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Research Report

Vertical prism adaptation, but not sound presentation, modulates the visuospatial representation: A manual line-bisection study

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ABSTRACT

The present study aimed at testing whether vertical prism adaptation (PA) can modulate vertical visuospatial representation, assessed with a vertical manual line-bisection (MLB) task (Experiment 1). In a second time, we wanted to investigate the potential influence of sound presentation during such a task. Sound is a spatially valued element that has previously been reported to modify horizontal visuospatial representation. In Experiment 2, we presented either a high pitch, a low pitch, or no sound during the same MLB as in Experiment 1. With this experiment, we also searched for an eventual interaction between the effect of sound presentation and the potential cognitive aftereffects of vertical PA on visual representation.

Both Experiments 1 and 2 were constructed with the same design and conducted with two distinct groups of young healthy right-handed participants. First, we assessed the initial sensorimotor state with an open-loop pointing task, and the initial representational state through a vertical MLB (with addition of sound for Experiment 2). Then participants were submitted to a 16-minute PA procedure and were tested again on the open-loop pointing task and the MLB to assess the aftereffects following prism removal.

Our results showed sensorimotor aftereffects following both upward and downward PA, in a direction opposed to the optical deviation used. The early aftereffects measured following PA were symmetrical, but at the end of the experiment the residual aftereffects were smaller following downward PA than upward PA. We also provide a new insight on the aftereffects of vertical PA on visuospatial representation, showing that downward PA (but not upward PA) can produce an upward bias on the manual line-bisection task. This is the first proof of such cognitive aftereffects following vertical PA. However, we found no effect of sound presentation on the vertical visual space representation and no interaction between PA and sound presentation.

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1. Introduction

1.1. Prism adaption and its representational aftereffects

Prism adaptation (PA) is an experimental paradigm classically used to induce short-term sensorimotor plasticity. Although this paradigm appeared more than a century ago to study sensorimotor function in humans (Kornheiser, 1976; Stratton, 1897), interest has increased for the last two decades, with the highlight of cognitive aftereffects following PA to a lateral optical deviation in both pathological (Rossetti et al., 1998) and healthy humans (Colent et al., 2000). PA consists of manually pointing toward visual targets, while wearing glasses, which classically shift the visual field laterally (e.g., Michel, 2016). At first, errors are made in the direction of the optical shift induced by prisms. Then, trial after trial, the performance gets better and the magnitude of error decreases to reach the same level of accuracy as before prism exposure. Finally, after prism removal, another error appears toward the opposite direction of the deviation induced by the glasses (e.g., Redding et al., 2005). This latter pointing error testifies to the development of “true adaptation” and is called sensorimotor aftereffects (e.g., Prablanc et al., 2020). Twenty-five years ago, Rossetti et al. (1998) showed that PA to a rightward optical deviation can produce therapeutical effects in patients suffering of unilateral spatial neglect (USN), which is a common behavior occurring after a neurological lesion. USN appears as “a failure to report, respond, or orient to contralateral stimuli that is not caused by an elemental sensorimotor deficit” (e.g., Heilman et al., 2000). Among the therapeutical effects, one can identify a visuospatial representational shift toward the left part of the space, which was initially neglected. This study was the first proof of cognitive aftereffects of PA. Colent et al. (2000) then showed that such representational aftereffects can also occur after PA to a leftward optical deviation in healthy individuals, producing a representational shift to the right, which can be considered as a mild neglect simulation. Then literature has grown about these cognitive aftereffects of PA (Michel, 2016 for a review), showing that they can occur not only in visuospatial representation, but also in the representation of spatially valued elements like numbers (Loftus et al., 2009), letters (Nicholls et al., 2008), body representation (Michel, Rossetti et al., 2003), and more recently on auditory frequency representation (Bonnet et al., 2021, 2022; Michel et al., 2019).

1.2. Line bisections: tasks for the assessment of visuospatial representation

Classically, spatial representation is studied in the horizontal dimension with simple paper/pencil tasks, or tasks requiring a verbal response to a visuospatial stimulus. Some classical paradigms are the line-extension task (e.g., Bisiach et al., 1998), the Landmark task (e.g., Fink et al., 2001) or the line-bisection task (e.g., Jewell & McCourt, 2000). The line-bisection task is one of the most used paradigms to assess visuospatial representation, because of its ease to implement with healthy persons as well as with clinical populations (e.g., Halligan, 1995). In the manual version of the line-bisection task (MLB), participants have to indicate, as accurately as possible, the center of a line presented in front of them by tracing a bisection mark with a pencil. In its perceptual version (i.e., the Landmark task), participants have to judge whether a presented line is bisected to the right or to the left of its true center (e.g., Milner et al., 1992). Performance in bisection tasks is characterized by a well-known bias toward the left part of the space (called pseudoneglect) for horizontal lines (e.g., McCourt & Jewell, 1999), and a bias toward the higher part of the space (called altitudinal bias) for vertical lines (e.g., Jeerakathil & Kirk, 1994). These biases reflect an overrepresentation of the left and the upper part of the space, that seems to be due to an imbalance in the implied structures of the brain. The right hemisphere has clearly been shown to be dominant for visuospatial functions, maybe because of a facilitated involvement of the right parietofrontal network (e.g., de Schotten et al., 2011). This dominance would lead to an overrepresentation of the contralateral space (i.e., the left hemispace), inducing a leftward bias on the response of the participant. The altitudinal bias has also been partly explained by this hemispheric asymmetry, as suggested in a case study on a right temporal lobe damaged patient, which exhibited a downward bias on vertical MLB, suggesting a right-lateralized treatment of the visuospatial information from the upper part of the space (Morris et al., 2020). Another explanation for the altitudinal bias could be an asymmetry of activation between the ventral and the dorsal visual pathways, implied preferentially in the processing of information from the upper and the lower part of the visual field, respectively (Goodale & Milner, 1992; Previc, 1990). Churches et al. (2017) suggested that the upward attentional shift is due to a greater activation of the ventral stream relative to the dorsal stream (see also Drain & Reuter-Lorenz, 1996). Because of an absence of correlation between vertical and horizontal biases in different visuospatial judgment tasks, they conclude that these biases would rely on different cognitive mechanisms. The treatment of information in the vertical dimension would rely on an object-based strategy, involving preferentially the ventral visual stream, whereas the treatment of the horizontal dimension would rather rely on a space-based strategy, involving preferentially the dorsal visual stream (Churches et al., 2017; Duecker & Sack, 2015). This postulate about a ventral processing in vertical bisection tasks is in line with previous data of Claunch et al. (2012), showing that using a face memorization task (known to recruit the ventral visual stream) while performing a vertical MLB, increased the upward altitudinal bias, as compared to the bias observed while memorizing spatial locations, or seeing faces without the need to recognize them (tasks that do not recruit the ventral visual stream). The ventral visual stream dominance would thus contribute to the upward altitudinal bias.

1.3. Scarcity of studies about vertical PA

Although the aftereffects of lateral PA on visuospatial representation have been extensively studied through the horizontal line-bisection task, literature about the representational aftereffects of vertical PA is still scarce. More generally, very few studies have been conducted on vertical PA (Bonnet et al., 2022; Bultitude et al., 2012; Martin et al., 2001). Recently, sensorimotor aftereffects have been shown to occur following adaptation to both an upward and a downward optical deviation (Bonnet et al., 2022). This was the first proof of symmetrical sensorimotor aftereffects on visuomanual pointing following vertical PA (i.e., directed toward the opposite direction of the optical deviation used), as it is usually observed following horizontal PA. To date, no study has reported cognitive visuospatial aftereffects following vertical PA.

