. (1997). Target size and displacement along the axis of implied gravitational attraction: Effects of implied weight and evidence of representational gravity. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *23*, 1484-1493.
- Hubbard, T. L. (1998). Some effects of representational friction, target size, and memory averaging on memory for vertically moving targets. *Canadian Journal of Experimental Psychology*, *52*, 44-49.
- Hubbard, T. L. (2005). Representational momentum and related displacements in spatial memory: A review of the findings. *Psychonomic Bulletin and Review*, *12*, 822-851.
- Hubbard, T. L. (2006). Computational theory and cognition in representational momentum and related types of displacement: A reply to Kerzel. *Psychonomic Bulletin and Review*, *13*, 174-177.
- Hubbard, T. L. (2014). Forms of momentum across space: Representational, operational, and attentional. *Psychonomic Bulletin & Review*, *21*, 1371-1403.

- Hubbard, T. L., & Bharucha, J. J. (1988). Judged displacement in apparent vertical and horizontal motion. *Perception & Psychophysics*, *44*, 211-221.
- Hubbard, T. L., & Ruppel, S. (1999). Representational momentum and the landmark attraction effect. *Canadian Journal of Experimental Psychology*, *53*(3), 242-256.
- Jenkin, H. L., Howard, I. P. (1998). Retinal and gravitational frames of reference in ambiguous figure recognition. *Investigative Ophthalmology & Visual Science*, *39*, S858.
- Jenkin, H. L., Jenkin, M., Dyde, R. T., & Harris, L. R. (2004). Shape-from shading depends on visual, gravitational, and body-orientation cues. *Perception*, *33*, 1453-1461.
- Jenkin, M. R., Dyde, R. T., Jenkin, H. L., Zacher, J. E., & Harris, L. R. (2011). Perceptual upright: the relative effectiveness of dynamic and static images under different gravity States. *Seeing and Perceiving*, *24*(1), 53-64.
- Kerzel, D., & Gegenfurtner, K. R. (2003). Neuronal processing delays are compensated in the sensorimotor branch of the visual system. *Current Biology*, *13*, 1975-1978.
- Kerzel, D. (2000). Eye movements and visible persistence explain the mislocalization of the final position of a moving target. *Vision Research*, *40*, 3703-3715.
- Kerzel, D. (2003a). Centripetal force draws the eyes, not memory of the target, toward the center. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *29*, 458-466.
- Kerzel, D. (2003b). Mental extrapolation of target position is strongest with weak motion signals and motor responses. *Vision Research*, *43*, 2623-2635.
- Kerzel, D. (2006). Why eye movements and perceptual factors have to be controlled in studies on "representational momentum". *Psychonomic Bulletin and Review*, *13*, 166-173.
- Kerzel, D., Jordan, J. S., & Müsseler, J. (2001). The role of perception in the mislocalization of the final position of a moving target. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 829-840.

- Lacquaniti, F., Bosco, G., Indovina, I., La Scaleia, B., Maffei, V., Moscatelli, A., & Zago, M. (2013). Visual gravitational motion and the vestibular system in humans. *Frontiers of Integrative Neuroscience*, 7, 101.
- MacNeilage, P. R., Ganesan, N., Angelaki, D. R. (2008). Computational approaches to spatial orientation: from transfer functions to dynamic Bayesian inference. *Journal of Neurophysiology*, 100, 2981-2996.
- Mars, F., Popov, K., & Vercher, J. L. (2001). Supramodal effects of galvanic vestibular stimulation on the subjective vertical. *NeuroReport*, 12, 2991–2994.
- McIntyre, J., Zago, M., Berthoz, A., & Lacquaniti, F. (2001). Does the brain model Newton's laws? *Nature Neuroscience*, 4, 693-694.
- Michelson, P. L., McCaslin, D. L., Jacobson, G. P., Petrak, M., English, L., & Hatton, K. (2018). Assessment of Subjective Visual Vertical (SVV) Using the "Bucket Test" and the Virtual SVV System. *American Journal of Audiology*, 27(3), 249–259.
- Mitrani, L., & Dimitrov, G. (1978). Pursuit eye movements of a disappearing moving target. *Vision Research*, 18, 537-539.
- Mittelstaedt, H. (1983). A new solution to the problem of the subjective vertical. *Naturwissenschaften*, 70, 272–281.
- Mittelstaedt, H. (1986). The subjective vertical as a function of visual and extraretinal cues. *Acta Psychologica*, 63, 63–85.
- Nagai, M., Kazai, K., & Yagi, A. (2002). Larger forward memory displacement in the direction of gravity. *Visual Cognition*, 9, 28-40.
- Oman, C. M. (2003). Human visual orientation in weightlessness. In L. Harris & M. Jenkin (Eds.), *Levels of perception* (pp. 375–398). New York: Springer.
- Peirce, J. W. (2007). PsychoPy – psychophysics software in python. *Journal of Neuroscience Methods*, 162, 8-13.

