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Vestibular modulation of multisensory integration during actual and vicarious tactile stimulation

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Abstract

The vestibular system has been shown to contribute to multisensory integration by balancing conflictual sensory information. It remains unclear whether such modulation of exteroceptive (e.g., vision), proprioceptive, and interoceptive (e.g., affective touch) sensory sources is influenced by epistemically different aspects of tactile stimulation (i.e., felt from within vs. seen, vicarious touch). In the current study, we aimed to (a) replicate previous findings regarding the effects of galvanic stimulation of the right vestibular network in multisensory integration, and (b) examine vestibular contributions to multisensory integration when touch is felt but not seen (and vice versa). During artificial vestibular stimulation (LGVS, i.e., right vestibular stimulation), RGVS (i.e., bilateral stimulation), and sham (i.e., placebo stimulation), healthy participants ($N = 36$, Experiment 1; $N = 37$, Experiment 2) looked at a rubber hand while either their own unseen hand or the rubber hand were touched by affective or neutral touch. We found that (a) LGVS led to enhancement of vision over proprioception during visual only conditions (replicating our previous findings), and (b) LGVS (versus sham) favored proprioception over vision when touch was felt (Experiment 1), with the opposite results when touch was vicariously perceived via vision (Experiment 2) and with no difference between affective and neutral touch. We showed how vestibular signals modulate the weight of each sensory modality according to the context in which they are perceived and that such modulation extends to different aspects of tactile stimulation: felt and seen touch are differentially balanced in multisensory integration according to their epistemic relevance.

KEYWORDS

affective touch, body ownership, multisensory integration, proprioception, vestibular stimulation, visual capture

1 | INTRODUCTION

During multisensory integration, signals from different sensory modalities are weighted according to their contextual reliability and combined to produce a unitary perceptual experience of the world (Ernst & Banks, 2002; Fetsch, Pouget, DeAngelis, & Angelaki, 2011; Stein, Stanford, & Rowland, 2014). Such experience includes our own body and the sense that our body belongs to us (body ownership; Gallagher, 2000). Body ownership has been extensively studied using the rubber hand illusion (RHI; Botvinick & Cohen, 1998),

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during which participants watch a fake hand being touched in or out of synchrony with their own unseen hand. As a result of synchronous stroking of the rubber hand and participant's hand, individuals may feel subjective feelings of ownership of the rubber hand and/or a shift in the perceived location of their own real hand toward the position of the rubber hand (proprioceptive drift). The amount of shift resulting from the experimental condition is obtained by asking participants, before and after the stroking, to report where they feel their own index finger to be. Then, the difference between post- versus pre-measurements is calculated to obtain the proprioceptive drift.

The RHI has provided significant insight into how conflict between vision of a synchronously touched rubber hand and proprioception of the real hand's location is resolved by information from one modality (vision) dominating over the others (proprioception and touch; Folegatti, de Vignemont, Pavani, Rossetti, & Farne, 2009; Pavani, Spence, & Driver, 2000; van Beers, Wolpert, & Haggard, 2002). This "visual capture" effect, characterized by a dominance of visual cues over other modalities (Rock & Victor, 1964), occurs in particular when vision is deemed contextually most reliable (e.g., when we process visuo-proprioceptive signals in the horizontal plane; van Beers et al., 2002). However, not all sensory conflictual situations are solved with a dominance of vision over proprioception. For example, an illusory feeling of movement is often experienced while sitting on a stationary train and observing an adjacent train beginning to move past. In such instances, the vestibular system, primarily involved in regulating balance and coordination during self-motion, also contributes to multisensory integration, providing information signaling an unresolved conflict between vision ("I see motion") and proprioception ("I feel I am not moving"), which often results in motion sickness (Bertolini & Straumann, 2016).

An increasing number of studies suggests that the functional role of the vestibular system extends beyond the regulation of posture and balance (Brandt & Dieterich, 1999). Neuroanatomical evidence (Fasold et al., 2002; zu Eulenburg, Caspers, Roski, & Eickhoff, 2012) indicates shared neural mechanisms for vestibular processes and other sensory modalities, such as vision (Brandt et al., 2002; Della-Justina et al., 2015; Seemungal et al., 2013), touch, and proprioception (Dijkerman & de Haan, 2007; Lackner & DiZio, 2005). A partial overlap between the vestibular network and brain regions linked to multisensory integration has also been identified, with activations in the temporoparietal junction, inferior parietal lobule, insula, and cingulate cortex (Lopez, 2016; Lopez, Blanke, & Mast, 2012). In order to test the influence of vestibular signals on body ownership, several studies implemented artificial vestibular stimulation to activate the peripheral vestibular organs (such as galvanic vestibular stimulation, GVS; see Utz, Dimova, Oppenländer, & Kerkhoff, 2010). Neuroimaging findings showed that such peripheral stimulation leads to the activation of the right vestibular network when the anode is positioned on the left vestibular nerve and the cathode on the right (i.e., LGVS). The opposite configuration leads to bilateral activation of both vestibular networks (i.e., RGVS; Fink et al., 2003; Utz et al., 2010). However, results from studies employing GVS to investigate the influence of vestibular activation on body ownership have not always been consistent. Different studies suggest a differential mechanism underlying right-hemisphere vestibular effects on body ownership: while some authors suggest that vestibular stimulation increases the weight of proprioception (Ferrè, Berlot, & Haggard, 2015), others posits the opposite (Lopez, Lenggenhager, & Blanke, 2010).