1.4. *Sound: a spatially valued element able to interact with visuospatial representation?*

As introduced before, horizontal visuospatial representation is not immutable, and can be modified by different factors, others than lateral PA (e.g., Colent et al., 2000). The one that drew our attention was sound presentation, which has already been shown to have an impact on visuospatial representation. Sound is a spatially valued element (Pratt, 1930). Previous work showed the existence of a "SMARC effect" (Spatial Musical Association of Response Codes), inducing faster and more accurate responses to high-pitch sound stimuli when responding with a button located upwards or rightwards, whereas faster and more accurate responses were observed for low-pitch sound stimuli when responding with a button located downwards or leftwards (Lidji et al., 2007; Rusconi et al., 2006). These studies also pointed differences between participants having a strong musical background and those having not: musicians present a spatial representation of pitch both in the horizontal and the vertical dimensions, whereas nonmusicians would present a spatial representation only in the vertical dimension (Lidji et al., 2007). According to Ishihara et al. (2013), the existence of a SMARC effect suggest a spatial mapping of auditory pitches representation in the brain, so they wondered if the presentation of high or low sounds could modulate performance on a visuospatial representational task. In a first experiment, they proposed to healthy persons to do a horizontal and a vertical MLB task, while hearing either a high pitch (1760 Hz), a low pitch (110 Hz), or a white noise. They found that in the horizontal dimension there was a significant effect of pitch on MLB performance with a leftward bias induced by low pitches and a rightward bias induced by high pitches. In the vertical dimension, they replicated the well-documented upward altitudinal bias, but they observed no pitch effect on the bisection performance. One can wonder if using other displays for this task to make it more sensitive could favor the appearance of a pitch effect on vertical MLB. For instance, increasing the difference between the high and low sounds or modifying the line length could lead to a better expression of the representational modulation.

1.5. *Objectives and hypotheses*

The present study aimed first at evaluating whether vertical PA can produce visuospatial representational aftereffects on a vertical MLB (Experiment 1). A second objective was to assess if the presentation of sounds when performing such a representational task in the vertical dimension could produce a bias, and could interact with the representational aftereffects of vertical PA (Experiment 2).

Concerning Experiment 1, different hypotheses can be considered. Based on previous literature about the aftereffects of PA on auditory frequencies, for which only PA to a downward optical deviation produces a representational bias of sound toward higher frequencies (Bonnet et al., 2022), one can imagine that PA to a downward optical deviation only should produce representational aftereffects in MLB, shifting the subjective center of the line upwards.

Another hypothesis can be formulated based on knowledge about the aftereffects of lateral PA on visuospatial tasks, where aftereffects only occur following PA toward the direction of the initial bias (e.g., Goedert et al., 2010). In this view, the expected effect would be observed only following upward PA, because of the upward altitudinal bias on MLB. The aftereffect following upward PA would be characterized by a shift of the subjective center of the line downwards.

One can also imagine other hypotheses if considering that vertical and horizontal PA rely on totally independent mechanisms. One can predict an absence of visuospatial representational aftereffects of vertical PA on MLB, as it was the case on the Landmark task (Bonnet et al., 2022).

For Experiment 2, we hypothesized that low pitch presentation during the MLB should produce a representational bias toward the lower part of the space, and high pitch presentation should induce a representational bias toward the upper part of the space. In the case of a significant effect of PA and sound presentation on visuospatial representation, we expected that these two effects would be potentiated or annulated, according to the respective directions of the induced bias. Namely, if downward PA induces an upward bias on MLB, the presentation of a high pitch sound during this task would exacerbate this bias, whereas a low pitch would diminish the expression of this PA-induced bias.

2. Experiment 1

2.1. *Material and methods*

2.1.1. *Participants*

An *a priori* sample size estimation was performed using G*Power 3.1 (Faul et al., 2007) to estimate the number of participants required for this study (Experiments 1 and 2). We used previous data of Colent et al. (2000) on representational aftereffects of lateral PA, assessed by the perceptual version of the line-bisection task ($N = 7$ for each optical deviation). This previous work seems close enough to the purpose of this study, although PA and line bisection were not performed in the same orientation (i.e., horizontally in the study of Colent et al., 2000; vertically in the present study). Colent et al. (2000) found that leftward PA shifted the initial leftward bias (i.e., pseudoneglect) toward the right side. Performance was expressed in mm from the left end of the 250 mm line. The obtained values were 123.98 ± 1.0 mm in pretest and 125.1 ± 1.2 mm in posttest. With an estimated effect size of $d = .98$, G*Power gives a required sample size of $N = 11$ (with $\alpha = .05$ and power $= .80$). For the present study, each group was above this minimal sample size.

Thirty-two young healthy adults (12 men, 20 women; $M_{age} = 21.3 \pm 2.6$ years old) participated to Experiment 1. They were all right-handed (Edinburgh score > .5). They had a normal or corrected-to-normal vision and had no antecedents of neurological or psychiatric disorders. After receiving information about the experiment, they all provided a written consent to participate in this study. This study was approved by the Committee for Ethical Research of Université Bourgogne Franche-Comté (CERUBFC-2021-10-07-029).

Participants were randomly attributed to a Downward Optical Deviation group ($N = 15$) or an Upward Optical Deviation group ($N = 14$). Since we focused on aftereffects of PA, only participants with a significant adaptation were included in the statistical analysis. Thus, three participants were excluded from the experiment because they showed no significant adaptation to the downward optical deviation.

2.1.2. *Design and experimental set-up*

Participants came at the lab where they were submitted to a 1h15 protocol. First, they performed an MLB task, and an open-loop pointing task (Pretest), followed by the PA procedure. The development of sensorimotor adaptation was immediately assessed by a second open-loop pointing task (Posttest), and they performed a second MLB task to evaluate the representational aftereffects of PA. Finally, they did a last open-loop pointing task to check if sensorimotor aftereffects lasted until the end of the experiment (Late-test).

Participants were seated on an adjustable stool in front of a 924×520 mm touchscreen with a resolution of 1280×720 pixels oriented vertically. Their gaze was aligned with the middle of the screen for every task by mean of a fixed chin support with an eye-screen distance of 450 mm. The experiment was performed in the dark, with only the light of the screen to avoid visual distraction. Participant were told to keep their eyes closed between the different parts of the experiment to prevent vision of their hand, which could lead to more deadaptation by matching visual and proprioceptive information available for action.

2.1.3. *Manual line-bisection task (MLB)*

An MLB was performed before (Pretest) and after (Posttest) PA. For this task, participants had their left hand on their left knee and their right hand (effector for the task) reposing on a table just in front of their chest. This set-up allowed the dissociation of the reference position of each hand to avoid sensory conflict due to a mismatch between visual, proprioceptive and tactile information from the adapted hand compared to the nonadapted one. Such a mismatch could have led to deadaptation. In this position, both hands were hidden from eyes before the beginning of the reaching movement, also to avoid visual feedback of hand positions in the peripheral vision and minimize deadaptation.

Thirty-six black lines were presented vertically on a white background. Each line was 300 mm long and 2 mm thick and was placed on the middle of the screen. Participant had to mark with a stylus the middle of each line, and the mark, which appeared as a 2 pixels thick line, remained visible for a few seconds. The length of the bisection mark made by the participant was free, as they were only told to focus on the accuracy of the point where they cross the vertical line. A gray screen was presented as a mask between each trial to avoid the participant to mark the next line based on the memory of their previous mark. During this task, the participant was told to do very slow movements to reach the screen to avoid any sensorimotor interference and thus limit the contribution of sensorimotor aftereffects on the representational task for the posttest. This performance criterion was very important to isolate visuospatial representation from sensorimotor bias during the MLB task. Before the beginning of the experiment, the participant was trained with three lines to get familiar with the task and to check if the task was well understood.

2.1.4. *Open-loop pointing task*

For this task, the initial position of participants' right hand was on a support in front of their nose, with the index on a 1×1 cm rough mark. The task was realized with the right index finger. Open-loop pointing was performed just before and immediately after PA to check sensorimotor adaptation of the participant. A third open-loop pointing was realized at the end of the experiment to ensure that the aftereffects lasted at least for all the duration of the bisection task. In the open-loop pointing task, a black dot (diameter = 6 mm) was presented on the middle of the screen. The participant was told to open their eyes, to look at the target and then to close their eyes before pointing to the target as accurately as possible. Occulting glasses (PLATO Visual Occlusion Spectacles, Translucent Technologies Inc.) were used to avoid any accidental eye opening during the movement, and thus to prevent the participant from taking visual cues about their hand position, which would have led to deadaptation. Then participant was told to keep their finger on the screen and their hand was brought back to the starting point by the experimenter. This precaution was taken to limit participant's deadaptation and to replace their hand strictly in the same position for each trial.

