INTEGRATION OF VISUAL AND PROPRIOCEPTIVE AFFERENTS IN KINESTHESIA

M. GUERRAZ, [a,b]* S. PROVOST, [b] R. NARISON, [b]
A. BRUGNON, [b] S. VIROLLE [b] AND J.-P. BRESCIANI [a]

[a] *Laboratory of Psychology and NeuroCognition, UMR 5105 CNRS – University of Savoie, BP 1104, 73011 Chambéry Cedex, France*

[b] *Department of Psychology, University of Savoie, BP 1104, 73011 Chambéry Cedex, France*

Abstract—Proprioceptive signals are of prime importance in kinesthesia. However, in conditions of visuo-proprioceptive conflicts, strong visual-evoked biases can be observed. In three experiments, we parsed the interaction between visual and proprioceptive afferents using the 'mirror box' paradigm. Participants' left arm, the image of which was reflected in a mirror, was passively moved into flexion/extension or remained static. In Experiment 1 proprioceptive afferents of the unseen static right arm were masked with diffuse arm vibration. In Experiments 2 and 3, afferent signals were enhanced by muscle vibration of biceps or triceps stretch receptors. Illusory arm movements were evaluated with subjective reports and matching adjustments. Results revealed that participants did not experience kinesthetic illusions when the mirror reflected the image of a static arm while proprioceptive afferents conveyed signals of a moving arm (Experiment 2). In this specific case, vision apparently contributed much more strongly to the final percept than proprioceptive signals. However, in most circumstances, the percept reflected integration of both afferent signals (Experiments 1–3). For instance, when both sensory channels conveyed signals of arm displacement but in the opposite direction, kinesthetic illusions occurred but were either proprioceptively (vibration illusion) or visually driven (mirror illusion), according to individual sensorial preferences (Experiments 2 and 3). These results indicate that kinesthesia is the product of cooperative integration processes in which the final percept strongly depends on the experimental conditions as well as sensorial preferences. The observed changes in the relative contribution of each input across experimental conditions likely reflect reliability-dependent weights. © 2012 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: multisensory integration, vibration, kinesthesia, mirror illusion.

INTRODUCTION

Kinesthesia refers to the sense of position and movement of our limbs and trunk. Among proprioceptive afferents, the principal muscle receptor involved in kinesthesia is the muscle spindle that has been widely investigated by the use of vibration. Specifically, vibration, applied to a muscle–tendon, activates mainly the primary spindle endings (Ia fibers), for which the firing rate seems to be interpreted by the CNS as an elongation of that muscle (Burke et al., 1976; Roll et al., 1989, 2009). When vibration is applied on one particular muscle, the erroneous interpretation induces motor effects (Eklund, 1972; Goodwin et al., 1972; Roll and Roll, 1988; Romaiguere et al., 1991; Caudron et al., 2008, 2010) or illusory sensation of joint displacement also called vibratory illusion (Goodwin et al., 1972; Gilhodes et al., 1986; Ceyte et al., 2007). For instance, vibration, applied on either the biceps or triceps of an unseen static arm, induces illusion of arm displacement in the direction that would have stretched the receptor bearing muscle (Goodwin et al., 1972; Roll and Roll, 1988). In contrast, when applied to the whole body/segments (such as using a road drill) or concurrently on two antagonist muscles, vibration substantially degrades afferent proprioceptive responsiveness and therefore position perception (Ribot et al., 1986; Roll et al., 1989; Bock et al., 2007).