A previous study from our group (Ponzo, Kirsch, Fotopoulou, & Jenkinson, 2018) aimed to clarify these conflicting findings, while assessing how vestibular and interoceptive signals (i.e., feelings about the physiological condition of one's own body; Ceunen, Vlaeyen, & Van Diest, 2016; Craig, 2002) interact to shape body ownership. Recent research indicates that body ownership is modulated by interoceptive signals (Suzuki, Garfinkel, Critchley, & Seth, 2013; Tsakiris, Tajadura-Jimenez, & Costantini, 2011) and can be enhanced by applying gentle touch at slow velocities that activate specialized nerve fibers (C- tactile [CT] afferents), which provide interoceptive information in the form of tactile pleasure (Crucianelli, Krahé, Jenkinson, & Fotopoulou, 2018; Crucianelli, Metcalf, Fotopoulou, & Jenkinson, 2013; Lloyd, Gillis, Lewis, Farrell, & Morrison, 2013; Loken, Wessberg, Morrison, McGlone, & Olausson, 2009; van Stralen et al., 2014). In our previous study, GVS was administered during a RHI procedure using slow affective, CT-optimal or fast emotionally neutral, CT-suboptimal touch. We found that right-hemisphere vestibular stimulation increased proprioceptive drift during vision only conditions and synchronous visuo-tactile conditions. However, we did not find any observable effect on subjective embodiment (Ponzo et al., 2018). Moreover, the enhancement of proprioceptive drift during right vestibular stimulation was greater following affective compared with neutral touch conditions. These findings were interpreted as a right-hemisphere stimulation-induced enhancement of vision over proprioception (see also Martinaud, Besharati, Jenkinson, & Fotopoulou, 2017; Samad, Chung, & Shams, 2015). However, the specific mechanism by which touch enhances body ownership during LGVS remains unclear. Affective touch has been shown to elicit comparable feelings of pleasure and neural activation in the posterior insula, when experienced directly on one's own skin as well as when observed on someone else's skin (i.e., vicarious affective touch; Morrison, Bjornsdotter, & Olausson, 2011; Morrison, Löken, et al., 2011). Hence, the contribution of affective touch to body ownership may not only depend on its felt components but also on its seen vicarious aspects. Thus, the vestibular system may differentially modulate such contribution according to the way that touch is perceived.

The current work sought to address this outstanding ambiguity, by dissociating felt and seen touch during two RHI experiments with concurrent GVS. We included conditions during which slow (affective) or fast (neutral) touch was applied only to the real hand without concurrent touch on the rubber hand (Experiment 1) and vice versa (Experiment 2). This was done to determine whether the enhancement of proprioceptive drift was driven by the seen or the felt component of affective touch. We firstly aimed to replicate our previous findings (Ponzo et al., 2018), showing that vision of a rubber hand during right-hemisphere vestibular stimulation leads to increased proprioceptive drifts toward the rubber hand, even without touch (visual capture of proprioception). Secondly, we aimed to explore whether vestibular stimulation would favor proprioception over vision when touch is felt but not seen, but favor vision over proprioception when touch is seen but not felt. We hypothesized that administering affective touch only on participant's own hand during LGVS would lead to smaller proprioceptive drifts (i.e., disruption of a previously induced visual capture), compared with neutral fast touch, while affective touch on the rubber hand only would have opposite effects (i.e., enhancement of visual capture) due to the vicarious properties of affective touch. We did not expect to observe changes in embodiment questionnaire scores, since all touch conditions in the current study involved visuo-tactile asynchrony, consistently found not to elicit increased embodiment feelings (Costantini et al., 2016; Rohde, Di Luca, & Ernst, 2011).

2 | METHOD

2.1 | Participants

In Experiment 1, 36 right-handed, healthy participants (23 female, age range = 18–48 years, $M = 24.39$; $SD = 6.01$) were recruited via an institutional subject pool. Two participants were excluded from the analysis (they scored more than 2.5 *SD* away from the mean in more than two distributions). The final sample consisted of 34 participants (22 female; age range = 18–48 years, $M = 24.24$, $SD = 5.90$). Thirty-seven new healthy participants (24 female, age range: 18–44, $M = 22.27$; $SD = 5.35$ years) took part in Experiment 2. Two participants were excluded (see above for criteria), with a final sample of 35 participants (22 female; age range = 18–44, $M = 22.26$; $SD = 5.44$).

Exclusion criteria included psychiatric/neurological history, vestibular disturbances, pregnancy, or metal plates in participants' body, and previous participation in GVS studies (due to the necessary deception involved in sham conditions). Both studies were approved by an institutional ethics committee, and all participants gave written consent.

2.2 | Experimental design

We applied GVS (LGVS, RGVS, sham) during a RHI task in a within-subjects block design, with the order of the three GVS blocks counterbalanced across the sample. Each of the three GVS blocks comprised two stroking conditions (slow affective at 3 cm/s or fast neutral at 18 cm/s touch (Crucianelli et al., 2013), administered in a counterbalanced order across participants), each preceded by a visual only condition (pure visual capture; see Figure 1a,b). Stroking conditions (Figure 1c) were administered to explore whether touch on participant's hand only during LGVS would reduce a previously induced visual capture, with the prediction that affective touch would have a further disrupting effect than neutral touch.

Two outcome measures were collected: proprioceptive drift (i.e., the perceived shift of the participant's hand toward the rubber hand, in centimeters) and an embodiment questionnaire. Proprioceptive drift was assessed pre-GVS and post-GVS for each condition and calculated by subtracting the post-GVS estimate of the left hand's location from the pre-GVS one (Figure 1a and Section 2.4 for a detailed description of the proprioceptive drift procedure). At the end of each condition, participants completed the Embodiment Questionnaire (Longo, Schuur, Kammers, Tsakiris, & Haggard, 2008), presented on a computer in a randomized order (see online supporting information, Appendix S1, section 1). The answers to each question were averaged in order to obtain an overall embodiment score per condition.

The design and procedure for Experiment 2 were identical to Experiment 1 except that touch was applied on the rubber hand only (instead of participant's own hand) and that we predicted an enhancement rather than a disruption of visual capture effects.

2.3 | Experimental setup and materials

2.3.1 | GVS

We implemented a bipolar stimulation with fixed intensity (1 mA) and duration (2 min per condition), delivered via a direct current stimulator (neuroConn DC stimulator, neuroCare Group GmbH, München, Germany). The total amount of stimulation per GVS block was 8 min, with each experiment involving 24 min (including sham) of noncontinuous stimulation. Each GVS block was followed by a 20-min break in order to minimize possible stimulation aftereffects (Utz et al., 2010).

