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Fourier decomposition of spatial localization errors reveals an idiotropic dominance of an internal model of gravity

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ABSTRACT

Given its conspicuous nature, gravity has been acknowledged by several research lines as a prime factor in structuring the spatial perception of one's environment. One such line of enquiry has focused on errors in spatial localization aimed at the vanishing location of moving objects – it has been systematically reported that humans mislocalize spatial positions forward, in the direction of motion (representational momentum) and downward in the direction of gravity (representational gravity). Moreover, spatial localization errors were found to evolve dynamically with time in a pattern congruent with an anticipated trajectory (representational trajectory). The present study attempts to ascertain the degree to which vestibular information plays a role in these phenomena. Human observers performed a spatial localization task while tilted to varying degrees and referring to the vanishing locations of targets moving along several directions. A Fourier decomposition of the obtained spatial localization errors revealed that although spatial errors were increased "downward" mainly along the body's longitudinal axis (idiotropic dominance), the degree of misalignment between the latter and physical gravity modulated the time course of the localization responses. This pattern is surmised to reflect increased uncertainty about the internal model when faced with conflicting cues regarding the perceived "downward" direction.

1. Introduction

Successful interactions with and within an environment imply for any living creature to abide by physical principles which, more often than not, manifest in dynamic patterns. That neural pathways relay information with sizeable delays (cf. e.g., Nijhawan, 1994, 2008; Nijhawan & Kirschfeld, 2003) further heightens the fundamental ordeals faced by an animal pushed to act in a timely manner.

Accordingly, several scholars have hypothesized that at some level neural systems might capitalize on the invariance of physical properties by developing internal models (see, e.g., Angelaki et al., 2004; Grush, 2005; Poon & Merfeld, 2005; Shepard, 1984; Snyder, 1999; Tin & Poon, 2005) – that is, neural structures that explicitly mimic the relationship between physical variables in a predictive manner and so as to overcome ambiguities in sensory processing due to noise and transmission delays. Internal models are nowadays thought to play a paramount role in human perceptual functions.

By virtue of its ubiquity in earthly environments, gravity has been widely acknowledged as one such physical invariant. For instance, the very interpretation of the information conveyed by the otolith organs (utricle and saccule in the inner ear's vestibular system; see, e.g., Clément, 2011; Clément & Bukley, 2007; Clément & Reschke, 2008) poses an important predicament: as stated by Einstein (1907) under the principle of equivalence, gravity is indistinguishable from a constant linear acceleration. That is, both a linear acceleration and a tilt relative to earth's gravity produce equivalent afferent signals, the meaning of which must be disambiguated by the nervous system (cf., e.g., Angelaki, Klier, & Snyder, 2009). It is now believed that neural structures explicitly solve the dynamics underlying vestibular signals (including signals from both the otoliths and the semi-circular canals) to provide an estimate of physical gravity (Angelaki et al., 2004; Hess & Angelaki, 1999; Merfeld, 1995; Merfeld, Zupan, & Peterka, 1999; Snyder, 1999).

The perception of gravity's direction and the perceptual vertical are furthermore determined by visual and somatosensory cues (including ankle joints, abdominal graviceptors and neck muscle afferents; Dyde, Jenkin, & Harris, 2006; Dyde et al., 2011; Haji-Khamneh & Harris, 2010; Harris et al., 2011; Howard & Hu, 2001; Lopez et al., 2009; Mittelstaedt, 1983; Mittelstaedt & Glasauer, 1993; Moscatelli & Lacquaniti, 2011; Oman, 2003). Human observers show, moreover, a general tendency to assume *a priori* that gravity is biased toward the body's longitudinal (supe-

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rior-inferior) axis – *idiotropic vector* (Mittelstaedt, 1983, 1986; for a similar approach under a Bayesian framework see De Vrijer, Medendorp, & Van Gisbergen, 2008) –, as revealed when participants tilted to varying degrees are asked to adjust a line or a rod to be aligned with the earth's gravitational pull (cf. Aubert's effect). Of importance, outcomes found with time-to-contact tasks and timing of interceptive actions strongly suggest that an internalized model of earth's gravitational acceleration is furthermore involved in the processing of visual sensory information (Indovina et al., 2005; Lacquaniti & Maioli, 1989; Lacquaniti et al., 2013; Moscatelli & Lacquaniti, 2011; Zago et al., 2004; see Baurés et al., 2007; for a critical review and Zago et al., 2008; for a response), even under microgravity conditions (McIntyre et al., 2001).

In the same vein, systematic mnesic spatial distortions have been found (Freyd & Finke, 1984; Hubbard, 1990, 2001; Hubbard, 2005) which seem to further support a pervasive role of an internal model of gravity in the visual representation of motion (De Sá Teixeira, Hecht, & Oliveira, 2013; De Sá Teixeira & Hecht, 2014a). Specifically, the memory for the last seen position occupied by a moving target that is suddenly halted has been found to be systematically displaced forward, in the direction of motion, and downward, in the direction of gravity (for a review see Hubbard, 2005). Under the hypothesis that these errors reflect mental analogues of physical properties, they were entitled, respectively, *representational momentum* and *representational gravity*.