Although of prime importance (Teasdale et al., 1993), proprioceptive afferents interact with other senses, such as vision, in the perception of position and movement (Maravita et al., 2003). For instance, a combination of synchronous visual and touch stimuli are sufficient to mislead the nervous system into self-attribution of a rubber hand (Botvinick and Cohen, 1998; Dummer et al., 2009). In this paradigm, when stimuli were temporally but not spatially congruent, intersensory bias occurred and the felt position of one's own hand is relocated toward the location of the rubber hand (Botvinick and Cohen, 1998; Kammers et al., 2009). Similarly, reflection of one moving hand through a mirror placed along the midline axis can give the appearance of symmetrical bimanual movements ("*mirror illusion*"). Such visual-evoked biases likely reflect "optimal" integration processes in which the relative weight of each sensory input is proportional to its reliability (Ernst and Bülthoff, 2004).

The purpose of our study was to parse further the interaction between visual and proprioceptive afferents in kinesthesia. Healthy participants were required to report illusory right arm displacement evoked by a combination of visual and proprioceptive manipulation. Visual afferents were manipulated through the mirror box paradigm in which participants could see the reflection of their passively moved left arm through a mirror orientated parallel to their midsagittal axis. Proprioceptive afferents on the unseen right arm were either degraded/masked

*Correspondence to: M. Guerraz, Laboratory of Psychology and NeuroCognition, UMR 5105 CNRS – University of Savoie, BP 1104, 73011 Chambéry Cedex, France. Tel: +33-4-79-75-91-86; fax: +33-4-79-75-83-99.
E-mail address: Michel.guerraz@univ-savoie.fr (M. Guerraz).

through diffuse vibrotactile stimulation (Experiment 1) or enhanced by targeted muscle vibration (Experiments 2 and 3). The interaction between visual and proprioceptive signals was evaluated in uni- or bimodal stimulation conditions in which the two sensory channels conveyed either congruent (co-directional) or opposite (contra-directional) signals about arm displacement.

EXPERIMENTAL PROCEDURES

Participants

Fifteen participants (10 females, 5 males, 14 right-handed), ranging in age from 18 to 29 years (mean age = 21.2 years) participated in Experiment 1. Eleven right-handed participants (8 females, 3 males), ranging in age from 20 to 29 years (mean age 21.8 years) participated in Experiment 2, four of whom already participated in Experiment 1. One of these participants did not experience any vibratory illusion and was not further considered for the experiment. Eighteen participants (12 females, 6 males, 17 right-handed), ranging in age from 18 to 28 years (mean age 21.5 years) participated in Experiment 3. One of the participants of Experiment 3 participated in Experiment 2 and none in Experiment 1. None of the participants had a history of visual, proprioceptive or neuromuscular disease. All volunteered and provided written informed consent prior to participating in the experiment. The experiment was performed in accordance to the ethical standards laid down in the 1964 Declaration of Helsinki and approved by the Local Ethics Committee of the University of Savoie.

Material

Participants sat in front of a large custom-built box. A mirror measuring 65 ∗ 65 cm was positioned vertically in the middle of that box, with the reflective surface facing to the participants left and oriented parallel to his midsagittal axis (Fig. 1). Participants' forearms were positioned on each side of the mirror and were supported by two manipulanda devices. The distances between the manipulanda and the mirror were adjusted so that the mirror image of the left arm coincided with the position of the right arm. The manipulanda consisted in wooden arms mounted with handles on which subjects positioned their forearms and hands. The right manipulandum was fixed while the left manipulandum was motorized (low noise DC motor) and could rotate (via a remote controller) to move participant's left elbow into flexion or extension. Manipulandum rotation velocity was fixed at 3.8 deg/s. Participants' forearms were adjusted on the manipulandum so that the axis of rotation of the motorized device precisely coincided with the participant's elbow joint.

In Experiments 1–3, participants were asked to match with their right foot what they felt in their right arm. To do so, participants' right foot was tapped to a paddle that could also rotate at a point close to the heel. In order to increase the range of motion of the feet, each participant's right leg was slightly extended.

Both the left manipulandum and paddle displacements were recorded with an electromagnetic motion capture system (Polhemus Fastrak, USA). A sensor was positioned on each device so that continuous signals of the angles of the manipulandum and the foot were provided. Data were collected with a sampling frequency of 40 Hz.