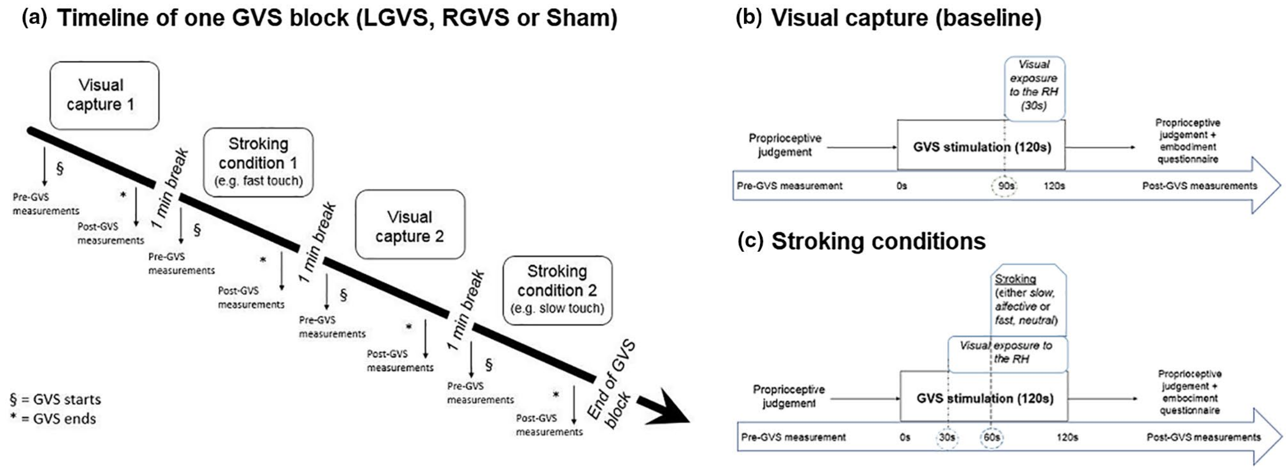

FIGURE 1 (a) Time line of one prototypical GVS block. At the beginning of each of the three GVS blocks (either LGVS, RGVS, or sham), participants undertook the first visual capture baseline, with measures taken before and after stimulation. Subsequently, one of the two stroking conditions was conducted in a counterbalanced order, with measures taken before and after stimulation. (b) Time line of visual capture baselines. Before the visual capture condition started, participants performed a proprioceptive judgment (pre-GVS measurement). Immediately afterward, the vestibular or sham stimulation commenced, lasting for 2 min, during which participants sat with their eyes open. During the last 30 s of vestibular or sham stimulation, the experimenter opened the box lid and instructed the participant to look at the rubber hand until told otherwise. After 120 s (total) stimulation, the lid was closed, and participants immediately performed a second proprioceptive judgment and completed the embodiment questionnaire (post-GVS measurements). (c) Time line of stroking conditions. Both stroking conditions (slow affective or fast neutral touch) followed the same structure. Participants made an initial (pre-GVS measurement) proprioceptive judgment, followed immediately by vestibular or sham stimulation lasting for 120 s. After 30 s of vestibular stimulation, the rubber hand was revealed by the experimenter, and participants were asked to continuously look at it for 30 s. Then, the experimenter started stroking participant's (Experiment 1) or rubber hand's (Experiment 2) forearm slowly or fast for 60 s, while the participant was asked to keep looking at the rubber hand. At the end of the 2 min, both tactile and vestibular stimulation ended, and participants performed a second proprioceptive judgment and answered the embodiment questionnaire (post-GVS measurements)

GVS was delivered via two 3 × 3 cm carbon rubber electrodes fixed either on the participants' mastoid bones (LGVS and RGVS) or neck (sham) using a rubber band. During LGVS (i.e., left-anodal/right-cathodal stimulation, affecting the right-hemisphere vestibular network), the anode was on the left mastoid process and the cathode on the right. During RGVS (i.e., left-cathodal/right-anodal, affecting both vestibular networks), the inverse configuration was used. During sham, the electrodes were placed on the nape (~5 cm below the end of the mastoid processes).

2.3.2 | Rubber hand illusion

The apparatus was the same as detailed in our previous study (Ponzo et al., 2018), with the exception of the distance between the rubber and participant's hand (see Figure 2). A black wooden box (62 cm × 43 cm × 26 cm), was positioned on a table 10 cm from the participant's torso. The box was divided in two equal halves by black cardboard. Two spots were marked on the table with tape, one for the left rubber hand's index finger and one for the participant's left index finger. On the upper side of the box, there was a measuring tape, used to record proprioceptive drift and visible to the experimenter only. Participants wore a black cloth covering their shoulders and arms throughout the experiment in order to minimize the influence of external visual cues. Stroking was delivered on participant's forearm or on the rubber hand using a make-up brush (Natural Hair Blush Brush, N° 7, The Boots Company) by trained experimenters, expert in controlling for speed, pressure, and uniformity of the applied touch (as in Crucianelli et al., 2013, and Krahé, Drabek, Paloyelis, & Fotopoulou, 2016; see Triscoli, Olausson, Sailer, Ignell, & Croy, 2013, for advantages and limitations of mechanical vs. human-applied affective touch).

2.4 | Experimental procedure

Participants positioned their left forearm in the box, and the experimenter aligned their index finger with the rubber hand (hidden from participant's view). Each condition started with a proprioceptive judgment (pre-GVS measurement; see Ponzo et al., 2018), followed by GVS stimulation. Each proprioceptive judgment was obtained as follows (as in Lloyd et al., 2013): the experimenter continuously moved the tip of a pen along the top of the closed box (~1 cm/s), starting either from the left- or right-hand side of the box. Participants were asked to verbally stop the experimenter when the pen reached the point vertically in line with the perceived position of the