- Peirce, J. W. (2009). Generating stimuli for neuroscience using PsychoPy. *Frontiers in Neuroinformatics*, 2, 10.
- Piscicelli, C., & Pérennou, D. (2017). Visual verticality perception after stroke: A systematic review of methodological approaches and suggestions for standardization. *Annals of Physical and Rehabilitation Medicine*, 60(3), 208–216.
- Pola, J., & Wyatt, H. J. (1997). Offset dynamics of human smooth pursuit eye movements: effects of target presence and subject attention. *Vision Research*, 37(18), 2579-2595.
- Reed, C. L., & Vinson, N. G. (1996). Conceptual effects on representational momentum. *Journal of Experimental Psychology: Human Perception and Performance*, 22, 839-850.
- Sekuler, R., & Armstrong, R. (1978). Fourier analysis of polar coordinate data in visual physiology and psychophysics. *Behavior Research Methods & Instrumentation*, 10, 8-14.
- Tesio, L., Longo, S., & Rota, V. (2011). The subjective visual vertical: validation of a simple test. *International journal of rehabilitation research. Internationale Zeitschrift fur Rehabilitationsforschung*, 34(4), 307–315.
- Tin, C., & Poon, C.-S. (2005). Internal models in sensorimotor integration: Perspectives from adaptive control theory. *Journal of Neural Engineering*, 2, S147–S163.
- Tresilian, J.R. (2004). Interceptive action: What's time-to-contact got to do with it? In H. Hecht & G. J. P. Savelsbergh (Eds.), *Time-to-contact* (pp. 109–140). Amsterdam: Elsevier.
- Tresilian, J.R. (2005). Hitting a moving target: Perception and action in the timing of rapid interceptions. *Perception & Psychophysics*, 67, 129–149.
- Volkening, K., Bergmann, J., Keller, I., Wuehr, M., Müller, F., & Jahn, K. (2014). Verticality perception during and after galvanic vestibular stimulation. *Neuroscience Letters*, 581, 75–79.

Wenderoth, P. M. (1974). The Distinction between the Rod-and-Frame Illusion and the Rod-and-Frame Test. *Perception*, *3*(2), 205–212.

Zago, M., & Lacquaniti, F. (2005). Cognitive, perceptual and action-oriented representations of falling objects. *Neuropsychologia*, *43*(2), 178-188.

Zago, M., McIntyre, J., Senot, P., & Lacquaniti, F. (2008). Internal models and prediction of visual gravitational motion. *Vision Research*, *48*, 1532-1538.

Zupan, L., Merfeld, D., & Darlot, C. (2002). Using sensory weighting to model the influence of canal, otolith and visual cues on spatial orientation and eye movements. *Biological Cybernetics*, *86*, 209–230.

ⁱ https://www.nasa.gov/images/content/194016main_node-2_full.jpg

ⁱⁱ Notice that for b_2 , a negative value reflects on a rightward “tilt” and, therefore, the negative correlation with the SVV measures translates a similar trend.