Procedure

Proprioceptive masking (Experiment 1). The reference (right) forearm of the participant was positioned at an angle of 45 deg to the horizontal. The left arm was positioned at either 0 deg (extended elbow) or 90 deg (flexed elbow) to the horizontal. Participants' right foot was placed in the same position (flexed or extended) as the left forearm. Following a baseline epoch of ∼10 s without any arm displacement, the left forearm was passively moved, either in flexion or extension (according to the initial elbow position) at a constant velocity of 3.8 deg/s. Subjects were required not to resist to this passive displacement. In half of the trials, a vibrator (VB115, Techno Concept, France) attached to the right manipulandum was turned on 10 s before the forearm was passively moved and left on till the end of the trial (vibrotactile mask condition). This vibrator induced diffuse vibrations in participants' right hand/forearm at a frequency of 40 Hz, which is sufficient to induce noise in proprioceptive afferents (Ribot et al., 1986; Cordo et al., 1995). In the other half of the trials, the vibrator was turned off (no mask condition).

Three visual conditions were carried out: (1) mirror vision: subjects were looking at their left moving forearm through the mirror. In this condition, both the moving arm and the reflected arm were visible; (2) no mirror vision: subjects were looking at their left moving forearm while the mirror was obstructed. In this condition, only the moving arm was visible; (3) no vision: subjects closed their eyes throughout the trial. The three visual conditions (mirror vision, no mirror vision, and no vision) were paired with the two vibrotactile mask conditions (vibrotactile mask and no mask) giving six experimental conditions in total in a within-subject design. Each condition was repeated four times in pseudo-random order for a total of 24 trials per participant.

Simulated muscle stretch and mirror vision (Experiment 2). The referenced (right) forearm and the left forearm (as well as the participants' right foot) were positioned at an angle of 45 deg to the horizontal prior to trial onset. The vibrator was positioned directly on the belly of either the biceps or triceps of participants' right reference arm. Following a baseline epoch of ∼10 s, the vibrator was turned on. The vibration frequency was 90 Hz (0.8 mm), a frequency known to be optimal to induce illusory arm displacements (Roll and Roll, 1988). When the vibrator was turned on, the left forearm (which image was reflected in the mirror) remained either static or was passively moved at a constant velocity of 3.8 deg/s to either an angle of 0 deg (extended arm) or 90 deg (flexed arm) to the horizontal. The simulated muscle stretch induced by the vibration applied to the right reference arm was therefore congruent or opposite to the passive displacement of the left arm. Specifically, vibrating the right biceps simulates a biceps stretch that is "congruent" with a passive left elbow extension, and "opposite in direction" to a passive left elbow flexion. Similarly, vibrating the triceps simulates a triceps stretch, "congruent" with a left elbow flexion, and "opposite" to a passive left elbow extension. Conditions in which the left arm was static (reflection of a static arm through the mirror) were considered as "neutral". Because illusory forearm movements evoked by biceps and triceps vibration are oppositely directed but otherwise symmetrical, the experimental trials were divided into three experimental conditions with *congruent*, *opposite* and *neutral* trials.

Two visual conditions were carried out: (1) mirror vision: subjects were looking at their left moving forearm in the mirror. In this condition, both the moving arm and the reflected arm were visible; (2) no vision: subjects closed their eyes throughout the trial.

The two visual conditions (mirror vision, no vision) were paired with the three congruency conditions (congruent, opposite, and neutral) giving six experimental conditions in total in a within-subject design. Each condition was repeated four times in pseudo-random order giving a total of 24 trials per participant.

Illusions were quoted as positive when the felt displacement was in the direction of the simulated muscle stretch (illusory flexion and extension with triceps and biceps vibration, respectively).