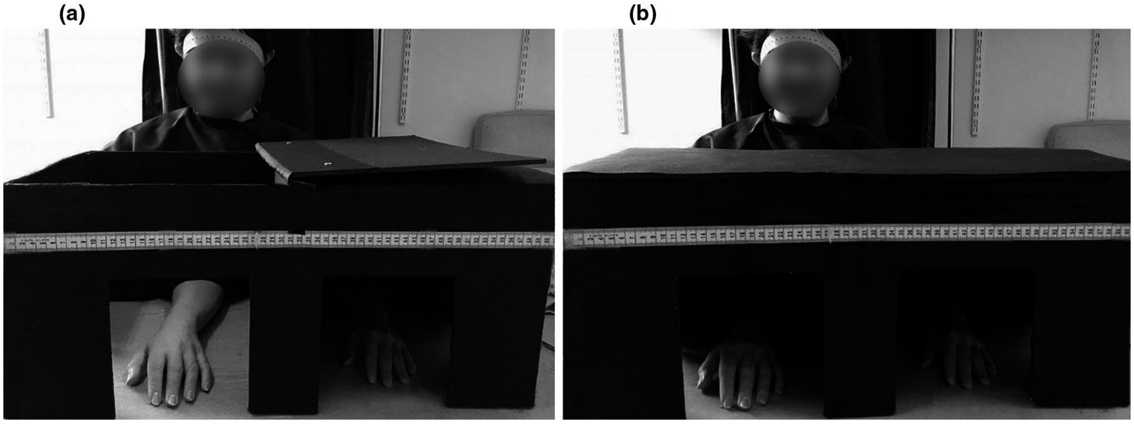

FIGURE 2 Participants placed their left hand into the left half of the box, while the rubber hand was positioned in the right half, in line with the center of participant's torso (distance between rubber hand and participant's hand = 27.5 cm). Both the participant's and rubber hand's left index fingers were located on the marked spots. (a) While the box was open, participants were asked to look inside and observe the rubber hand. (b) Before and after each condition, with the box closed and covered by a black carton, participants performed a proprioceptive judgment (see Experimental procedure)

participant's left index finger. The experimenter recorded the actual position of participant's finger and the perceived position (pre-GVS measurement of proprioceptive drift: actual finger position minus perceived finger position). During the first condition (visual capture, Figure 1b), the rubber hand was only revealed after 1 min 30 s of stimulation, and participants were asked to continuously look at the rubber hand for the last 30 s. Participants then performed a second proprioceptive judgment with the box closed and completed the embodiment questionnaire (post-GVS measurements).

After the first visual capture condition, there was a 1-min break, during which participants were asked to move their left arm to reduce any cumulative effects. During the break (in Experiment 1 only), two adjacent 9 × 4 cm areas were drawn with a washable marker on the participant's left forearm, to control for stroking pressure (i.e., by maintaining the brush within the marked borders) and habituation (i.e., by alternating between the two areas following each stroke; Crucianelli et al., 2013). Subsequently, one of the two stroking conditions began (slow or fast velocity), with a pre-GVS proprioceptive judgment (Figure 1c). Immediately afterward, the vestibular stimulation started, and for the first 30 s participants sat without performing any task. Then, the experimenter opened the lid and asked participants to focus on the rubber hand. After 30 s of visual only exposure to the rubber hand, the experimenter started stroking the participants' forearm (Experiment 1) or the rubber hand (Experiment 2), either slowly at 3 cm/s (i.e., single touch = 3 s) or fast at 18 cm/s (i.e., single touch = 0.5 s) for 60 s. Touch was always administered proximally to distally, and each stroke was followed by a 1-s pause. Participants were instructed to maintain their gaze on the rubber hand. After 120 s, the vestibular-tactile stimulation ended, the post-GVS proprioceptive judgment was obtained, and participants answered the embodiment questionnaire (post-GVS measurements). The second visual capture and stroking conditions of the block began after a 1-min break.

2.5 | Manipulation checks

At the end of the experiment, with no vestibular stimulation applied, participants were asked to rate the pleasantness of two sets of stroking (at 3 cm/s and 18 cm/s) to ensure that they perceived slow touch as more pleasant than fast touch (Crucianelli et al., 2013, 2018; Loken et al., 2009; Ponzo et al., 2018). In Experiment 2, we included an extra block of trials in which we asked participants to rate pleasantness of strokes observed on the rubber hand only (the vicarious and actual stroking block were counterbalanced—see supporting information, Appendix S1, section 2.2.4), to check whether they would rate the seen affective touch as more pleasant than the seen neutral touch. This was confirmed by parametric and nonparametric tests (see Appendix S1, 2.1.4 and 2.2.4). Participants were then asked to report any physical sensation associated with the vestibular stimulation and to guess in which of the three configurations they thought they had received vestibular stimulation (Appendix S1, 2.1.4 and 2.2.4).

2.6 | Data analysis

As several of the proprioceptive drifts distributions were non-normal in Experiment 1 and Experiment 2, we ran nonparametric analyses on the distributions of interest. When distributions were normal, we used repeated measures analysis of variance (ANOVA), followed up by paired samples *t* tests (with Bonferroni corrections for multiple comparisons). When data were not normally distributed, we calculated main effects by averaging the values of the proprioceptive drifts across one factor. We then compared these values using Friedman's ANOVA when the factor had three levels, followed up by Bonferroni-corrected ($\alpha = 0.025$) Wilcoxon signed-rank tests and Wilcoxon signed-rank test when the factor had only two levels. Two-way interactions were obtained by subtracting one level of the factor of interest from the other one and then analyzed with Friedman's ANOVA and Wilcoxon signed-rank tests. In both experiments, to investigate subjective feelings of embodiment, we ran the analyses detailed above and in the supporting information on the embodiment questionnaire scores (see Appendix S1, sections 2.1.1 and 2.2.1).

In all the parametric analysis reported below, we used Greenhouse-Geisser corrections for repeated measures designs (in accordance with the guidelines outlined in Jennings, 1987) and report the *p* values and effect sizes accordingly.

Data were analyzed using the IBM Statistical Package for Social Sciences (SPSS) for Windows, version 25 (Armonk, NY) and plotted using the *ggplot2* package for R (Wickham, 2016).

3 | RESULTS

3.1 | Experiment 1

3.1.1 | Visual capture

We first aimed to replicate previous findings of increased visual capture following LGVS (Ponzo et al., 2018), with the hypothesis of a right-hemisphere-specific effect of vestibular stimulation on visual capture. To do so, we ran a one-way repeated measures ANOVA on the averages of the two visual capture conditions in the three GVS configurations to explore main effects of stimulation and a Wilcoxon signed-rank test to explore main effects of order (owing to lack of normality in one of the distributions). We found a significant main effect of stimulation, $F(2, 66) = 6.110$, $p = 0.004$, $\eta_p^2 = 0.156$, $\varepsilon = 0.987$, but no main effect of order ($Z = 0.222$, $p = 0.824$, $r = 0.027$; Figure 3a). We also ran a Friedman's ANOVA to investigate the interaction between the two factors, which was not significant, $\chi^2(2) = 0.993$, $p = 0.609$. Given that the averages of the two visual capture conditions were normal, we followed up via planned contrasts paired samples *t* tests (Bonferroni-corrected, $\alpha = 0.025$), revealing significantly greater proprioceptive drift following LGVS compared to sham (LGVS: $M = 1.75$ cm, $SD = 2.62$; sham: $M = 0.15$ cm, $SD = 2.16$; LGVS vs. sham: $t(33) = 3.410$, $p = 0.002$, $d = 0.59$) and RGVS (RGVS: $M = 0.50$ cm, $SD = 2.10$; LGVS vs. RGVS: $t(33) = 2.459$, $p = 0.019$, $d = 0.42$; Figure 3b).