2.1.5. *Prism adaptation (PA)*

PA was achieved by the procedure used in previous studies (e.g., Michel, Pisella et al., 2003), adapted to the vertical dimension by Bonnet et al. (2022). The task duration, the number of movements and the strength of optical shift were chosen to maximize the likelihood to obtain aftereffects. Participants wore prismatic glasses inducing an upward or a downward optical deviation (15°). They had to perform four blocks of 81 pointing movements (total: 324 movements) to nine colored targets presented vertically on the screen (diameter of targets = 6 mm; intertarget space = 4 cm; colors = green, yellow, red, blue, black). The order of pointing was pseudorandomized to have the same number of movements to each target. Participants were told to point to targets as fast and accurately as possible with their right index finger and to come back at their starting position on their own at a normal speed. The task duration was about 16 min. Between blocks, participants were allowed to relax for 1 min, eyes closed, without moving their head or touching another part of their body with the adapting arm to avoid sensory conflicts that could led to deadaptation. This resting time was important to develop a greater adaptation (Taub & Goldberg, 1973), but also to reduce fatigue that appears due to the amount of rapid vertical movements of the arm.

2.1.6. *Statistical analysis*

All the statistical analyses were computed with Jamovi (The jamovi project, 2021). All data respected assumptions for parametric analysis, with a normal distribution assessed with a Shapiro–Wilk test, analyses thus consisted in one sample t tests, paired sample t tests, and repeated-measures ANOVA. The significance threshold was set to $\alpha = .05$.

2.2. *Results of Experiment 1*

2.2.1. *Open-loop pointing task*

2.2.1.1. Sensorimotor initial bias. A one sample t test (comparison of the pointing performance to 0, which corresponds to the objective position of the target) performed on open-loop pointing showed that in Pretest, errors were significantly directed toward the lower part of the space for both the Downward Optical Deviation group, $t(14) = 3.436$, $p = .004$, $d = -.887$, and the Upward Optical Deviation group, $t(13) = 3.756$, $p = .002$, $d = -1.004$ (Fig. 1). An independent sample t test showed no difference between the initial bias of the Downward and the Upward Optical Deviation groups ($t < 1$).

2.2.1.2. Sensorimotor aftereffects of PA. Separate analyses were conducted for the Downward and the Upward Optical Deviation groups to assess the aftereffects of PA according to the deviation used. A repeated-measures ANOVA was performed on open-loop pointing errors with Session (pre, post, or late) as within-subject factor (Fig. 1). Paired sample t tests were then realized to reveal differences between pointing errors before and after prism exposure.

The ANOVA showed a significant effect of Session for the Downward Optical Deviation group, $F(2, 28) = 77.44$, $p < .001$, $\eta^2 = .502$. Then, planned comparisons were performed with paired sample t tests and a Bonferroni correction of p. They revealed that the pointing errors were significantly shifted toward the upper part of the space in Posttest, $t(14) = -11.572$, $p < .001$, $d = -2.988$, and Late-test, $t(14) = -3.804$, $p = .004$, $d = -.982$, compared to the Pretest.

For the Upward Optical Deviation group, the ANOVA also showed a significant effect of Session, $F(2, 26) = 47.99$, $p < .001$, $\eta^2 = .370$. The planned comparisons performed with paired sample t tests and a Bonferroni correction of p revealed that the pointing errors were significantly shifted toward the lower part of the space in Posttest, $t(13) = 8.303$, $p < .001$, $d = 2.219$, and Late-test, $t(13) = 5.519$, $p < .001$, $d = 1.475$, compared to the Pretest.

Independent sample t tests were conducted on the absolute value of magnitude of sensorimotor effects between the Downward and the Upward Optical Deviation groups. No difference was found between groups on the magnitude of adaptation (Posttest − Pretest; $t < 1$; Fig. 2A). The deadaptation (Immediate aftereffects − Late aftereffects) was significantly greater for the Downward Optical Deviation group than for the Upward Optical Deviation group, $t(27) = 3.566$, $p = .001$, $d = 1.325$ (Fig. 2C), but the difference between magnitudes of adaptation at the end of the experiment (Late-test − Pretest) failed to reach significance, $t(27) = -1.907$, $p = .067$ (Fig. 2B).

2.2.2. *Vertical manual line-bisection task*

2.2.2.1. Representational initial bias. A one sample t test (comparison to 0, which corresponds to the objective center of the line) performed on line-bisection performance for the Pretest—to assess initial representational bias—showed that errors were significantly oriented toward the upper part of the space, $t(28) = 2.341$, $p = .027$, $d = .435$. This initial error is called altitudinal bias. An independent sample t test conducted on Pretest data between the two optical deviation groups revealed no significant difference ($t < 1$).

2.2.2.2. Representational aftereffects of PA. Paired t tests were used to assess the difference between Pretest and Posttest for Downward and Upward Optical Deviation groups separately. Errors in line-bisection task were significantly shifted toward the upper part of the space following adaptation to a Downward Optical Deviation, $t(14) = -3.37$, $p = .005$, $d = -.871$ (Fig. 3A), but no difference was observed between Pretest and Posttest after adaptation to an Upward Optical Deviation ($t < 1$; Fig. 3B).

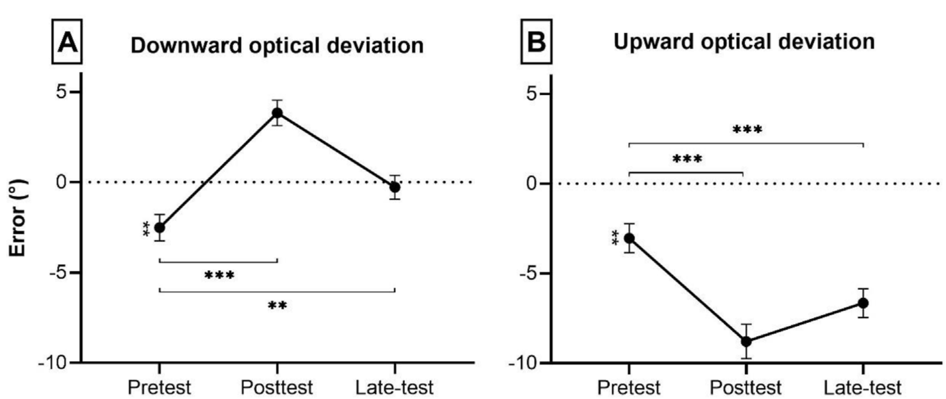

Fig. 1 – Average pointing errors on the open-loop pointing task (Experiment 1). *Note.* Measures of the pointing error (expressed in degrees) on open-loop pointing were made before PA (Pretest), just following PA (Posttest), and at the end of the experiment (Late-test) to assess sensorimotor adaptation. Mean results with standard errors are displayed on panel A for the group adapted to a downward optical deviation, and on panel B for the group adapted to an upward optical deviation. A comparison to 0 was performed for the Pretest only, revealing a significant downward pointing error for each group. Comparisons between the Pretest and Posttest, and between the Pretest and the Late-test revealed significant differences. **$p < .01$. ***$p < .001$.

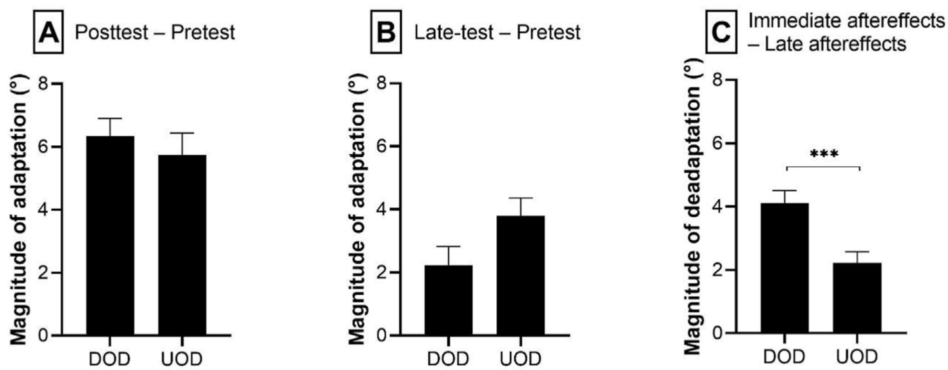

Fig. 2 – Magnitude of adaptation and deadaptation for each optical deviation (Experiment 1). *Note.* The absolute value of magnitude of sensorimotor effects was compared between the Downward (DOD) and the Upward Optical Deviation (UOD) groups. Panel A displays the magnitude of adaptation following PA (Posttest – Pretest). Panel B displays the magnitude of residual adaptation at the end of the experiment (Late-test – Pretest). Panel C displays the magnitude of deadaptation (i.e., the loss of sensorimotor aftereffects) between immediate aftereffects (Posttest – Pretest) and late aftereffects (Late-test – Pretest). Error bars represent standard errors. ******p* < .001.