A

B
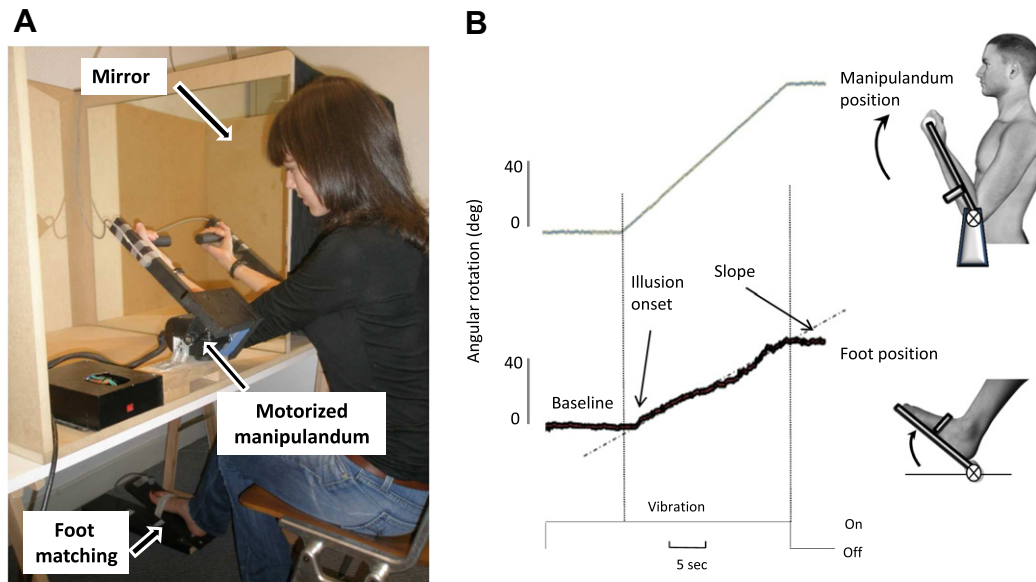
Fig. 1. (A) Mirror box apparatus. The participant sat at a table facing a box which was compartmented by a mirror reflecting the image of his (her) left arm. This mirror could be covered according to the experimental condition. The manipulandum supporting the left arm was motorized and could move the arm into flexion or extension at a velocity of 3.8 deg/s. The right arm (reference arm) was systematically static and out of sight (hidden behind a black curtain). Participants right leg was slightly extended with the foot taped to a paddle which rotated just below the heel. (B) The upper trace shows the rotation of the left arm (into flexion in that trial) supported by the motorized manipulandum. The middle trace shows a typical foot matching adjustment from which movement illusion speed was calculated (as the slope of the foot matching response based on a least squares linear regression fitted over a period from Illusion onset to the end of the trial).

Unimodal versus bimodal stimulation (Experiment 3). Both the referenced (right) forearm and the left forearm were positioned at an angle of 45 deg to the horizontal prior to trial onset. Each trial consisted of a baseline epoch of ~10 s, followed by a 12-s epoch of stimulation which varied according to the experimental condition. Two unimodal conditions were manipulated: (1) *vibration only*: the vibrator attached to either the biceps or triceps of the right arm was turned on (90 Hz) for 12 s. In this experimental condition, participants left arm remained static and eyes were closed. (2) "*Mirror vision only*" condition: the left forearm was passively moved at a constant velocity of 3.8 deg/s to either an angle of 0 deg (extended arm) or 90 deg (flexed arm) to the horizontal (mirror vision only) for 12 s. In the mirror condition, the vibrator was switched off. Visual and proprioceptive stimulation were combined in two bimodal conditions, similar to those manipulated in Experiment 2: (3) "*congruent condition*": the vibrator attached to either the biceps or triceps of the right arm was turned on (90 Hz) while the left forearm was passively moved in a congruent way to either an angle of 0 deg (extended arm) or 90 deg (flexed arm) to the horizontal. (4) "*Opposite*" condition: the vibrator attached to either the biceps or triceps of the right arm was turned on while the left forearm was passively moved in the opposite direction. Each condition was repeated six times giving a total of 24 trials per participant.