3.1.2 | Stroking conditions—Raw proprioceptive drifts

In order to examine the effects of vestibular stimulation on proprioceptive drifts following stroking, we ran a Friedman's ANOVA on the averaged values of the two stroking conditions, which did not show any difference between the three GVS configurations, $\chi^2(2) = 3.173$, $p = 0.205$. We then averaged the proprioceptive drift values across the different GVS configurations and used a Wilcoxon signed-rank test in order to check for differences due to the stroking conditions, which did not yield significant results ($Z = 1.402$, $p = 0.161$, $r = 0.17$). The interaction between the two factors was tested by subtracting the values of fast touch from the slow touch ones within each GVS configuration and then comparing the differentials via a Friedman's ANOVA, which did not reveal a difference between the conditions, $\chi^2(2) = 1.111$, $p = 0.574$ (Figure 4).

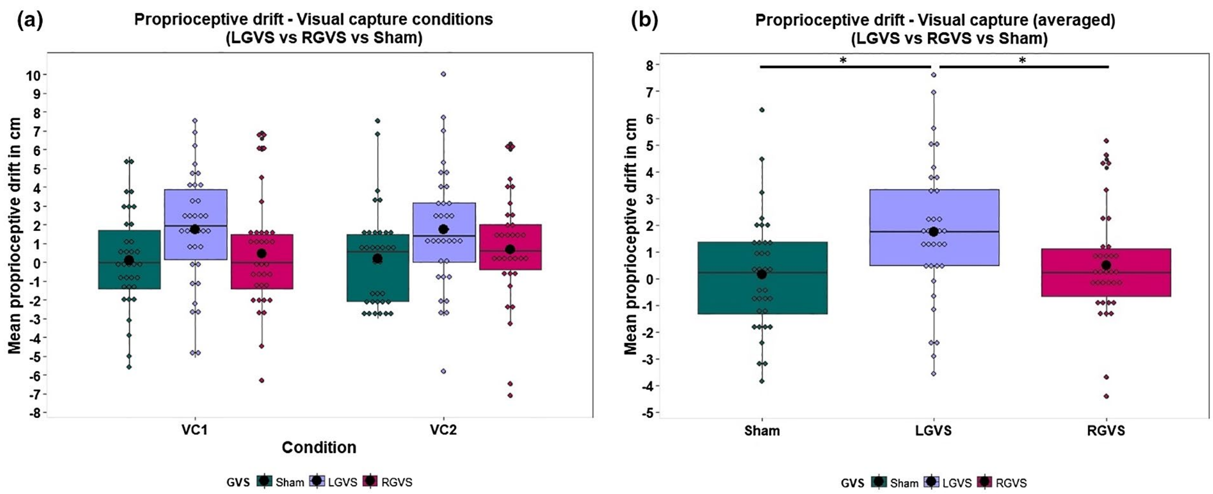

FIGURE 3 Mean values of the proprioceptive drift measured in cm in sham, LGVS, and RGVS. (a) Visual capture conditions 1 and 2 as performed by the participants during the block. (b) Visual capture baselines averaged. Solid line = median; black dot = mean; upper whisker = min(max(x), Q_3 + 1.5 × IQR); lower whisker = max(min(x), Q_1 − 1.5 × IQR). *$p < 0.05$

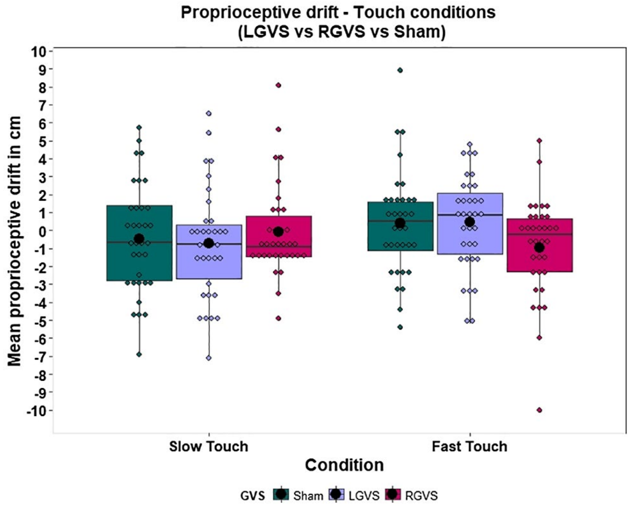

FIGURE 4 Mean values of the proprioceptive drifts in the different stroking conditions (slow affective touch and fast neutral touch) measured in cm and in the three different vestibular configurations (sham, LGVS, RGVS). Solid line = median; black dot = mean; upper whisker = min(max(x), Q_3 + 1.5 × IQR); lower whisker = max(min(x), Q_1 − 1.5 × IQR)

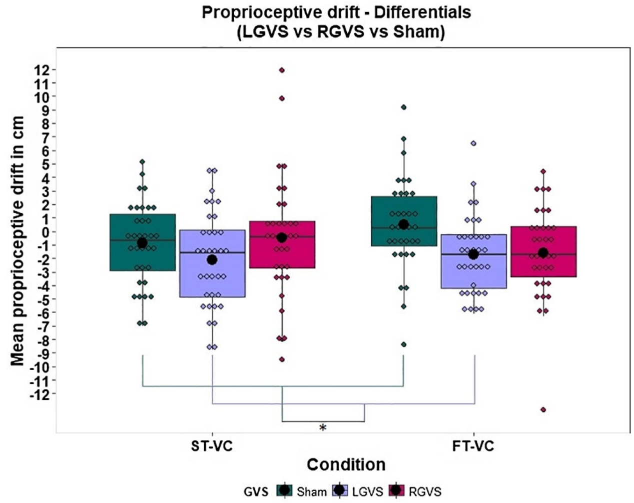

FIGURE 5 Mean values of the differential scores obtained from the subtraction of the proprioceptive drift values of the visual capture baselines from the stroking condition ones measured in cm and in the three different vestibular configurations (sham, LGVS, RGVS). ST = slow affective touch; FT = fast neutral touch; solid line = median; black dot = mean; upper whisker = min(max(x), Q_3 + 1.5 × IQR); lower whisker = max(min(x), Q_1 − 1.5 × IQR). $^*p < 0.05$

