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RESEARCH REPORT

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Vestibular contribution to spatial encoding

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Abstract

Determining the spatial relation between objects and our location in the surroundings is essential for survival. Vestibular inputs provide key information about the position and movement of our head in the three-dimensional space, contributing to spatial navigation. Yet, their role in encoding spatial localisation of environmental targets remains to be fully understood. We probed the accuracy and precision of healthy participants' representations of environmental space by measuring their ability to encode the spatial location of visual targets (Experiment 1). Participants were asked to detect a visual light and then walk towards it. Vestibular signalling was artificially disrupted using stochastic galvanic vestibular stimulation (sGVS) applied selectively during encoding targets' location. sGVS impaired the accuracy and precision of locating the environmental visual targets. Importantly, this effect was specific to the visual modality. The location of acoustic targets was not influenced by vestibular alterations (Experiment 2). Our findings indicate that the vestibular system plays a role in localising visual targets in the surrounding environment, suggesting a crucial functional interaction between vestibular and visual signals for the encoding of the spatial relationship between our body position and the surrounding objects.

KEYWORDS

galvanic vestibular stimulation, sensory localisation, spatial encoding, spatial navigation, vestibular system

1 INTRODUCTION

Humans successfully interact with the external world by recruiting different sources of information. In novel environments, grasping the spatial relationship between our position and the surrounding objects, known as an egocentric reference, becomes exceptionally important: This enables us to accurately gauge the distance to targets we want to reach or avoid. Distance estimates are mainly based on visual cues (Sun et al., 2004). This is unsurprising given that the visual system is key in representing spatial information based on its high spatial acuity (Alais & Burr, 2004). Navigators combine both static (i.e., convergence and binocular disparity) and dynamic visual cues (i.e., optic flow) to represent the external space. However, other sensory modalities provide distance

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information. That is, when vision is degraded or becomes unavailable, auditory cues provide distance information about environmental objects outside the navigator's perspective, though less accurately than visual ones (Kolarik et al., 2016; Nardi et al., 2020; Zahorik et al., 2005).

Humans constantly integrate visual and auditory signals with self-motion cues to represent distances (Chen et al., 2017; Nardini et al., 2008; Zanchi et al., 2022). Selfmotion cues are defined as the ability to perceive the movements of own body and to discriminate between different duration, directions and types of motions (i.e., rotations vs translations) and stem from both proprioceptive and vestibular systems. The vestibular system consists of a set of organs that continuously detects the motion of one's head in space: The semicircular canals signal rotational accelerations on three orthogonal planes-yaw, pitch and roll-whereas the otoliths detect linear and translational acceleration, including gravity. Hence, the vestibular system plays a crucial role in various self-motion tasks and serves as the perceptual foundation for accomplishing efficient path integration. This involves updating our spatial position and movements by considering inertial cues, allowing us to navigate effectively (Loomis, 1999). Recent research has demonstrated a vestibular contribution to higher cognitive functions, such as spatial navigation, visuospatial memory, travelled distance processing and spatial perception (Bigelow & Agrawal, 2015; Deshpande & Patla, 2005; Ferrè et al., 2013; Ferrè & Haggard, 2020; Hilliard et al., 2019; Israël et al., 1995; Ivanenko et al., 1997). Both animal and human studies have shown that vestibular damage leads to one's inability to explore the environment (Dallal et al., 2015; Xie et al., 2017). For instance, artificially interfering with vestibular inputs during walking causes a systematic change in the planned trajectory (Bent et al., 2000; Carlsen et al., 2005; Fitzpatrick et al., 1999; Karn & Cinelli, 2019). Critically, vestibular projections do not target a primary unimodal sensory area. Instead, they connect with a cortical network that processes information from various sensory systems, including visual, auditory, haptic and proprioceptive inputs (Angelaki & Cullen, 2008). This interaction with other senses highlights the integrative nature of the vestibular system.

Let us consider a scenario where we aim to grab the newspaper situated directly ahead of us but on the opposite side of the room. Such goal-directed locomotion task requires the successful encoding of the egocentric distance between the goal target (i.e., the newspaper) and our starting position (i.e., where we are in the room) and then the updating of our own position in space based on self-motion. Although vestibular signals contribute to self-motion and spatial navigation (Xie et al., 2017; Yoder & Taube, 2014), extant research has not

determined how vestibular cues play a role in these processes. Here, we have investigated whether vestibular cues contribute to spatial encoding of environmental objects in a spatial navigation task that requires participants to walk to the position of a previously learned target. In particular, we have explored whether this vestibular contribution to spatial encoding is selective for visual targets (Experiment 1) or might also influence acoustic target encoding (Experiment 2). Specifically, we hypothesized that disrupting vestibular signals would impair the encoding accuracy and increase variability of performance regardless of the physical distance of the learned target. Our study aims to broaden knowledge about how vestibular information contributes to efficient goal-directed spatial navigation, as well as consider how vestibular inputs play a role in the cognitive processes that allow for generating a coherent spatial estimation of external environments.