2.2.2.3. Absence of correlation between initial bias and cognitive aftereffects. No correlation was found between the magnitude of the initial altitudinal bias (i.e., the error, in mm, between the true center of the line and the bisection mark made by the participant) and the magnitude of representational aftereffects induced by downward PA (i.e., the difference of error, in mm, between pretest and posttest on the line-bisection task), $r(13) = -.39$, $p = .152$. This analysis was only performed for the Downward Optical Deviation group, since the Upward Optical Deviation did not produce a significant aftereffect on visuospatial representation.

2.2.3. *Absence of correlation between sensorimotor and cognitive aftereffects*

For the Downward Optical Deviation group, which showed a significant effect of vertical PA on spatial representation, no correlation was found between the magnitude of sensorimotor aftereffects (open-loop pointing task) and the magnitude of representational aftereffects (line-bisection task), $r(13) = .16$, $p = .577$.

2.3. *Discussion of Experiment 1*

We found an initial sensorimotor bias directed toward the lower part of the space for both deviation groups. The downward action of gravity on the moving limb could explain such a bias, that was already observed on this kind of open-loop pointing task before (Bonnet et al., 2022). PA to a downward optical deviation shifted this bias upwards, whereas PA to an upward optical deviation exacerbated this initial downward bias. The magnitude of aftereffects was the same between these two optical deviations. This result replicates the previous study of Bonnet et al. (2022), showing that both vertical PA to an upward and a downward optical deviation produce

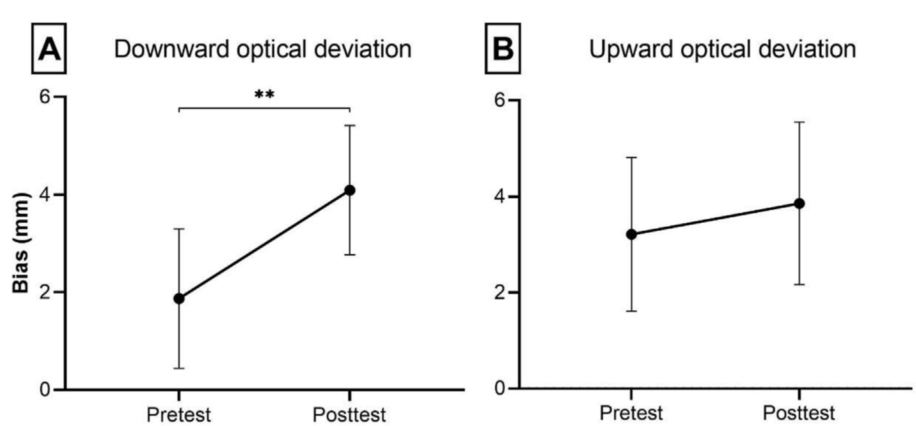

Fig. 3 – Average bias on the manual line-bisection (Experiment 1). *Note.* Measures of the bias on the MLB were performed before (Pretest) and following PA (Posttest). Panel A displays the mean results with standard errors for the group adapted to a downward optical deviation. Panel B displays the mean results with standard errors for the group adapted to an upward optical deviation. *****p* < .01.

sensorimotor aftereffects in the opposite direction of the optical deviation. Further analyses about the strength of these sensorimotor aftereffects showed that PA to an upward optical deviation produced more robust sensorimotor aftereffects (downwards), with less deadaptation in Late-test than what is observed for the upward aftereffects induced by a downward PA. This difference may be explained by the action of gravity. Indeed, gravity acts on the moving limb downwards, namely in the same direction as the sensorimotor aftereffects of PA to an upward optical deviation. Inversely, gravity tends to pull the arm in the opposite direction of the upward sensorimotor aftereffects of a downward PA.

At a representational level, an initial “altitudinal” bias was observed on line-bisection task performance. This bias, directed toward the higher part of the space, is consistent with previous studies on vertical MLB task (Jeerakathil & Kirk, 1994; Mańkowska et al., 2018). Downward adaptation induced a shift of the initial representational bias upwards, whereas no representational aftereffects were observed following an upward adaptation. This is the first demonstration of such visuospatial representational aftereffects following vertical PA. Unlike in the horizontal dimension, aftereffects of vertical PA were not reflected by a shift of the initial bias toward the other side (e.g., Goedert et al., 2010), but by an increase in the initial altitudinal bias in the same direction (upwards), only following downward PA. No correlation was found between the magnitude of the initial altitudinal bias and the magnitude of representational aftereffects. This result differs from what is observed in the lateral dimension, where a greater initial bias predicts a greater shift of the bias after PA (e.g., Goedert et al., 2010).

No correlation was found between the magnitude of sensorimotor aftereffects and the magnitude of representational aftereffects following PA to a downward optical deviation, indicating that the observed bias on MLB task cannot be attributed to a sensorimotor bias induced by prisms. Such a result was obtained while precaution was taken in the experimental set-up and careful indications were given to the participants by the experimenter to avoid sensorimotor contamination (See Material and Methods). Consequently, our results are in line with previous work on lateral PA where there was also no correlation between the magnitude of sensorimotor aftereffects and the magnitude of cognitive effects following adaptation (Berberovic, 2003; Fortis et al., 2011; Girardi et al., 2004; Guinet & Michel, 2013; Herlihey et al., 2012; Schintu et al., 2014).

In Experiment 1, we showed that PA to a downward optical deviation can exacerbate the initial altitudinal bias toward the upper part of the space. Based on this observation and considering the multiple sources of information available to build spatial representation, one can wonder if other factors can modulate this representation. Ishihara et al. (2013) investigated the impact of sound height on visuospatial representation, through an MLB task performed both in the horizontal and the vertical dimension. Horizontally, the results showed that hearing a high pitch shifted the visual subjective center of the line toward the right, while hearing a low pitch shifted this center toward the left. However, such an effect was not observed in the vertical dimension. In Experiment 2, we aimed at testing whether an effect of sound presentation could occur on vertical visuospatial representation. Compared with Ishihara's protocol, we wanted to make the experimental conditions more sensitive to favor the occurrence of pitch effect on the MLB. We decided to increase the difference in frequency between the higher and the lower sound frequency displayed to the participants while bisecting the lines (from 110 Hz for the low pitch and 1760 Hz for the high pitch in Ishihara et al. to 100 Hz for the low pitch and 3000 Hz for the high pitch in the present study). The line length was also increased from 200 mm to 300 mm, to favor the observation of an eventual bias, since a longer line is known to increase the magnitude of representational biases on line-bisection tasks (e.g., Jewell & McCourt, 2000). Finally, we aimed at testing whether there could be an additive effect of sound presentation and of PA on vertical visuospatial representation.

3. Experiment 2

3.1. *Material and methods*

3.1.1. *Participants*

Since this protocol was very close to Experiment 1, the sample size estimation was identical for this second experiment (see 2.1.1 Participants).

Thirty-one young healthy adults (9 men, 22 women; $M_{age} = 21.8 \pm 4.3$ years old) participated to Experiment 2. None of them participated in Experiment 1, so that they were totally naïve to the purpose of the experiment. They were all right-handed (Edinburgh score > .5). They had a normal or corrected-to-normal vision and had no antecedents of neurological or psychiatric disorders. After receiving information about the experiment, they all provided a written consent to participate in this study. This study was approved by the Committee for Ethical Research of Université Bourgogne Franche-Comté (CERUBFC-2021-10-07-029).

Participants were randomly attributed to a Downward Optical Deviation group ($N = 15$) or an Upward Optical Deviation group ($N = 15$). Since we focused on aftereffects of PA, only participants with a significant adaptation were included in the statistical analysis. Thus, one participant was excluded from the experiment because he showed no significant sensorimotor adaptation to the downward optical deviation.

3.1.2. *Design and experimental set-up*

Experiment 2 was similar as Experiment 1. The only difference was on the MLB task, which included the presentation of sounds while the participant was performing the task. The questionnaire used before the experiment was extended to collect information about the musical background of the participants to allow a categorization of participants according to their musical background. Based on criterion of the study of Bonnet et al. (2021), we categorized participants as musicians if they had more than five years of musical training and were still playing music.