3.1.3 | Disruption of visual capture—Differential scores

To examine the effects of touch in disrupting a previously induced visual capture, differential scores were calculated by subtracting the proprioceptive drift score obtained during the stroking condition from its immediately preceding visual capture baseline and analyzed via a repeated measures ANOVA (followed by Bonferroni-corrected paired samples *t* tests). A 3 × 2 repeated measures ANOVA on the differential scores revealed a main effect of stimulation, $F(2, 66) = 5.054$, $p = 0.011$, $\eta_p^2 = 0.133$, $\varepsilon = 0.926$, but no main effect of velocity, $F(1, 33) = 0.199$, $p = 0.659$, $\eta_p^2 = 0.006$, and no significant two-way interactions (Figure 5; Stimulation × Velocity, $F(2, 66) = 2.167$, $p = 0.128$, $\eta_p^2 = 0.062$, $\varepsilon = 0.904$). Post hoc paired samples *t* tests comparing each type of GVS regardless of touch velocity (Bonferroni-corrected, $\alpha = 0.0167$) indicated that LGVS led to significantly greater disruption of visual capture (i.e., smaller proprioceptive drifts) in comparison with sham (LGVS: $M = -1.90$ cm, $SD = 2.45$; sham: $M = -0.18$ cm, $SD = 2.02$; $t(33) = 3.591$, $p = 0.001$, $d = 0.62$) but not RGVS (RGVS: $M = -1.02$ cm, $SD = 2.75$; $t(33) = -1.453$, $p = 0.156$, $d = 0.25$), with no difference between RGVS and sham, $t(33) = -1.583$, $p = 0.123$, $d = 0.27$.

3.2 | Experiment 2

3.2.1 | Visual capture

A Friedman's ANOVA performed on the proprioceptive drift values of the two visual capture conditions (Figure 6a) showed a main effect of stimulation, $\chi^2(2) = 8.647$, $p = 0.013$, and a Wilcoxon signed-rank test ($Z = 2.039$, $p = 0.041$, $r = 0.24$) showed a main effect of order, with the first visual capture condition being higher than the second one (first: $Mdn = 0.67$, *IQR* (interquartile range) = 1.77; second: $Mdn = 0.5$, $IQR = 1.80$), but no interaction between the factors, $\chi^2(2) = 0.844$, $p = 0.656$. To follow up the significant main effect of stimulation, Wilcoxon signed-rank tests ($\alpha = 0.025$) were used, which were not significant (LGVS: $Mdn = 1.25$, $IQR = 1.85$; sham: $Mdn = 0.75$, $IQR = 1.4$; LGVS vs. sham: $Z = 0.949$, $p = 0.342$, $r = 0.11$; LGVS vs. RGVS: RGVS: $Mdn = 0.20$; $IQR = 2.25$; LGVS vs. RGVS: $Z = 1.950$, $p = 0.051$, $r = 0.23$; Figure 6b).

3.2.2 | Visual capture (combined)

To check whether increasing the sample size to include data from both experiments ($N = 69$) would lead to the same results outlined in Experiment 1 and (partly) replicated in Experiment 2, we ran a Friedman's ANOVA on the average of the two visual capture conditions, revealing a main effect of stimulation, $\chi^2(2) = 19.737$, $p < 0.0001$ (Figure 7), further investigated via post hoc Wilcoxon signed-rank test (Bonferroni-corrected, $\alpha = 0.025$). Such comparisons showed that LGVS led to greater proprioceptive drifts in comparison with both sham ($Z = 3.121$; $p = 0.002$, $r = 0.27$) and RGVS ($Z = 2.822$; $p = 0.005$, $r = 0.24$). There were no main effects of order ($Z = 1.193$; $p = 0.233$, $r = 0.10$) or interaction, $\chi^2(2)$ $=0.007$, $p = 0.996$.

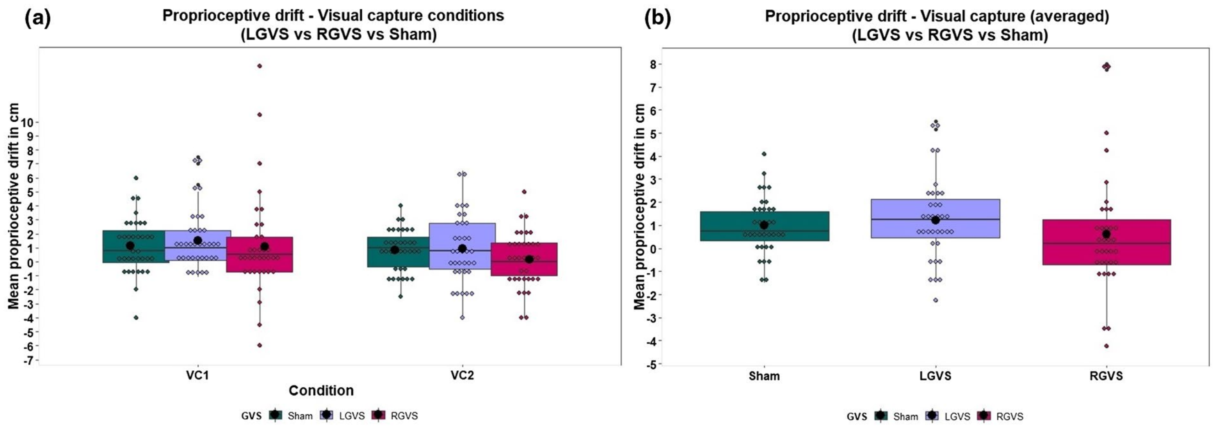

FIGURE 6 Mean values of the proprioceptive drift measured in cm in sham, LGVS, and RGVS. (a) Visual capture conditions 1 and 2 as performed by the participants during the block. (b) Visual capture baselines averaged. Solid line = median; black dot = mean; upper whisker = min(max(x), Q_3 + 1.5 × IQR); lower whisker = max(min(x), Q_1 − 1.5 × IQR). *$p < 0.05$