EXPERIMENT 1: SPATIAL 2 **ENCODING OF VISUAL TARGETS**

2.1 | Participants

Twenty healthy participants were recruited (mean age \pm SD: 29.5 \pm 5.84 years old) for Experiment 1. Nineteen participants were right-handed as assessed using the Edinburgh handedness inventory (Oldfield, 1971). None of the participants had a history of neurological, vestibular or psychiatric disorders. Informed consent was obtained before participation. All participants were naïve to the aims of the experiment. The research ethics committee of Birkbeck University of London (United Kingdom) approved the experimental protocol. The study adhered to the ethical standards of the Declaration of Helsinki.

2.2 1 Stochastic vestibular stimulation

The vestibular stimulation was delivered using a commercial stimulator (Good Vibrations Engineering Ltd., Nobleton, Ontario, Canada) controlled by MATLAB (R2019b, The MathWorks, United States). Carbon rubber electrodes (area: 10 cm²) covered with electrode gel were placed binaurally over the participants' mastoid processes and fixed with adhesive tape. First, researchers cleaned the area of application; then, they applied electrode gel to reduce the impedance. Vestibular stimulation consisted of an alternating sum-of-sines voltage with dominant frequencies at 0.16, 0.32, 0.43 and 0.61 Hz, generating a stochastic stimulation (stochastic galvanic vestibular stimulation, henceforth sGVS), which promotes a sense

of instability without consistent or directional illusory motion. Notably, the stimulation was delivered binaurally to avoid that the non-stimulated side could compensate for the stimulated one. The max intensity was 1 mA, and the total duration was 10 s. The study adopted these parameters to maximize the disruption of the vestibular signals (Fraser et al., 2015; MacDougall et al., 2006; Moore et al., 2006), eliciting a generic sensation of weak dizziness. Importantly, these effects do not outlast the stimulation (Fitzpatrick & Day, 2004). We also used sham stimulation to control for non-vestibular-specific effects. Researchers placed the electrodes for sham stimulation on the left and right side of the neck, about 5 cm below the GVS electrodes (Ferrè et al., 2013; Lopez et al., 2010).

2.3 | Experimental procedure

Experimental procedure is shown in Figure 1 (left panel). Verbal instructions about the task were provided to participants at the beginning of the experimental session. Participants wore a backpack containing the vestibular stimulator, and they were allowed to briefly familiarise themselves with sGVS-induced sensation before the actual task. The experiment took place in a $2.31 \times 3.91 \text{ m}^2$ darkened room. Participants stood behind

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a marked line on the floor along one of the two longest sides of the room (starting position). To reduce irrelevant environmental visual cues, participants wore sunglasses for the whole duration of the experiment. In the starting position, participants received 10 sec of sGVS or sham stimulation while standing still. During the last 500 ms of the stimulation, researchers switched on one of the three visual targets, which consisted of LED lights laying on the floor in a straight line directly in front of participants. To prevent participants from deviating from the straightahead direction, we placed a strip of soft material on the floor that could be used as a reference while walking. Crucially, this strip could not provide additional spatial information about the distance of the targets, being available along the whole straight line from the starting position and the opposite wall. From the starting position, the closest light was at a distance of 2.26 m, the middle one was at 2.53 m and the furthest was at 2.87 m. To reduce light reflection on the walls, each light has been dimmed using a black opaque piece of nylon. Visual targets were remotely controlled via MATLAB (R2019b, The MathWorks, United States). When both the visual target and the stimulation went off, participants were incited to reach the position of the recently learned target by walking. Researchers instructed each participant to align their heels and back with the remembered position of the



FIGURE 1 Experimental procedure and Experiment 1 results. Left panel: experimental procedure. In the encoding phase, participants were instructed to focus on the switched-on target while stimulated with sGVS or sham. In the walking phase, participants had to reach the estimated position of the target (stimulation off). Then, the experimenter measured their performance in target localization. Right panel: results from Experiment 1, on accuracy (upper panel) and precision (lower panel).

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target. The experimenter measured the distance with a laser meter (RS PRO RSLDM-50H, precision ±1.5 mm, Class 2, 1268821, RS PRO, RSLDM-50H). After the measure, the researcher invited the participants to return to the starting position for the next trial. No participant referred to feel strong dizziness or pain during the stimulation. The experimental session was divided into two blocks with 15 trials each. In each block, only sGVS trials or sham trials were administered. The order of stimulation type was counterbalanced across participants, whereas the distance of the targets on each trial was randomized across each block (5 repetitions for each distance). The whole experiment lasted 45 min.