3.1.3. *Sound*

Sound was broadcast with a Sennheiser HD 200 headphone at a mean intensity of 70 dB, using normal equal-loudness level contours (ISO226: 2003) to find an equally perceived intensity within the different frequencies. The sound stimuli were two sine waves of distinct frequencies (low = 100 Hz; high = 3000 Hz). Participants had to bisect 36 lines during the task (i.e., 12 lines with a low pitch, 12 lines with a high pitch and 12 lines with no sound). The stimuli appeared pseudorandomly within 12 blocks of three lines (1 per condition), based on Ishihara et al. (2013), who found that sound stimuli modulated line-bisection performance in the horizontal dimension only when presented alternatively.

3.2. *Results of Experiment 2*

3.2.1. *Open-loop pointing task*

3.2.1.1. SENSORIMOTOR INITIAL BIAS. A one sample *t* test (comparison of the pointing performance to 0, which corresponds to the objective position of the target) performed on open-loop pointing showed that in Pretest, errors were significantly directed toward the lower part of the space for both the Downward Optical Deviation group, $t(14) = -4.296$, $p < .001$, $d = -1.109$, and the Upward Optical Deviation group, $t(14) = -5.751$, $p < .001$, $d = -1.485$ (Fig. 4). An independent sample *t* test showed no difference between initial bias of the Downward and the Upward Optical Deviation groups ($t < 1$).

3.2.1.2. SENSORIMOTOR AFTEREFFECTS OF PA. Separate analyses were conducted for the Downward and the Upward Optical Deviation groups to assess the aftereffects of PA according to the deviation used. A repeated-measures ANOVA was performed on open-loop pointing errors with Session (pre, post, or late) as within-subject factor (Fig. 4).

For the Downward Optical Deviation group (Fig. 4A), the ANOVA showed a significant effect of Session, $F(2, 28) = 103.476$, $p < .001$, $\eta^2 = .398$. Then, planned comparisons, performed with paired sample *t* tests and a Bonferroni correction of *p*, revealed that pointing errors were significantly shifted toward the upper part of the space in Posttest, $t(14) = -11.793$, $p < .001$, $d = -3.045$, and Late-test, $t(14) = -5.371$, $p < .001$, $d = -1.387$, compared to the Pretest.

For the Upward Optical Deviation group (Fig. 4B), the ANOVA also showed a significant effect of Session, $F(2, 28) = 89.710$, $p < .001$, $\eta^2 = .494$. The planned comparisons, performed with paired sample *t* tests and a Bonferroni correction of *p*, revealed that pointing errors were significantly shifted toward the lower part of the space in Posttest, $t(14) = 14.414$, $p < .001$, $d = 3.722$, and Late-test, $t(14) = 6.725$, $p < .001$, $d = 1.736$, compared to the Pretest.

Independent sample *t* tests were conducted on the absolute value of magnitude of sensorimotor aftereffects between the Downward and the Upward Optical Deviation groups (Fig. 5). No difference was found between groups on the magnitude of adaptation (Posttest − Pretest, $t < 1$; Fig. 5A). The deadaptation (Immediate aftereffects − Late aftereffects) was significantly greater for the Downward Optical Deviation group than for the Upward Optical Deviation group, $t(28) = 3.214$, $p = .003$, $d = 1.174$ (Fig. 5C), but the difference between magnitudes of adaptation at the end of the experiment failed to reach significance (Late-test − Pretest, $t(28) = -1.938$, $p = .063$; Fig. 5B).

3.2.2. *Vertical manual line-bisection task*

3.2.2.1. REPRESENTATIONAL INITIAL BIAS. A one sample *t* test (comparison to 0, which corresponds to the objective center of the line) performed on line-bisection performance for the Pretest—to assess initial representational bias—showed that errors were significantly oriented toward the upper part of the space, $t(29) = 3.193$, $p = .003$, $d = .583$. This initial error is called altitudinal bias. An independent sample *t* test conducted on Pretest data between the two groups revealed no significant difference ($t < 1$).

3.2.2.2. ABSENCE OF SOUND EFFECT ON INITIAL REPRESENTATIONAL BIAS. Three one sample *t* tests (comparison to 0) were conducted to assess whether there was an initial altitudinal bias for each pitch condition on the line-bisection task (pretest). A significant upward bias was found for each condition [Low pitch: $t(29) = 3.543$, $p = .001$, $d = .647$; High pitch: $t(29) = 2.956$, $p = .006$, $d = .540$; No sound: $t(29) = 2.863$, $p = .008$, $d = .523$].

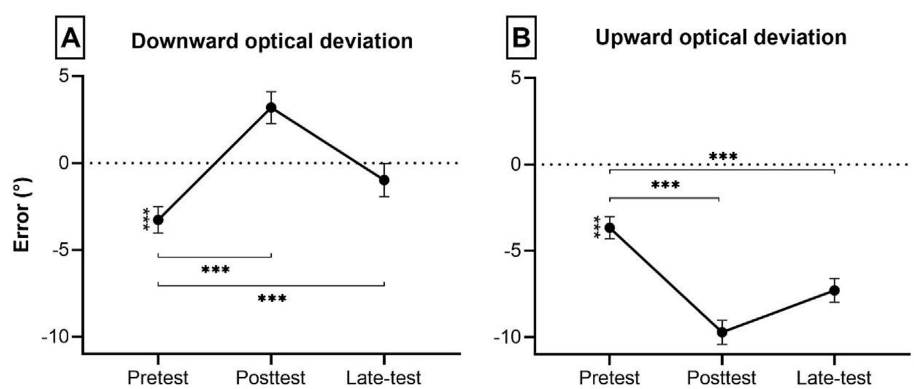

Fig. 4 – Average pointing errors on the open-loop pointing task (Experiment 2). *Note.* Measures of the pointing error (expressed in degrees) on open-loop pointing were made before PA (Pretest), just following PA (Posttest), and at the end of the experiment (Late-test) to assess sensorimotor adaptation. Mean results with standard errors are displayed on panel A for the group adapted to a downward optical deviation, and on panel B for the group adapted to an upward optical deviation. A comparison to 0 was performed for the Pretest only, revealing a significant downward pointing error for each group. Comparisons between the Pretest and Posttest, and between the Pretest and the Late-test revealed significant differences. ***$p < .001$.

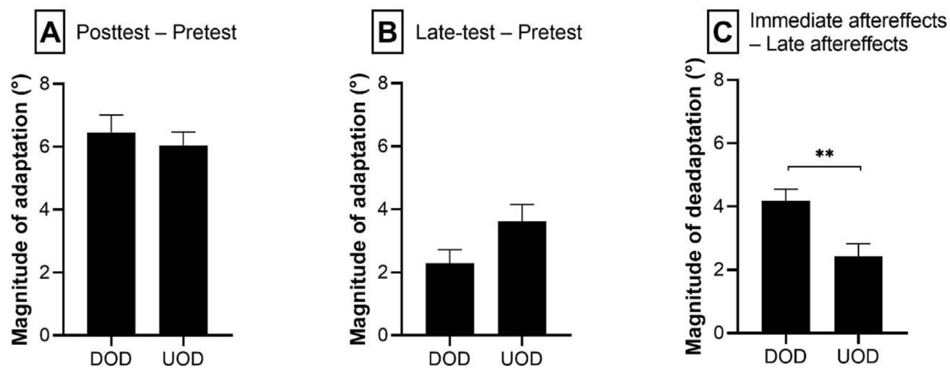

Fig. 5 – Magnitude of adaptation and deadaptation for each optical deviation (Experiment 2). ***Note*****. The absolute value of magnitude of sensorimotor effects was compared between the Downward (DOD) and the Upward Optical Deviation (UOD) groups. Panel A displays the magnitude of adaptation following PA (Posttest – Pretest). Panel B displays the magnitude of residual adaptation at the end of the experiment (Late-test – Pretest). Panel C displays the magnitude of deadaptation (i.e., the loss of sensorimotor aftereffects) between immediate aftereffects (Posttest – Pretest) and late aftereffects (Late-test – Pretest). Error bars represent standard errors. $^{**}p < .01$.**

A repeated-measures ANOVA with Pitch (low, high, no sound) as within-subject factor revealed no difference between the three conditions on the Pretest of line-bisection task, $F(2, 58) = 1.651$, $p = .200$.