In the three experiments, participants moved actively and synchronously their two arms into flexion–extension before each trial. This allowed the two arms to have a similar immediate history of contraction and length changes before trials (see Gregory et al., 1988; Proske et al., 1993; Proske, 2006 for discussion concerning muscle thixotropy).

Measures of kinesthetic illusion

Subjective reports. At the end of each trial, participants were required to rank the direction (flexion or extension) and speed of the felt displacement (illusion) of the right arm on a subjective scale from 0 to 20 with steps of one. Zero corresponded to the absence of felt displacement of the referenced arm, 10 being a felt displacement whose velocity was equal to that of the passively moved left forearm. Twenty corresponded to a felt displacement whose velocity was twice as important. Prior to the experiment, subjects experienced trials with passive displacement of the left forearm to become familiar with subjective rating.

Matching task. During each trial, the participants' task was to match with his right foot what he felt in his right arm (Fig. 1). The foot matching task was used to measure movement illusion speed (deg/s). It was calculated as the slope of angular foot displacement based on a least squares linear regression fitted over a period of 5 s (200 data points) from illusion onset. When no illusion occurred, movement illusion speed was zero. Within the analysis period, the profile of the matching adjustment (when an illusion was experienced) was approximately linear, as suggested by the strong correlation coefficient observed for each trial and subject (mean Pearson coefficient $r = 0.97$). Illusion onset was defined as the time at which the angular position of the foot was beyond three standard deviations from the mean baseline position of the foot calculated over a 5-s epoch before manipulandum displacement. Because of the unusual aspect of such a foot matching task, participants undertook familiarization trials prior to the experiment. At the end of each experimental session, participants undertook a further four trials to test matching accuracy in which they were required to match the passive displacement of the left forearm (either in flexion or extension) with their right foot indicator. These trials were used to normalize velocity measurements of experimental trials.

Statistics

Data from the matching task and subjective report were analyzed using a 3 × 2 [vision (mirror vision, vision, and no vision), mask interference (no mask, mask)] and a 3 × 2 [congruence

(congruent, opposite, and neutral), vision (mirror vision, no vision)] repeated measures ANOVAs (within-subject design) in Experiments 1 and 2, respectively. The reported values are Huynh–Feldt corrected and post hoc tests were performed using Holm's correction for multiple comparisons. In Experiment 3, predicted and observed results were compared with t-tests. Spearman coefficient was used for correlation analysis.

RESULTS

Proprioceptive masking (Experiment 1)

Subjective reports. Reflection of the passively moving left arm through the mirror-evoked illusions of right arm displacement ("mirror illusion") in the same direction. Mirror illusion was experienced in 98% and 96% of the trials when the vibrotactile mask was present or absent, respectively. Passive displacement of the left arm evoked occasional illusions of right arm displacement in the other two visual conditions (no mirror: 35%; no vision: 31%) when the vibrotactile mask was present. When the vibrotactile mask was off, very few illusions were reported (no mirror: 13%; no vision: 12%). Kinesthetic illusion did never occur when the left arm was static (baseline epoch).

The ANOVA revealed a significant main effect of "vision" ($F(2, 28) = 224$, $p < .01$). In particular, the mean estimate of right arm displacement was significantly larger ($p < .05$) in the *mirror condition* (mean = 7.8, SD = 1.6) than in the other two conditions (mean = 0.56, SD = 0.9 and mean = 0.76, SD = 1.55 for the *no mirror* and *no vision* conditions, respectively) which did not differ from one another ($p > .05$).

The main effect of the "mask" also reached significance ($F(1, 14) = 23.5$, $p < .01$). Specifically, the mean score with vibrotactile mask was larger than that without mask for all three visual conditions (Fig. 2a). However, the interaction between "vision" and "mask" was close to significance ($F(2, 28) = 2.7$, $p = .085$), indicating that mask did not quite have the same effect for all visual conditions. This was confirmed by post hoc analysis that revealed that the difference between the *mask* and *no mask* conditions reached significance only in the "*mirror vision*" condition ($p < .05$).