3.2.3 | Visual capture of vicarious touch

In order to examine the effects of vestibular stimulation on proprioceptive drifts following seen touch (Figure 8), we conducted a Friedman's ANOVA on the averaged values of the two stroking conditions, which showed a main effect of stimulation, $\chi^2(2) = 7.667$, $p = 0.022$. To explore this main effect of stimulation, we ran post hoc Wilcoxon signed-rank test (Bonferroni-corrected, $\alpha = 0.0167$), confirming that LGVS increased proprioceptive drifts in comparison with sham (LGVS: $Mdn = 0.80$, $IQR = 2.5$; sham: $Mdn = 0.65$, $IQR = 2$; $Z = 2.786$, $p = 0.005$, $r = 0.33$) but not RGVS (RGVS: $Mdn = 0.65$, $IQR = 1.85$; $Z = 1.223$, $p = 0.221$, $r = 0.15$), with no difference between sham and RGVS ($Z = 1.172$, $p = 0.241$, $r = 0.14$) and regardless of the type of touch. No effect of order ($Z = 0.118$, $p = 0.732$, $r = 0.01$) or interaction, $\chi^2(2) = 2.162$, $p = 0.339$, were significant.

4 | DISCUSSION

We used GVS during an adapted RHI to explore vestibular contributions to multisensory integration aiming to (a) replicate our previous findings on visual capture of proprioception (i.e., LGVS leads to greater proprioceptive drifts toward the rubber hand even without touch), and (b) investigate the role of right-hemisphere vestibular stimulation in sensory conflict (i.e., touch felt but not seen and vice versa). Specifically, we hypothesized that (a) LGVS would lead to smaller proprioceptive drifts during tactile stimulation of participants' skin (i.e., touch felt but not seen) in comparison with RGVS and sham (disruption of visual capture), but in favor of vision when touch is seen but not felt (visual capture of vicarious touch), and (b) both effects would be enhanced by applying affective slow touch in comparison with neutral fast touch.

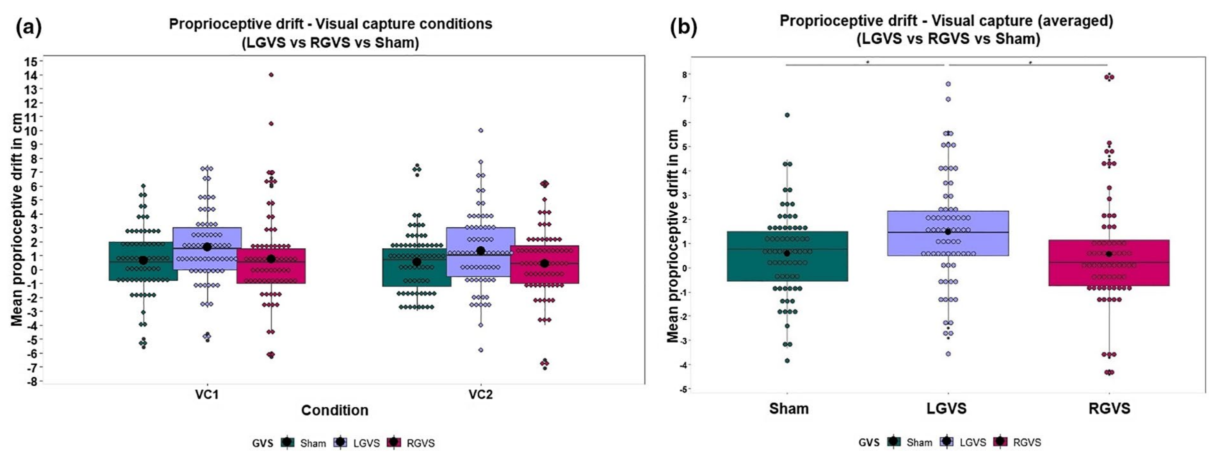

FIGURE 7 Mean values of the proprioceptive drift measured in cm in sham, LGVS, and RGVS. (a) Visual capture conditions 1 and 2 as performed by the participants during the block for both Experiment 1 and 2. (b) Visual capture baselines averaged. Solid line = median; black dot = mean; upper whisker = min(max(x), Q_3 + 1.5 × IQR); lower whisker = max(min(x), Q_1 − 1.5 × IQR). *$p < 0.05$

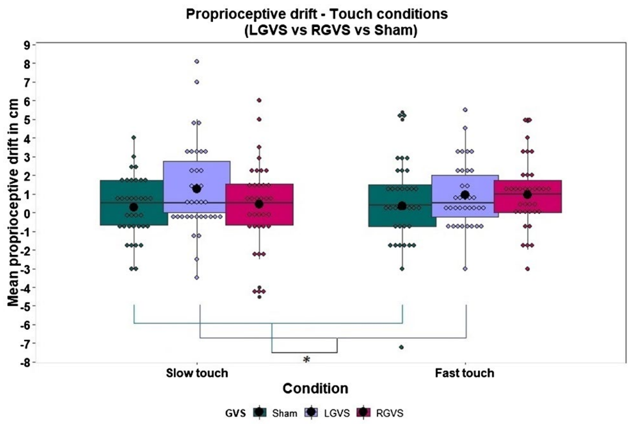

FIGURE 8 Mean values of the proprioceptive drifts in the different stroking conditions (slow affective touch and fast neutral touch) measured in cm and in the three different vestibular configurations (sham, LGVS, RGVS). Solid line = median; black dot = mean; upper whisker = min(max(x), Q_3 + 1.5 × IQR); lower whisker = max(min(x), Q_1 − 1.5 × IQR). $*p < 0.05$