2.4 Results

For each participant and trial, we computed the difference between the target and walked distance. First, we checked that the participants actually perceived and processed the three different distances simply by measuring their walked distances for each target in the sham block. Then, we calculated the mean error (higher error means lower accuracy) and the standard deviation (SD, higher SD means lower precision). Data were analysed using the RStudio software (Version 3.6.2; 2019).

Participants' walked distances increased as the physical target distance increased (mean \pm SD: Short = 1.96 ± 0.22 , Medium = 2.22 ± 0.24 ; Long = 2.58 ± 0.25). A repeated-measures analysis of variance (ANOVA) on the walked distances indeed showed a main effect of target distance (generalised eta squared was used as effect size; η_G^2 : $F_{(2,38)} = 241.1$, p < .0001, $\eta_G^2 = .53$. In particular, pairwise comparisons with Bonferroni correction revealed a significant difference for each pairwise comparison: Short vs Medium: $t_{(19)} = -8.76$, p < .001, Cohen's d = -1.96; Short vs Long: $t_{(19)} = -22$, p < .001, Cohen's d = -4.91 and Medium vs Long: $t_{(19)} = -13.3$, p < .001, Cohen's d = -2.97, suggesting that participants distinguished the three visual target distances and walked accordingly. As we were not interested in the effect of vestibular stimulation on specific distances in space, henceforth we have collapsed the estimates for the three visual distances for our comparisons between sGVS and sham conditions.

We hypothesized that sGVS would impair distance error and increase SD independently from the physical distance of the target. We then directly compared sGVS and sham errors and SD with planned comparisons. A significant increase in error values was found during sGVS compared with sham condition $(t_{(19)} = 1.79)$, p = .04, Cohen's d = 0.4), indicating lower accuracy for visual distance estimates. A significant increase in SD

values during sGVS also emerged ($t_{(19)} = 2.21$, p = .03, Cohen's d = 0.5), suggesting a lower precision in sGVS compared with sham condition. Thus, our results suggest worse accuracy and precision when vestibular signals are disrupted by the sGVS during the encoding of the location of visual targets (Figure 1, right panel).

The disruption of vestibular signals on the encoding of the location of visual targets induced a significant worsening of navigation performance. Specifically, we observed a systematically lower accuracy and precision during sGVS. Our results demonstrate the contribution of the vestibular system in estimating the location of visual targets, suggesting a functional interaction between vestibular and visual inputs during the encoding of spatial cues. It remains unclear whether the vestibular system plays a role in the general estimation of spatial distance or whether this contribution is sensory-specific for visually encoded targets. For this reason, we tested whether vestibular alterations similarly influence the spatial encoding of acoustic targets (Experiment 2).

EXPERIMENT 2: SPATIAL 3 ENCODING OF ACOUSTIC TARGETS

3.1 **Participants**

A different group of 20 healthy participants (mean age \pm SD: 29 \pm 6.7 years old) was recruited in Experiment 2. Seventeen were right-handed as assessed using the Edinburgh handedness inventory (Oldfield, 1971). The inclusion criteria were the same as Experiment 1. The study obtained informed consent before the experiment. All participants were naïve to the aims of the experiment. The research ethics committee of Birkbeck University of London (United Kingdom) approved the experimental protocol. The study adhered to the ethical standards of the Declaration of Helsinki.

3.2 **Experimental procedure**

The experimental set-up and procedure were similar to Experiment 1; but in Experiment 2, the targets consisted of auditory cues delivered by three loudspeakers (Stilgut YB202STGD, $6.6 \times 6.6 \times 6$ cm) laying on the floor along one of the two longest sides of the experimental room. The speakers were connected with jack cables to the experimental computer through an external sound card (Xonar U5, Asus). Each loudspeaker played a 500 ms pink noise sound. From the starting position, the closest loudspeaker was at a distance of 1.96 m, the middle one was at 2.53 m, and the furthest was at 3.24 m. As

localising auditory stimuli is more challenging than localising visual ones (Kolarik et al., 2016), we moved the loudspeakers apart relative to the visual targets in Experiment 1. This was meant to help participants with the discrimination of the three distances. Similar to Experiment 1, the experimenter controlled when and which acoustic target would be switched on and off by pressing a key on the experimental computer keyboard, which remotely controlled the speakers via MATLAB (R2019b, The Math-Works, United States). Also for this experiment, no participant felt strong dizziness or pain during stimulation.