Representational momentum was first reported by Freyd and Finke (1984) using implied motion displays and a *same-different* spatial judgement task. Upon seeing a moving target that suddenly disappeared and if further shown a static object (mnesic probe) nearby that vanishing location, human observers were found to be more prone to report that the latter occupies the last seen position of the target when it is actually slightly displaced forward along the direction of motion. The magnitude of the mnesic displacement was furthermore found to be proportional with the target's implied velocity (Freyd & Finke, 1985) and to increase with time (by varying the retention interval between the target's disappearance and the presentation of the mnesic probe) until a peak at about 300 ms (Freyd & Johnson, 1987), in line with the reasoning that it reflected an analogue of physical momentum. Importantly, similar displacements were found with static photographs and drawings conveying dynamic information (Freyd, 1983, 1987; Freyd, Pantzer, & Cheng, 1988), in particular when in congruence with the expected effects of gravitational pull (cf. Bertamini, 1993; see also Nagai, Kazai, & Yagi, 2002), implying that a representational analogue of gravity might also play a role in mnesic spatial distortions.

A significant enlargement of the study of representational momentum was triggered with research led by Hubbard (Hubbard, 1995, 1996, 1997, 1998, 2005; Hubbard & Bharucha, 1988). Noteworthy in these studies was the use of continuous linear motion displays (as opposed to implied movement) coupled with a behavioural localization task – participants were required to indicate the remembered vanishing position of the target by adjusting a cursor controllable with a computer mouse. Notice that whereas in a same-different paradigm participants' responses are constrained to the locations of the mnesic probe, as chosen by the researcher, the behavioural localization responses are only limited by the extent of the presentation window (i.e., computer screen). This particular aspect of localization responses rendered visible a systematic tendency to indicate target's positions biased downward, toward gravity, for horizontally moving targets (Hubbard, 1990; Hubbard & Bharucha, 1988), vertically moving targets (thus modulating the magnitude of representational momentum; Hubbard, 2001; Hubbard & Bharucha, 1988), and even static targets (Motes et al., 2008). Taken together, these outcomes have been interpreted as reflecting an independent functioning of an internal analogue of gravity which, jointly with representational momentum, would affect spatial perception (Hubbard, 1995, 2005), allegedly in order to cope with transmission delays in neural perceptual-motor cycles (Ashida, 2004; Hubbard, 2005; Kerzel & Gegenfurtner, 2003).

Recently, it was found that behavioural localizations aimed at the remembered vanishing positions of horizontally moving targets evolve with time in a pattern that seems to mimic an anticipated course – representational trajectory (De Sá Teixeira, Hecht, & Oliveira, 2013; experiment 1; see also De Sá Teixeira & Oliveira, 2013). Specifically, during the first 300 ms after target offset, the remembered vanishing location drifts forward along the motion axis; from 300 ms beyond (up until at least 1200–1400 ms; cf. De Sá Teixeira & Hecht, 2014b), the remembered position drifts downward in the direction of gravity with no further increase in the forward displacement. Constraining eye movements, which were found to account for representational momentum due to an overshoot of smooth pursuit eye movements coupled with a foveal bias (tendency to mislocalize the spatial location of a target towards the direction of gaze; De Sá Teixeira & Oliveira, 2014; Kerzel, 2000, 2002, 2003, 2006; Kerzel, Jordan, & Müsseler, 2001), prevents the initial increase forward with time, but not the temporal evolution of downward errors, evident even for times below 300 ms. However, if left unconstrained, gaze drifts forward and downward with time in a pattern that closely mimics the behavioural responses (De Sá Teixeira, Hecht, & Oliveira, 2013, experiment 2). In an extension of these results, targets shown descending toward the gravity pull were found to be mislocalized increasingly downward for times until 300 ms, stabilizing afterwards. Conversely, targets moving upward (against gravity) lead to small and constant errors, sometimes in a direction opposite to motion (De Sá Teixeira & Hecht, 2014a; De Sá Teixeira & Oliveira, 2014). Finally, static targets were remembered as being displaced downward in the direction of gravity and more so for longer retention intervals between target offset and response (De Sá Teixeira & Hecht, 2014a). As participants necessarily take some time to respond, it might be possible that the rate at which the remembered location drifts downward has been underestimated in these studies, although no correlation between response times and downward mnesic errors has been found (cf. De Sá Teixeira & Hecht, 2014a; De Sá Teixeira & Oliveira, 2014). Nothwithstanding, these outcomes seem to suggest that although representational momentum and representational gravity act along specific and independent spatial axes (respectively, motion and gravity axis), their joint dynamics are closely coupled in determining the anticipated course of the target.

Even though representational gravity has been defined as an error downward in the direction of gravity (e.g., Hubbard, 2005), which would imply that the internal model of gravity was based on world coordinates, few studies attempted to disentangle the physical direction of gravity (as sensed with the otolith organs) from the observer's body orientation – idiotropic vector – (but see Nagai, Kazai, & Yagi, 2002), known to significantly influence the perception of the vertical direction (cf. e.g., Mittelstaedt, 1983, 1986; Oman, 2003). Recently, evidence was found that given a behavioural localization task and linearly moving targets, human observers tend to make a systematic error in the direction of their feet (idiotropic down) when lying on a lateral decubitus posture, orthogonal to the gravity's pull. Moreover, and although the memory for the last location of the target increases downward with time when upright, no dynamic evolution of the errors (representational trajectory) was found when participants' body was orthogonal to gravity (De Sá Teixeira & Hecht, 2014b). These findings would entail that an internal model of gravity critically depends on the degree of alignment between the observer's body and the