3.2.2.3. Musical background. According to the questionnaire they had to answer, five participants were categorized as musicians in the Upward Optical Deviation group, and one in the Downward Optical Deviation group. A further statistical analysis conducted on nonmusicians only revealed very similar results as those obtained for the entire group, with no effect of sound on the MLB, as assessed by a repeated measures ANOVA with Pitch (low, high, no sound) as within-subject factor ($F < 1$).

3.2.2.4. Representational aftereffects of PA and absence of sound effect. Separate analyses were then conducted for Downward and Upward Optical Deviation groups to assess the aftereffects of both PA and pitch influence according to the deviation used. A two-way repeated-measures ANOVA was realized with Session (pre, post, late) and Pitch (low, high, no pitch) as within-subject factors.

For the Downward Optical Deviation group, the ANOVA showed a significant upward effect of Session on line-bisection performance, $F(1, 14) = 5.041$, $p = .041$, $\eta^2 = .026$ (Fig. 6A), but no effect of Pitch, $F(2, 28) = 1.636$, $p = .213$ and no Pitch $\times$ Session interaction ($F < 1$).

For the Upward Optical Deviation group, the ANOVA showed no effect of Session ($F < 1$; Fig. 6B), no effect of Pitch, $F(2, 28) = 2.101$, $p = .141$, and no Pitch $\times$ Session interaction, $F(2, 28) = 1.279$, $p = .294$.

3.2.2.5. Absence of correlation between initial bias and cognitive aftereffects. No correlation was found between the magnitude of the initial altitudinal bias (i.e., the error, in mm, between the true center of the line and the bisection mark made by the participant) and the magnitude of representational aftereffects induced by PA (i.e., the difference of error, in mm, between pretest and posttest on the line-bisection task), $r(13) = -.05$, $p = .856$. This analysis was only performed for the Downward Optical Deviation, since the Upward Optical Deviation did not provide a significant shift in visuospatial representation.

3.2.2.6. Absence of correlation between sensorimotor and cognitive aftereffects. For the Downward Optical Deviation group, which showed a significant effect of vertical PA on visuospatial representation, no correlation was found between the magnitude of sensorimotor aftereffects (i.e., the difference of error, in degrees, between pretest and posttest on the open-loop pointing task) and the magnitude of representational aftereffects (i.e., the difference of error, in mm, between pretest and posttest on the line-bisection task), $r(13) = -.23$, $p = .404$.

3.2.3. *Symmetrical sensorimotor adaptation and asymmetrical deadaptation between downward and upward optical deviations*

We wanted to check if increasing the number of participants would lead to a reinforcement or a vanishing of the tendential difference observed between the magnitude of residual aftereffects of upward and downward PA. Since Experiments 1 and 2 consisted exactly in the same sensorimotor protocol, with an identical duration of every task, the same number, direction and amplitude of pointing movements, and since no participant performed both experiments, we performed the following analysis by combining sensorimotor data from Experiment 1 ($N = 29$) and Experiment 2 ($N = 30$) together (Fig. 7). This allowed us to obtain a larger sample size of $N = 59$ participants. We observed symmetrical sensorimotor aftereffects following downward and upward PA. Namely, the difference between amplitudes of adaptation (Posttest – Pretest) in Downward Optical Deviation and Upward Optical Deviation groups remained nonsignificant ($t < 1$; Fig. 7A). However, the amplitude of deadaptation (Immediate aftereffects – Late aftereffects) was greater for the Downward Optical Deviation group,

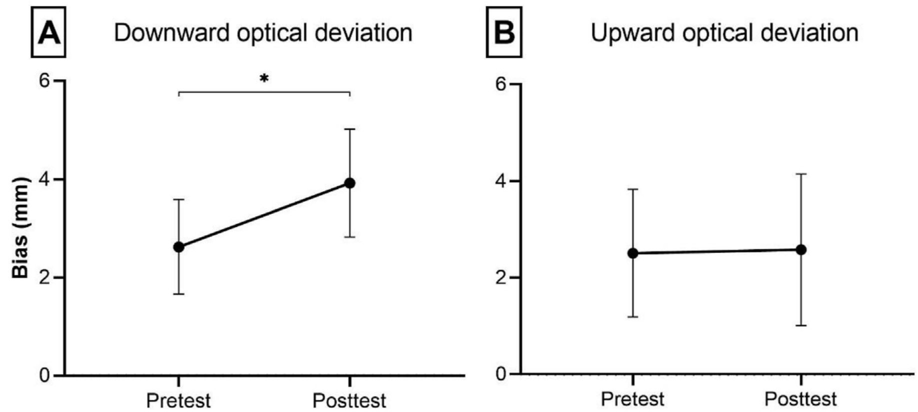

Fig. 6 – Average bias on the manual line-bisection (Experiment 2). ***Note*****. Measures of the bias on the MLB were performed before (Pretest) and following PA (Posttest). These graphs represent data of MLB averaged over all pitch conditions (low, high, no sound), since no difference was found between them. Panel A displays the mean results with standard errors for the group adapted to the downward optical deviation. Panel B displays the mean results with standard errors for the group adapted to the upward optical deviation. *p < .05.**

$t(57) = 4.859$, $p < .001$, $d = 1.265$ (Fig. 7C). The amplitude of residual adaptation at the end of the experiment (Late-test – Pretest) appeared to be significantly greater for the Upward Optical Deviation group, $t(57) = -2.756$, $p = .008$, $d = -.718$ (Fig. 7B).

3.3. *Discussion of Experiment 2*

In Experiment 2, we replicated our results from Experiment 1 about sensorimotor aftereffects of vertical PA. An initial sensorimotor bias directed toward the lower part of the space was thus observed on the open-loop pointing task. This downward bias was shifted toward the higher part of the space following PA to a downward optical deviation and exacerbated following PA to an upward optical deviation. These sensorimotor aftereffects were symmetrical in terms of magnitude of the pointing bias induced by PA. Further analysis on the robustness of these sensorimotor aftereffects were performed by combining open-loop data of both Experiments 1 and 2. It showed that downward aftereffects following upward PA were more robust than upward aftereffects following downward PA (i.e., there was less deadaptation and the remaining sensorimotor aftereffects at the end of the experiment were larger following upward PA).

At a representational level, we also observed the initial altitudinal bias directed toward the higher part of the space. This bias was observed for all pitch conditions (low, high, no sound). We did not observe any effect of sound presentation on line-bisection performance, and no combined/interactive effect of PA and sound presentation. The only significant effect was an increase of the initial upward bias following downward PA, independently to sound presentation. With

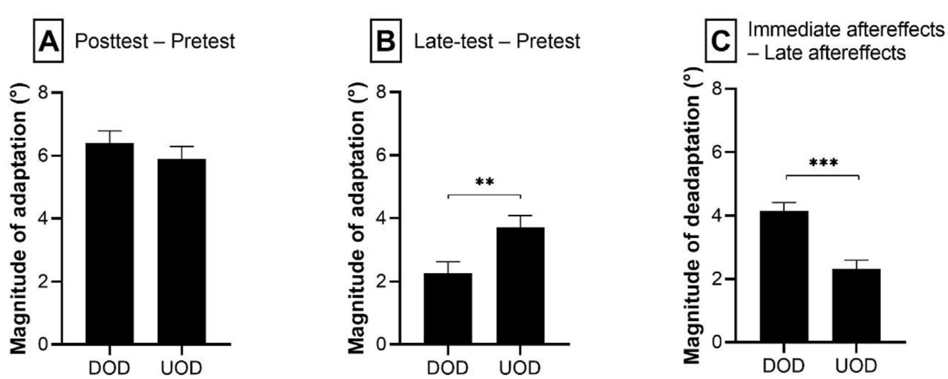

Fig. 7 – Magnitude of adaptation and deadaptation for each optical deviation (Experiments 1 and 2). ***Note*****. This figure shows the compiled sensorimotor results of Experiments 1 and 2. The absolute value of magnitude of sensorimotor effects was compared between the Downward (DOD) and the Upward Optical Deviation (UOD) groups. Panel A displays the magnitude of adaptation following the PA (Posttest – Pretest). Panel B displays the magnitude of residual adaptation at the end of the experiment (Late-test – Pretest). Panel C displays the magnitude of deadaptation (i.e., the loss of sensorimotor aftereffects) between immediate aftereffects (Posttest – Pretest) and late aftereffects (Late-test – Pretest). Error bars represent standard errors. **p < .01. ***p < .001.**

this second experiment, we thus strongly replicate the main result of Experiment 1 about the representational aftereffects of vertical PA, illustrated here for the first time.