3.3 | Results

Data were analysed as in Experiment 1. Participants' walked distances increased as the physical target distance increased (Mean \pm SD: Short = 2.19 \pm 0.43, Medium = 2.31 \pm 0.41; Long = 2.58 \pm 0.32). The repeated-measures ANOVA on the walked distance revealed a main effect of target distance: $F_{(2,38)} = 10.27$, p < .001, $\eta^2_G = 0.15$. Pairwise comparisons with Bonferroni corrections (Short vs Medium: $t_{(19)} = -1.17$, p = .77, Cohen's d = -0.26; Short vs Long: $t_{(19)} = -3.83$, p = .003, Cohen's d = -0.86;

Medium vs Long: $t_{(19)} = -4.62$, p < .001, Cohen's d = -1.03) suggest that participants distinguished at least short vs long and medium vs long, with less ability to distinguish the two closer distances. This result does not surprise us considering the challenging nature of reaching an acoustic target in depth.

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No difference between sGVS and sham in error values was found ($t_{(19)} = -1.04$, p = .31, Cohen's d = -0.23) (left and upper panel of Figure 2). Supporting this, we calculated the Bayes factors (BF₁₀; Rouder et al., 2009) using the *ttestBF* function from the BayesFactor package (Morey & Rouder, 2018) in RStudio, adopting a scale *r* on the effect size of .707. The obtained value supported the absence of difference between sGVS and sham, BF₁₀ = 0.37 (BF₁₀ lower than 1 is considered in favour of the null hypothesis). Similarly, direct comparison on SD values showed no difference between sGVS and sham condition ($t_{(19)} = 0.31$, p = .76, Cohen's d = 0.07); the Bayes factor supports this absence of difference on SD (BF₁₀ = 0.3) (left and lower panel of Figure 2).

In contrast to the pattern of results observed in the localisation of visual targets, these results seem to suggest no effect of vestibular disturbance on the encoding of the spatial location of auditory cues. To compare the effects



FIGURE 2 Experiment 2 results and between experiments comparison. Left panel: results from Experiment 2, on accuracy (upper panel) and precision (lower panel). Right panel: index of GVS impact on localisation measured for both experiments on accuracy (upper panel) and precision (lower panel).

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of sGVS on visual versus auditory localisation, we conducted a mixed ANOVA on the error and SD with sensory condition (visual, auditory) and stimulation (sGVS, sham) as between and within factors respectively; generalised eta squared (η_G^2) was used as effect size. Error and SD were standardized (z-scores) to account for the different magnitude of values for reaching visual and acoustic targets. The analysis on the standardized error revealed a significant interaction between sensory condition and stimulation ($F_{(1,38)} = 4.204$, p = .04, $\eta^2_G = 0.008$). Direct comparison revealed a significant difference between sGVS and sham in visual localisation $(t_{(19)} = 1.78)$, p = .04, Cohen's d = 0.26), but not in auditory localisation $(t_{(19)} = -1.03, p = .84,$ Cohen's d = -0.09). No difference was found between the error values in the sham conditions in the two experiments $(t_{(33.9)} = -0.65,$ p = .51, Cohens' d = -0.20). A similar analysis on standardized SD values revealed a significant interaction between sensory condition and stimulation $(F_{(1,38)} =$ 5.346, p = .02, $\eta_G^2 = 0.02$). Direct comparison revealed a significant difference between sGVS and sham in visual localisation ($t_{(19)} = 1.95$, p = .03, Cohen's d = 0.45), but not in auditory localisation $(t_{(19)} = -1.31, p = .89,$ Cohen's d = -0.29). No difference was found between the SD values in the sham conditions in the two experiments $(t_{(31.3)} = -1.28, p = .21, \text{ Cohen's } d = -0.39)$. To further investigate whether disruption of vestibular inputs on spatial encoding is sensory-specific, we calculated an index (the difference between sGVS and sham conditions in visual vs. auditory error and SD) to measure the effect of sGVS on spatial localization. The index computed for error yielded a significant difference between acoustic and visual targets' reaching performance $(t_{(19)} = 2.07, p = .04, \text{ Cohen's } d = 0.65; \text{ right and upper}$ panel of Figure 2). Conversely, the index computed for SD showed no significant difference between the two experiments ($t_{(19)} = 1.10$, p = .28, Cohen's d = 0.35; right and lower panel of Figure 2). The high inter-individual SD that we identified in Experiment 2 may explain the lack of significance between the two indexes on precision.

GENERAL DISCUSSION 4

Interaction between different sensory cues characterizes the spatial encoding of environmental features. In the present study, we systematically investigated the contribution of vestibular signals to the spatial encoding of visual and acoustic targets. Our results demonstrated that vestibular inputs play a clear role in the encoding of visual (Experiment 1) but not acoustic (Experiment 2) targets to be reached by walking.