In Experiment 1, we successfully replicated our previous findings: LGVS led to greater visual capture in comparison with sham and RGVS during mere observation of a rubber hand; that is, participants showed significantly greater proprioceptive drift toward the rubber hand following right-hemisphere vestibular stimulation. In Experiment 2, we found a similar, yet milder, pattern: LGVS led to greater proprioceptive drifts but not significantly more than RGVS and sham. This reduction of the effect in Experiment 2 might be due to the different experimental manipulations (felt vs. seen touch in the conditions following the visual capture ones) and/or higher individual variability in the sample. However, these findings suggest that stimulation of the right vestibular network may modulate multisensory integration by increasing the weight of vision over proprioception in a visuo-proprioceptive conflict. As we argued elsewhere (Ponzo et al., 2018), such visual capture effect may be due to a temporary disruption of participants' body representation (Fink et al., 2003; Harris & Hoover, 2015). The vestibular system may reduce the relative weight of somatosensory stimuli while increasing the relevance of exteroceptive ones in order to allow the resolution of perceptual ambiguity (Zeller, Litvak, Friston, & Classen, 2015). This would be consistent with the visual capture effects observed in stroke patients with right peri-sylvian lesions (Martinaud et al., 2017) and with reports of symptoms remission following right-hemisphere vestibular stimulation in patients with dis-ownership feelings (Bisiach, Rusconi, & Vallar, 1991; Rode et al., 1992).

Our second main finding is that vestibular stimulation modulates visuo-tactile conflicts according to whether the touch is felt or seen. In Experiment 1, when touch was applied to participant's own hand (without concomitant tactile stimulation of the rubber hand), proprioceptive drifts were significantly smaller during LGVS in comparison with sham stimulation (but not RGVS). In Experiment 2, seen vicarious touch delivered to the rubber hand during LGVS led to increased proprioceptive drifts in comparison with sham (but not RGVS). Hence, vestibular signals (not necessarily in a lateralized fashion) may be dynamically contributing to multisensory integration according to the contextual relevance of the different modalities involved. This may explain some of the previous conflicting findings in vestibular stimulation studies, with some authors reporting proprioceptive enhancement over vision during LGVS and others suggesting the opposite pattern, with vestibular stimulation increasing vision over proprioception (e.g., Lopez et al., 2010; Ponzo et al., 2018 vs. Ferrè, Haggard, Bottini, & Iannetti, 2015; Pavlidou, Ferrè, & Lopez, 2018; Pfeiffer, Serino, & Blanke, 2014). When a rubber hand is in a plausible position in space, allowing its integration in participants' body representation (as in our previous and current studies), vestibular signals may contribute to solve perceptual ambiguity by weighting visual signals more than proprioceptive ones. Conversely, when a third sensory modality (touch) is introduced in an asymmetric fashion, such that incorporation of the rubber hand into participant's body representation would generate additional conflict (i.e., feeling touch that is not seen leads to increased perceptual ambiguity), vestibular signals do not favor visual cues over proprioceptive ones. However, when touch is seen but not felt (i.e., it is vicariously perceived via vision), vestibular signals seem to favor vision rather than proprioception, to reduce sensory conflict. In line with neuroimaging findings, suggesting an overlap between areas of the vestibular network and multisensory integration of exteroceptive and proprioceptive signals (Lopez et al., 2012; zu Eulenburg et al., 2012), we suggest that vestibular processing in the right temporo-parietal and insular areas may balance sensory inputs in order to solve ambiguous perceptual situations. Such weighting mechanism could be responsible for the enhancement or reduction of visual cues in visuo-proprioceptive-tactile conflicts according to whether the conflict between the different sensory sources can or cannot be solved via visual dominance over proprioception.

Finally, we did not find differences between affective and neutral touch in disrupting nor enhancing visual capture. This contradicts our hypothesis that the results we observed in our previous study may be due to either the felt or the vicarious properties of affective touch. One possibility is that our previous findings, rather than representing vestibular enhancement of felt or seen components of affective touch, may be explained by the presence of both, delivered in synchrony (Filippetti, Kirsch, Crucianelli, & Fotopoulou, 2019). Future studies should investigate differential contributions of visuo-tactile versus vicarious and tactile only affective touch to multisensory integration.

The current study also presents some methodological limitations. Given the length of each experimental session, we were not able to compare the felt and seen touch in a within-subject fashion. This was mainly due to the fact that we posited that our results may be hemispheric specific. However, without comparing LGVS with RGVS, such conclusion could not be made. Hence, we decided to devise two different experiments using all three GVS configurations, including RGVS. Future studies could look at a within-subject design, perhaps with experimental sessions spread over 2 consecutive days.

Additionally, our GVS device did not allow for fully blinded procedures. In order to reduce experimenter bias, the main experimenter who participated in the study design did not collect the data herself but supervised data collection after having extensively trained the assisting experimenters (one for each study). Future research could employ the same design with a more sophisticated device, allowing for double-blinding.

Finally, GVS may have applications for the treatment of certain clinical conditions. For example, vestibular stimulation has been found to temporarily improve symptoms such as unilateral neglect (Saj, Honoré, & Rousseaux, 2006), anosognosia for hemiplegia (unawareness of paralysis), and somatoparaphrenia (limb dis-ownership; Bisiach et al., 1991; Cappa, Sterzi, Vallar, & Bisiach, 1987). Vestibular stimulation has also been shown to reduce painful sensations in healthy volunteers (Ferrè, Haggard, et al., 2015) as well as in a single case of chronic pain following stroke (Spitoni et al., 2016). As such, future studies might explore the possible use of galvanic vestibular stimulation in the treatment of stroke-induced changes in awareness or the reduction of chronic pain, both of which currently lack an established, effective treatment (Turk, 2002; Turk & Okifuji, 2002). For example, chronic pain might be reduced by shifting patients' attention away from the felt pain and toward more pleasurable visual experiences. Based on our experimental findings, GVS might provide the mechanism by which this increase in the weight of visual information over proprioception could be achieved. Further clinical and experimental studies are needed to explore these ideas.

To conclude, we provide further evidence that the vestibular system may dynamically contribute to multisensory integration by weighting different sensory modalities according to the context in which they are experienced. In the current study, vestibular stimulation led to an increased dominance of visual information over proprioception during a visuo-proprioceptive conflict as well as during vicarious touch conditions (i.e., when touch was seen on the rubber hand but not felt on participant's hand) but a decrease of visual capture effects when touch was only felt on participant's hand but not seen on the rubber hand. These findings suggest that the vestibular network may modulate multisensory experience in a dynamic fashion in an attempt to solve sensory conflicts.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1

Table S1

Table S2

Figure S1

Figure S2

Experiment 1—Data set

Experiment 2—Data set

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