As observed in Experiment 1, no correlation was observed between the amplitude of sensorimotor aftereffects and the amplitude of representational aftereffects. No correlation was found between the magnitude of the initial altitudinal bias (i.e., the representational upward bias when bisecting a vertical line) and the magnitude of the representational aftereffects due to PA.

4. General discussion

4.1. Sensorimotor initial bias

For both Experiments 1 and 2, we found an initial sensorimotor bias directed toward the lower part of the space. This bias can probably be explained by the influence of gravity, which acts on the participant's arm downwards and thus may lower the hand trajectory. In a review on the effects of gravity on sensorimotor planning and control, White et al. (2020) underline that the nervous system includes an internal representation of gravity and can take advantage of it for the planning of movements. This integration of gravity would rely on multiple sensory cues (Bock, 1998), including vestibular (Lacquaniti et al., 2013), proprioceptive (Bringoux et al., 2012), tactile (Carriot et al., 2004), and visual information (Sciutti et al., 2012). In our study, during the open-loop pointing task, participants had to do movements in such an altered sensory context, namely with the absence of visual feedback of their moving hand during their movements and the absence of terminal error feedback when reaching the screen. It is likely that without visual feedback, it is more difficult to control/compensate gravitational influence, which would have a greater impact on pointing performance.

4.2. Sensorimotor aftereffects of vertical PA

For most participants, we observed that vertical PA affected the downward sensorimotor initial bias symmetrically. PA to an upward optical deviation exacerbated this bias, increasing the magnitude of downward pointing error, whereas PA to a downward optical deviation inverted the bias, pulling it toward the higher part of the space. This observation replicates our previous work (Bonnet et al., 2022), showing that vertical PA produces sensorimotor aftereffects in the opposite direction of the optical deviation used with a similar magnitude, as it is the case in lateral PA (e.g., Redding et al., 2005). The absolute value of the magnitude of adaptation in significantly adapted persons was not different between the two optical deviation groups. However, four participants did not adapt to the downward optical deviation, while all participants were correctly adapted to the upward optical deviation. This result suggests that in the vertical dimension, participants who are able to adapt do it similarly irrespective to the optical deviation used, but that some participants do not show the ability to adapt to the downward optical deviation.

When compiling sensorimotor data of Experiments 1 and 2, which consisted in the same open-loop pointing task, we observed that the group adapted to a downward optical deviation had less robustness in the sensorimotor aftereffects of PA. Indeed, although the magnitude of adaptation (i.e., the difference between pretest and posttest on the open-loop pointing task) was similar between the two groups, the magnitude of deadaptation (i.e., the decrease of sensorimotor aftereffects between the Posttest and the Late-test) was different. Namely, computing (Immediate aftereffects – Late aftereffects) revealed a significantly greater loss of aftereffects for the downward optical deviation group than for the upward optical deviation group. As a consequence, at the end of the experiment the amplitude of sensorimotor aftereffects was significantly lower for the downward optical deviation group than for the upward one. The present study confirms the possibility to adapt to both optical deviations, but with a faster decay of sensorimotor aftereffects following PA to a downward optical deviation.

Altogether, these results suggest that although vertical PA affected the sensorimotor initial bias symmetrically, the faster decay in sensorimotor aftereffects of vertical PA following a downward optical deviation could be attributed to a strong influence of gravity, which tends to pull the pointing arm downwards, while the aftereffects of downward PA tend to pull the pointing arm upwards. Consistent with this hypothesis, the more robust adaptation to an upward optical deviation would be due to an aftereffect directed downward, namely in the same direction as gravity.

4.3. Representational initial bias

Before adaptation, a significant altitudinal bias was observed in vertical line-bisection performance, directed toward the upper part of the space. This representational bias is consistent with previous literature on the Landmark Task (e.g., Bonnet et al., 2022; Fink et al., 2001) and the MLB (e.g., Claunch et al., 2012; Suavansri et al., 2012), reflecting an overrepresentation of the higher part of the space.

The altitudinal bias may be explained by an imbalance between visual streams for the processing of visual information, with a ventral dominance for the processing of the upward visual field. According to Previc (1990), the processing of the lower visual field seems to rely preferentially on the dorsal stream, whereas the processing of upper visual field would rely on the ventral stream (Drain & Reuter-Lorenz, 1996). In line with this view, Falchook et al. (2013) investigated vertical visuospatial representation by comparing the performance between an MLB and a manual line quadrisection (i.e., a task where participants are asked to put the transector 25% from the top or the bottom of the line). The line quadrisection was designed to require more focal attention, involving preferentially the ventral visual stream. They observed an increase of the upward altitudinal bias for the line quadrisection as compared with the vertical MLB, and interpret it as the consequence of a ventral stream involvement in this representational bias. More recently, Churches et al. (2017) suggested that the vertical line-bisection task relies on an object-based mechanism, involving preferentially the ventral visual pathway (Duecker & Sack, 2015; Goodale & Milner, 1992). This ventral dominance during vertical MLB would result in an overrepresentation of the upper part of the space, leading participants to put their mark above the true center of the line.

This explanation is in line with behavioral data of Claunch et al. (2012). They observed that when displaying a facial memorization task while participants were performing a vertical MLB, there was an increase of the upward altitudinal bias, as compared with the bias obtained without retention of the faces. Indeed, facial recognition is known to imply a specific object-based mechanism mostly recruiting the fusiform gyrus in the occipitotemporal (ventral) stream (Claunch et al., 2012; Kanwisher & Yovel, 2006). According to the authors, an increase in activity within the ventral stream would be responsible for the upward shift of the MLB bias. Clinical studies have also corroborated this view, highlighting that bilateral parieto-occipital lesions (i.e., affecting the dorsal visual pathway) lead patients to an upward bias, corresponding to a neglect of the inferior part of the space (Mennemeier et al., 1992), whereas bilateral temporo-occipital lesions (i.e., affecting the ventral visual pathway) lead patients to a downward bias, reflecting a neglect of the higher part of the space (Mennemeier et al., 1992; Shelton et al., 1990).

Another explanatory account for the occurrence of the altitudinal bias is the involvement of the right hemisphere, that could be responsible of the overrepresentation of the upper part of the space. It was proposed by some functional imagery studies on the Landmark task that the vertical and horizontal version of this task seems to rely on the same type of mechanisms, namely on a magnitude processing, relying on a right hemisphere involvement (Fink et al., 2001; Seydell-Greenwald et al., 2019; Walsh, 2003). In addition, Suavansri et al. (2012) suggested that the altitudinal bias would also rely on the involvement of the right hemisphere in the manual version of the line-bisection task, because this bias is increased when bisecting lines are presented in the left hemispace, as compared with those presented in the right hemispace. Clinical data from a case study on a patient with a unilateral right temporal lobe lesion seems to confirm this hypothesis, with a downward bias on vertical line-bisection, reflecting an upward neglect (Morris et al., 2020). Thus, additionally to the well-known left pseudoneglect observed in horizontal line-bisection task, the right hemisphere could also be responsible of the altitudinal bias.

Comparing to previous work using a perceptual line-bisection task (Bonnet et al., 2022), the observed altitudinal bias seems to be greater in the present study. This difference may account for the existence of an intentional bias linked to the use of a manual response during MLB (Suavansri et al., 2012).

4.4. *Representational aftereffects of PA*

In both experiments, whereas no representational aftereffects were found following adaptation to an upward optical deviation, we found that following PA to a downward optical deviation, the initial upward altitudinal bias on MLB was exacerbated, reflecting a change in vertical visuospatial representation. Thus, although the effect size was smaller in Experiment 2 ($\eta^2 = .026$, small effect) than in Experiment 1 ($d > .8$, large effect; Cohen, 1988), the representational aftereffects of vertical PA was replicated.