Our study reports for the first time an essential contribution of the vestibular system to the preparation phase of goal-directed locomotion in the absence of inertial selfmotion cues. Walking towards a previously observed target is a common behaviour in the daily life of the average human. However, the performance in this task is influenced by several factors, such as visual perception, self-motion, calibration of locomotion and vision and working memory (Rieser et al., 1990). Distance perception is overall accurate in the form of reaching the target by walking (e.g., Loomis et al., 1998; Loomis & Knapp, 2003; Rieser et al., 1990). Previous research has highlighted the importance of vestibular inputs in efficiently walking towards learned targets. In fact, when individuals were artificially stimulated with GVS while walking, their planned trajectory towards target locations underwent systematic changes, leading to impaired performance (Deshpande & Patla, 2005; Fitzpatrick et al., 1999; Karn & Cinelli, 2019). This impairment is likely attributed to a failure to update the current position and the perceived trajectory of the navigator. Here, we applied sGVS in the 'pure localisation estimate' phase, that is, the moment in which navigators had to estimate the egocentric distance between their own position and the location of targets before walking. In other words, no self-motion cues were strictly needed to compute these distance estimates. Nonetheless, we observed worse accuracy in estimating the distance of visual targets when participants were stimulated with sGVS than with sham. Even in the absence of actual movements, the vestibular system provides information about the spatial relationship between the head, gravitational force and environment. Critically, our findings line up with previous research that has described a vestibular contribution in complex spatial processing, such as converting motion information to distance information to maintain spatial orientation when visual signals are absent (Kaski et al., 2016; Seemungal, 2015). We demonstrated a vestibular contribution to spatial encoding that allows navigators to encode the spatial distance between a visual target and the body-even without self-motion information.

The vestibular system continuously process information about the position of the head relative to the gravitational acceleration, transforming cues from a head-centred framework into cues in world-centred coordinates (Angelaki & Cullen, 2008). Gravitational acceleration is detected by the vestibular otoliths. Gravity is a constant point of reference, and therefore, every head movement implies a calibration between the organism, its surrounding space and gravity. We suggest that sGVS might have interfered with graviception, disrupting a fundamental reference. Accordingly, it is well-known that galvanic vestibular stimulation stimulates the vestibular

nerve eliciting responses from both the semicircular canals and otoliths (Stephan et al., 2005). sGVS may have affected the processing in the cortical and subcortical vestibular network, that is, the insular cortex, temporoparietal junction, ventral premotor area, supplementary motor area, middle cingulate cortex, postcentral gyrus, thalamus and putamen (Lopez et al., 2012).

Our results indicate a sensory-specific interaction between visual and vestibular signals in spatial encoding. The interaction between visual and vestibular inputs has been extensively investigated both functionally and behaviourally. Crucially, vision and the vestibular system are already strictly connected at a low level of processing. Consider, for example, the vestibulo-ocular reflex (VOR), which is a reflex needed to preserve the image in the centre of the visual field when the head moves. Visual and vestibular interactions have been also largely described at higher levels of processing. Previous research demonstrated that path integration navigation strategy (i.e., based on self-motion) is combined with remembered visual landmarks while navigating without visual information (Kalia et al., 2013). In addition, visual and vestibular cues are dynamically integrated during goal-directed locomotion (Deshpande & Patla, 2005). Research indicates that visual and vestibular cortical areas inhibit each other for spatial orientation and motion perception, representing a functional connection between the two sensory systems (Brandt et al., 2002). This cortical interaction is interpreted as the tentative to reduce or prevent interference in case of visual-vestibular mismatch, shifting to the most reliable sensory modality (Brandt et al., 2002). In addition, in spatial contexts, dynamic visual information can cause after-effects on self-motion estimation based on vestibular cues (Cuturi & Macneilage, 2014), demonstrating the shared substrate of visual and vestibular processing (Gu et al., 2008). In the current work, we showed an additional specific visual-vestibular interaction in the static encoding of environmental visual targets contributing to one's ability to reach or avoid objects in space.

One might argue that the observed interaction between vestibular and visual inputs may be the consequence of the effect of sGVS on eye movements. Previous studies delivering a boxcar pulse of 1 mA reported static ocular torsions in the direction of the anode (e.g., Zink et al., 1998). Critically, a torsional eye movement effect would have impacted localisation precision but not accuracy; conversely, we observed a systematic disruption of performance accuracy. However, future studies may directly investigate this aspect by measuring eye movements during sGVS and targets encoding.

No effect of sGVS appeared among spatially encoding acoustic targets. Auditory information is generally less precise than visual cues for spatial tasks (Alais &

Burr, 2004), especially in distance perception (Zahorik et al., 2005). However, auditory cues in spatial encoding are the sole cues offering spatial information about objects outside the field of view when visual information is absent or less reliable (Kolarik et al., 2016; Nardi et al., 2020; Zahorik et al., 2005), allowing an egocentric representation of space of the body and the environment. Though the processing of auditory and vestibular cues interact both at central and peripheral levels (Smith, 2012), our results show that no interaction between the two systems occurs in the context of spatial encoding. Interestingly, previous research found a vestibular influence on auditory localization in the azimuthal plane (Lewald & Karnath, 2000). However, it is worth noticing that the human ability to determine the angular direction of a sound source in the horizontal plane is more accurate than distance estimation (Zahorik et al., 2005), which was the participants' task in the present study.

Although this study demonstrates overall a novel contribution of vestibular inputs in spatial encoding, our findings should be considered in light of some limitations. The experiments were carried out in a small room, preventing from exploring the effect of stimulation on the target distance encoding in larger and probably more ecological settings. In addition, the small size of the room hindered the possibility to deliver a higher number of target distances. Finally, the experiments involved reaching a previously learned target by actively walking up to their locations, including both vestibular and proprioceptive cues in the walking phase. Even though our aim was to interfere with vestibular signals during the target encoding and no stimulation was delivered during the goaldirected movement, future studies may be addressed to replace an active task with a passive one (e.g. in Israël et al., 1995; Ivanenko et al., 1997), reducing the required self-motion cues only to the vestibular ones.

To conclude, our results systematically demonstrate that even in the absence of inertial information deriving from self-motion, the vestibular system influences how one perceives the external world and how one particularly encodes visual spatial cues. The vestibular system is thus essential for building a coherent and efficient representation of space. We believe that this study provides critical insights not only into the understanding of vestibular processing but also into the well-known difficulties in spatial processing observed in individuals with vestibular loss.

AUTHOR CONTRIBUTIONS

S. Zanchi, L. F. Cuturi, M. Gori and E. R. Ferrè conceived the study and designed the experiments. S. Zanchi carried out the experiments, analysed the data and wrote the first draft of the article. All authors reviewed and approved the final version of the article for submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors upon request.

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REFERENCES

- Alais, D., & Burr, D. (2004). The ventriloquist effect results from near-optimal bimodal integration. *Current Biology*, 14(3), 257– 262. https://doi.org/10.1016/j.cub.2004.01.029
- Angelaki, D. E., & Cullen, K. E. (2008). Vestibular system: The many facets of a multimodal sense. *Annual Review of Neuroscience*, 31(1), 125–150. https://doi.org/10.1146/annurev.neuro. 31.060407.125555
- Bent, L. R., McFadyen, B. J., French Merkley, V., Kennedy, P. M., & Inglis, J. T. (2000). Magnitude effects of galvanic vestibular stimulation on the trajectory of human gait. *Neuroscience Letters*, 279(3), 157–160. https://doi.org/10.1016/S0304-3940(99)00989-1
- Bigelow, R. T., & Agrawal, Y. (2015). Vestibular involvement in cognition: Visuospatial ability, attention, executive function, and memory. *Journal of Vestibular Research: Equilibrium and Orientation*, 25(2), 73–89. https://doi.org/10.3233/VES-150544
- Brandt, T., Glasauer, S., Stephan, T., Bense, S., Yousry, T. A., Deutschlander, A., & Dieterich, M. (2002). Visual-vestibular and Visuovisual cortical interaction: New insights from fMRI and PET. Annals of the new York Academy of Sciences, 956, 3– 241. https://doi.org/10.1111/j.1749-6632.2002.tb02822.x
- Carlsen, A. N., Kennedy, P. M., Anderson, K. G., Cressman, E. K., Nagelkerke, P., & Chua, R. (2005). Identifying visual-vestibular contributions during target-directed locomotion. *Neuroscience Letters*, 384(3), 217–221. https://doi.org/10.1016/j.neulet.2005. 04.071