The development of such cognitive aftereffects following vertical PA is the crucial and new result of our study. To date, no other work reported this effect. Previous data of Bonnet et al. (2022) using the Landmark task reported no significant change of the visuospatial representation following vertical PA, despite using the same adaptative protocol. In the horizontal dimension, PA is known to produce smaller effects on the Landmark task than on MLB (Striemer et al., 2016). This greater expression of aftereffects on MLB than on the Landmark task may also exist in the vertical dimension, leading to a difference of significance between the study of Bonnet et al. (2022) and the present study.

The observed increase in the MLB bias upwards following downward PA could reflect an increase in the imbalance between processing of the upper and the lower part of the visual field. One can imagine a parallel with the lateral dimension, where recent works in cerebral imagery showed that PA acts on spatial judgment by modifying the imbalance between the left and right hemispheres (Clarke et al., 2022; Schintu et al., 2022). We thus hypothesize that vertical PA could act by modifying the activity of visual pathways. Downward PA could have a perturbating action on structures of the dorsal visual stream (Leigh et al., 2015), leading to an advantage of the ventral stream, thus increasing the overrepresentation of the upper part of the space. Nevertheless, literature about vertical PA is still very scarce and contains only few behavioral data. Thus, further work is needed using functional imagery to test this hypothesis because no imagery study has been conducted yet in this dimension.

4.5. *Absence of correlation between the altitudinal bias and the magnitude of representational aftereffects of PA*

In the lateral PA literature, the shift in visual subjective center following an adaptation procedure is known to be directed toward the opposite direction of the initial representational bias (i.e., pseudoneglect) of the subject, and to have an amplitude correlated to that of the initial bias. Subjects exhibiting a leftward initial bias (as it is the case for most young healthy persons), develop representational aftereffects following leftward PA, and subjects exhibiting a rightward initial bias, develop representational aftereffects following rightward PA (Goedert et al., 2010; Michel, 2016). In the present study, no correlation was found between the initial bias and the magnitude of the aftereffects induced by vertical PA. Both the initial upward altitudinal bias and the upward bias induced by downward PA had the same direction. These differences between horizontal and vertical PA may rely on the fact that PA does not act in the same way for these two dimensions. Regarding our initial hypotheses it is possible to conclude that only downward PA acts on visuospatial representation.

4.6. *Absence of correlation between the sensorimotor aftereffects and the representational aftereffects of PA*

During the MLB, participants were told to do very slow movements and to set the mark with the stylus as accurate as possible to avoid sensorimotor interference in this representational task (e.g., Colent et al., 2000; Michel, Pisella et al., 2003). Similarly, to the lateral dimension, no correlation was found between the sensorimotor bias observed in open-loop pointing task and the representational bias observed during the line-bisection task following prism removal (e.g., Schintu et al., 2014). The shift in line-bisection performance thus cannot be explained by sensorimotor aftereffects on the hand movement. Nevertheless, representational aftereffects strictly depend on the presence of sensorimotor aftereffects. Sensorimotor aftereffects testifies to the well adaptive development (Michel, 2016). The MLB bias following downward PA is thus the expression of a representational (cognitive) bias induced by prisms.

4.7. *Absence of effect of sound presentation on vertical visuospatial representation*

In Experiment 2, we focused on the effect of sound frequency on vertical MLB, and its potentially combined effect with PA. Previous literature has shown differences between musicians and nonmusicians in the processing of spatial representation of pitch height (Lidji et al., 2007; Rusconi et al., 2006). Musicians seem to show a spatial representation of sound frequencies that can influence their responses on a stimulus-response compatibility task both in the horizontal and the vertical dimensions. Nonmusicians are less sensitive to the horizontal dimension and show a spatial representation of pitch only in the vertical dimension, which has been highlighted as the "natural" dimension of spatial representation of sounds. Thus, in the present study about the processing of vertical space, we did not particularly focus on musical expertise. Nevertheless, to ensure that our result was not related to the musical background of participants, we assessed it with a questionnaire which allowed us to keep only nonmusicians ($N = 24$) for complementary analyses. As we expected, we found very similar results when performing our analysis on the whole sample or only on nonmusicians. Namely, we did not observe any effect of pitch on vertical MLB.

We observed a significant altitudinal bias for every pitch condition in vertical MLB (low, high and no sound), showing that this bias is robust enough to be unaffected by sound presentation. Actually, no difference in vertical MLB performance was found between the no sound and the sound conditions, excluding the hypothesis that the simple presence of sound modifies performance in this task. This result differs from what has been observed in the lateral dimension, where the leftward bisection bias was reduced by the mere presentation of sounds, independently of their frequency, as it was observed by Cattaneo et al. (2012), who presented a binaural white noise during visual and haptic bisection tasks.

The previous study of Ishihara et al. (2013) showed an effect of pitch on horizontal visuospatial representation, but not in the vertical dimension. We modified their protocol by increasing the line length from 200 mm to 300 mm as well as the gap between the low and high pitches, and the intensity of the broadcasted sound, especially for the higher pitch, expecting more effects to appear. A low pitch at 100 Hz (instead of 110 Hz) and a high pitch at 3000 Hz (instead of 1760 Hz) were broadcasted at a 70 dB (instead of 50 dB) intensity while the participant was performing the MLB. Our hypothesis was that high pitch should have exacerbated the upward initial altitudinal bias, whereas low pitch should have reduced or inverted this bias by inducing an overrepresentation of the lower part of the space. Even with these modifications of the protocol, we found no difference between the high and low pitch conditions on vertical MLB performance. Our results, combined with those of Ishihara et al., suggest that vertical visuospatial representation evaluated with an MLB seem not to be influenced by sound presentation. A possible interpretation could be that the vertical bisection bias (i.e., altitudinal bias) would be more robust than the more labile leftward bias (pseudoneglect) observed in the lateral dimension.

Another interpretation could be that no pitch effect was observed because vertical MLB relies on an object-based strategy rather than a space-based strategy (Churches et al., 2017; Claunch et al., 2012; Falchook et al., 2013). A perspective to further investigate the effect of pitch on visuospatial representation could be the use of another paradigm that would be more sensitive to the spatial dimension of the task. It would consist in indicating two polarized endpoint marks instead of a complete line, to explicitly identify an upper and a lower space marks. The participants should determine the midpoint between these two spatial marks. By doing this, pitch could have a greater influence on the participant's response because this task could favor the use of a space-based strategy, rather than the object-based strategy that seems to be favored in the vertical MLB.

5. Conclusion

Despite the great among of studies investigating horizontal PA, very few studies have been conducted in the vertical dimension. The present study brings the first proof of a visuospatial representational aftereffects of vertical PA, characterized by an upward shift of the subjective center of lines on an MLB task following PA to a downward optical deviation. The upward representational bias following downward PA could be due to a reorganization of the balance between the ventral and the dorsal visual streams. In a second time, we assessed the potential effect of sound presentation on the vertical MLB. We did not observe any effect of sound presentation on visuospatial representation, and no interaction between PA and sound presentation.

These results open new perspectives in the understanding of the aftereffects of vertical PA. First, neuroimaging studies are required to infer more precisely on the neural mechanisms involved in this dimension. Then, the presence of vertical representational aftereffects on healthy young people following vertical PA also allows us to think that maybe therapeutical effects could exist in people suffering from vertical neglects. It is known that, with aging, people present an elevation of the upward altitudinal bias (Mańkowska et al., 2018), probably due to a faster decay of performance of the dorsal pathway. Clinical studies are needed to evaluate whether patients presenting a vertical neglect or older people might benefit of a PA training to reduce their falling risk.

Ethical statement

This study was approved by the ethical committee of "Université Bourgogne Franche-Comté" (CERUBFC-2021-10-07-029).

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Transparency and openness (TOP) statement

No part of the study procedures or analyses was pre-registered prior to the research being conducted. We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. No analysis code was used for this study. All digital materials used and collected data for this study are available at https://osf.io/jvx37/

Open practices

The study in this article has earned Open Data and Open Materials badges for transparent practices. The data, materials are available at: https://osf.io/jvx37/.

CRediT authorship contribution statement

Vincent Ardonceau: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Bénédicte Poulin-Charronnat:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Clémence Bonnet:** Conceptualization, Methodology, Resources, Writing – original draft, Writing – review & editing. **Cyril Sirandré:** Software. **Carine Michel-Colent:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

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.

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