- Chen, X., McNamara, T. P., Kelly, J. W., & Wolbers, T. (2017). Cue combination in human spatial navigation. *Cognitive Psychology*, 95, 105–144. https://doi.org/10.1016/j.cogpsych. 2017.04.003
- Cuturi, L. F., & Macneilage, P. R. (2014). Optic flow induces nonvisual self-motion aftereffects. *Current Biology*, 24(23), 2817–2821. https://doi.org/10.1016/j.cub.2014.10.015
- Dallal, N. L., Yin, B., Nekovářová, T., Stuchlík, A., & Meck, W. H. (2015). Impact of vestibular lesions on allocentric navigation and interval timing: The role of self-initiated motion in spatial-temporal integration. *Timing and Time Perception*, 3(3–4), 269–305. https://doi.org/10.1163/22134468-03002053
- Deshpande, N., & Patla, A. E. (2005). Dynamic visual-vestibular integration during goal directed human locomotion. *Experimental Brain Research*, 166(2), 237–247. https://doi.org/10. 1007/s00221-005-2364-0
- Ferrè, E. R., & Haggard, P. (2020). Vestibular cognition: State-ofthe-art and future directions. *Cognitive Neuropsychology*, 37(7–8), 413–420. https://doi.org/10.1080/02643294.2020.1736018
- Ferrè, E. R., Longo, M. R., Fiori, F., & Haggard, P. (2013). Vestibular modulation of spatial perception. *Frontiers in Human Neuroscience*, 7(OCT), 1–7. https://doi.org/10.3389/ fnhum.2013.00660
- Fitzpatrick, R. C., & Day, B. L. (2004). Probing the human vestibular system with galvanic stimulation. *Journal of Applied Physi*ology, 96(6), 2301–2316. https://doi.org/10.1152/japplphysiol. 00008.2004
- Fitzpatrick, R. C., Wardman, D. L., & Taylor, J. L. (1999). Effects of galvanic vestibular stimulation during human walking. *Journal of Physiology*, 517(3), 931–939. https://doi.org/10.1111/ j.1469-7793.1999.0931s.x
- Fraser, L. E., Makooie, B., & Harris, L. R. (2015). The subjective visual vertical and the subjective haptic vertical access different gravity estimates. *PLoS ONE*, 10(12), 1–20. https://doi.org/ 10.1371/journal.pone.0145528
- Gu, Y., Angelaki, D. E., & DeAngelis, G. C. (2008). Neural correlates of multisensory cue integration in macaque MSTd. *Nature Neuroscience*, 11(10), 1201–1210. https://doi.org/10. 1038/nn.2191
- Hilliard, D., Passow, S., Thurm, F., Schuck, N. W., Garthe, A., Kempermann, G., & Li, S. C. (2019). Noisy galvanic vestibular stimulation modulates spatial memory in young healthy adults. *Scientific Reports*, 9(1), 1–11. https://doi.org/10.1038/ s41598-019-45757-0
- Israël, I., Sievering, D., & Koenig, E. (1995). Self-rotation estimate about the vertical axis. Acta Oto-Laryngologica, 115(1), 3–8. https://doi.org/10.3109/00016489509133338
- Ivanenko, Y., Grasso, R., Israël, I., & Berthoz, A. (1997). Spatial orientation in humans: Perception of angular whole-body displacements in two-dimensional trajectories. *Experimental Brain Research*, 117(3), 419–427. https://doi.org/10.1007/ s002210050236
- Kalia, A. A., Schrater, P. R., & Legge, G. E. (2013). Combining path integration and remembered landmarks when navigating without vision. *PLoS ONE*, 8(9), e72170. https://doi.org/10. 1371/journal.pone.0072170
- Karn, T., & Cinelli, M. E. (2019). The effect of galvanic vestibular stimulation on path trajectory during a path integration task.

Quarterly Journal of Experimental Psychology, 72(6), 1550-1560. https://doi.org/10.1177/1747021818798824

- Kaski, D., Quadir, S., Nigmatullina, Y., Malhotra, P. A., Bronstein, A. M., & Seemungal, B. M. (2016). Temporoparietal encoding of space and time during vestibular-guided orientation. Brain, 139(2), 392-403. https://doi.org/10.1093/brain/awv370
- Kolarik, A. J., Moore, B. C. J., Zahorik, P., Cirstea, S., & Pardhan, S. (2016). Auditory distance perception in humans: A review of cues, development, neuronal bases, and effects of sensory loss. Attention, Perception, and Psychophysics, 78(2), 373-395. https://doi.org/10.3758/s13414-015-1015-1
- Lewald, J., & Karnath, H. O. (2000). Vestibular influence on human auditory space perception. Journal of Neurophysiology, 84(2), 1107-1111. https://doi.org/10.1152/jn.2000.84.2.1107
- Loomis, J. M. (1999). Human navigation by path integration. Wayfinding Behavior. https://cir.nii.ac.jp/crid/ 1573668924947340544.bib?lang=en
- Loomis, J. M., Klatzky, R. L., Philbeck, J. W., & Golledge, R. G. (1998). Assessing auditory distance perception using perceptually directed action. Perception & Psychophysics, 60(6), 966-980. https://doi.org/10.3758/BF03211932
- Loomis, J. M., & Knapp, J. M. (2003). Visual perception of egocentric distance in real and virtual environments. In L. J. Hettinger & M. W. Haas (Eds.), Virtual and adaptive environments. Applications, implications, and human performance issues (1st ed., pp. 21-46). CRC Press.
- Lopez, C., Blanke, O., & Mast, F. W. (2012). The human vestibular cortex revealed by coordinate-based activation likelihood estimation meta-analysis. Neuroscience, 212, 159-179. https://doi. org/10.1016/j.neuroscience.2012.03.028
- Lopez, C., Lenggenhager, B., & Blanke, O. (2010). How vestibular stimulation interacts with illusory hand ownership. Consciousness and Cognition, 19(1), 33-47. https://doi.org/10.1016/j. concog.2009.12.003
- MacDougall, H. G., Moore, S. T., Curthoys, I. S., & Black, F. O. (2006). Modeling postural instability with galvanic vestibular stimulation. Experimental Brain Research, 172(2), 208-220. https://doi.org/10.1007/s00221-005-0329-y
- Moore, S. T., MacDougall, H. G., Peters, B. T., Bloomberg, J. J., Curthoys, I. S., & Cohen, H. S. (2006). Modeling locomotor dysfunction following spaceflight with galvanic vestibular stimulation. Experimental Brain Research, 174(4), 647-659. https://doi.org/10.1007/s00221-006-0528-1
- Morey, R. D., & Rouder, J. N. (2018). BayseFactor: computation of bayes factors for common designs.
- Nardi, D., Carpenter, S., Johnson, S., Gilliland, G., Melo, V., Pugliese, R., Coppola, V., & Kelly, D. (2020). Spatial reorientation with a geometric array of auditory cues. Quarterly Journal of Experimental Psychology, 75(2), 362-373. https://doi.org/10. 1177/1747021820913295
- Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of cue integration in human navigation. Current Biology, 18(9), 689-693. https://doi.org/10.1016/j.cub.2008.04.021
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia, 9(1), 97-113. https://doi.org/10.1016/0028-3932(71)90067-4

EJN European Journal of Neuroscience FENS Rieser, J. J., Ashmead, D. H., Talor, C. R., & Youngquist, G. A. (1990). Visual perception and the guidance of locomotion

675-689. https://doi.org/10.1068/p190675 Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. Psychonomic Bulletin and Review, 16(2), 225-237. https://doi.org/10.3758/PBR.16.2.225

without vision to previously seen targets. Perception, 19(5),

- Seemungal, B. M. (2015). The components of vestibular cognition -Motion versus spatial. Perception, 28, 507-524. https://doi.org/ 10.1163/22134808-00002507
- Smith, P. F. (2012). Interactions between the vestibular nucleus and the dorsal cochlear nucleus: Implications for tinnitus. Hearing Research, 292(1-2), 80-82. https://doi.org/10.1016/j.heares. 2012.08.006
- Stephan, T., Deutschländer, A., Nolte, A., Schneider, E., Wiesmann, M., Brandt, T., & Dieterich, M. (2005). Functional MRI of galvanic vestibular stimulation with alternating currents at different frequencies. NeuroImage, 26(3), 721-732. https://doi.org/10.1016/j.neuroimage.2005.02.049
- Sun, H. J., Campos, J. L., Young, M., Chan, G. S. W., & Ellard, C. G. (2004). The contributions of static visual cues, nonvisual cues, and optic flow in distance estimation. Perception, 33(1), 49-65. https://doi.org/10.1068/p5145
- Xie, Y., Bigelow, R. T., Frankenthaler, S. F., Studenski, S. A., Moffat, S. D., & Agrawal, Y. (2017). Vestibular loss in older adults is associated with impaired spatial navigation: Data from the triangle completion task. Frontiers in Neurology, 8(APR), 1-9. https://doi.org/10.3389/fneur.2017.00173
- Yoder, R. M., & Taube, J. S. (2014). The vestibular contribution to the head direction signal and navigation. Frontiers in Integrative Neuroscience, 8(APR), 1-13. https://doi.org/10.3389/fnint. 2014.00032
- Zahorik, P., Brungart, D. S., & Bronkhorst, A. W. (2005). Auditory distance perception in humans: A summary of past and present research. 91, 409-420.
- Zanchi, S., Cuturi, L. F., Sandini, G., & Gori, M. (2022). Interindividual differences influence multisensory processing during spatial navigation. Journal of Experimental Psychology: Human Perception and Performance, 48(2), 174–189. https://doi.org/10. 1037/xhp0000973.supp
- Zink, R., Bucher, S. F., Weiss, A., Brandt, T., & Dieterich, M. (1998). Effects of galvanic vestibular stimulation on otolithic and semicircular canal eye movements and perceived vertical. Electroencephalography and Clinical Neurophysiology, 107(3), 200-205. https://doi.org/10.1016/S0013-4694(98)00056-X

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