The foot matching task. Foot adjustments were consistent with subjective reports. The ANOVA showed a main effect of vision ($F(2, 28) = 67.9$, $p < .01$), the mean velocity of foot displacement being much larger in the *mirror vision* condition ($m = 3.3$ deg/s, SD = 1.2) than in both the *no mirror* ($m = 0.2$ deg/s, SD = 0.3) and *no vision* ($m = 0.26$ deg/s, SD = 0.5) conditions ($p < .05$, Fig. 2b). There was also a main effect of "mask" ($F(1, 14) = 4.8$, $p < .05$). As can be seen in Fig. 2b, illusion speed in the *vibrotactile mask* conditions was larger than in the *no mask* condition whatever the visual condition. There was no significant interaction between "vision" and "masking" ($F(2, 28) = 0.2$, $p > .05$).

Illusion onset was also measured in the two mirror conditions (with or without vibrotactile mask) in which illusion was experienced in the majority of instances. As can be seen in Fig. 2c, the latency of kinesthetic illusion in condition of mirror vision was much shorter with vibrotactile masking ($m = 3.26$ s, SD = 1.9) than without ($m = 6.7$ s, SD = 2.6) ($t(14) = 5.54$, $p < .01$).

Simulated muscle stretch and mirror vision (Experiment 2)

Subjective reports. Analysis of subjective reports showed significant main effects of both the "visual" ($F(1, 9) = 60.2$, $p < .01$) and "congruency" factors ($F(2, 18) = 12.1$, $p < .01$) as well as a significant interaction between them ($F(2, 18) = 21$, $p < .01$).

Simulated stretch in the absence of vision. In the absence of vision, and when the left arm was static, participants reported a kinesthetic illusion in response to muscle vibration, whose direction was a function of the vibrated muscle: an illusion of flexion and extension when vibration was applied over the right triceps and biceps, respectively. Although vibration applied to one muscle might to some extent spread to its antagonist, evoked forearm illusions attest that the stimulus was largely limited to the targeted muscle. When vision was occluded, moving the left arm in a direction congruent with or opposite to the simulated stretch had no effect on vibration-induced illusions (Fig. 4a) as confirmed by post hoc analysis ($p > .05$).

Simulated stretch with mirror vision (bimodal stimulation, Fig. 3). In the condition of mirror vision, strong kinesthetic illusions occurred when the passive displacement of the left arm was congruent with the simulated stretch (movement illusion speed: $m = 6.5$, SD = 2.5). When the left arm was either static ("neutral": $m = 0.4$, SD = 0.7) or was moving in a direction "opposite" to the simulated stretch ($m = -0.25$, SD 2.3) no consistent illusion occurred (see Fig. 4a). The congruent condition differed significantly from the other two conditions ($p < .05$), the latter being not significantly different from each other ($p > .05$). Although the speed of the mean movement illusion was close to zero in these latter conditions (see Fig. 4a), subjects hardly ever reported illusion in the "neutral" condition (left arm static: 15% of the trial) but often reported illusions in the "opposite" condition (62% of the trial). In the "opposite" condition, when an illusion was reported, it was either in the direction of the simulated stretch (proprioceptively driven) or in the opposite direction (visually driven); the illusions canceling each other when averaged. The inter-individual variability of perceptual estimates was therefore significantly larger in the "opposite" condition than in the "neutral" condition (Brown–Forsythe test, $p < .05$).

Comparison between mirror vision and no vision. Post-hoc analysis (Tukey) indicated that when passive displacement of the left arm was "congruent" with the simulated stretch, the kinesthetic illusion was similar in the two visual conditions (mirror vision and no vision) ($p > .05$). Therefore, adding congruent visual cues did
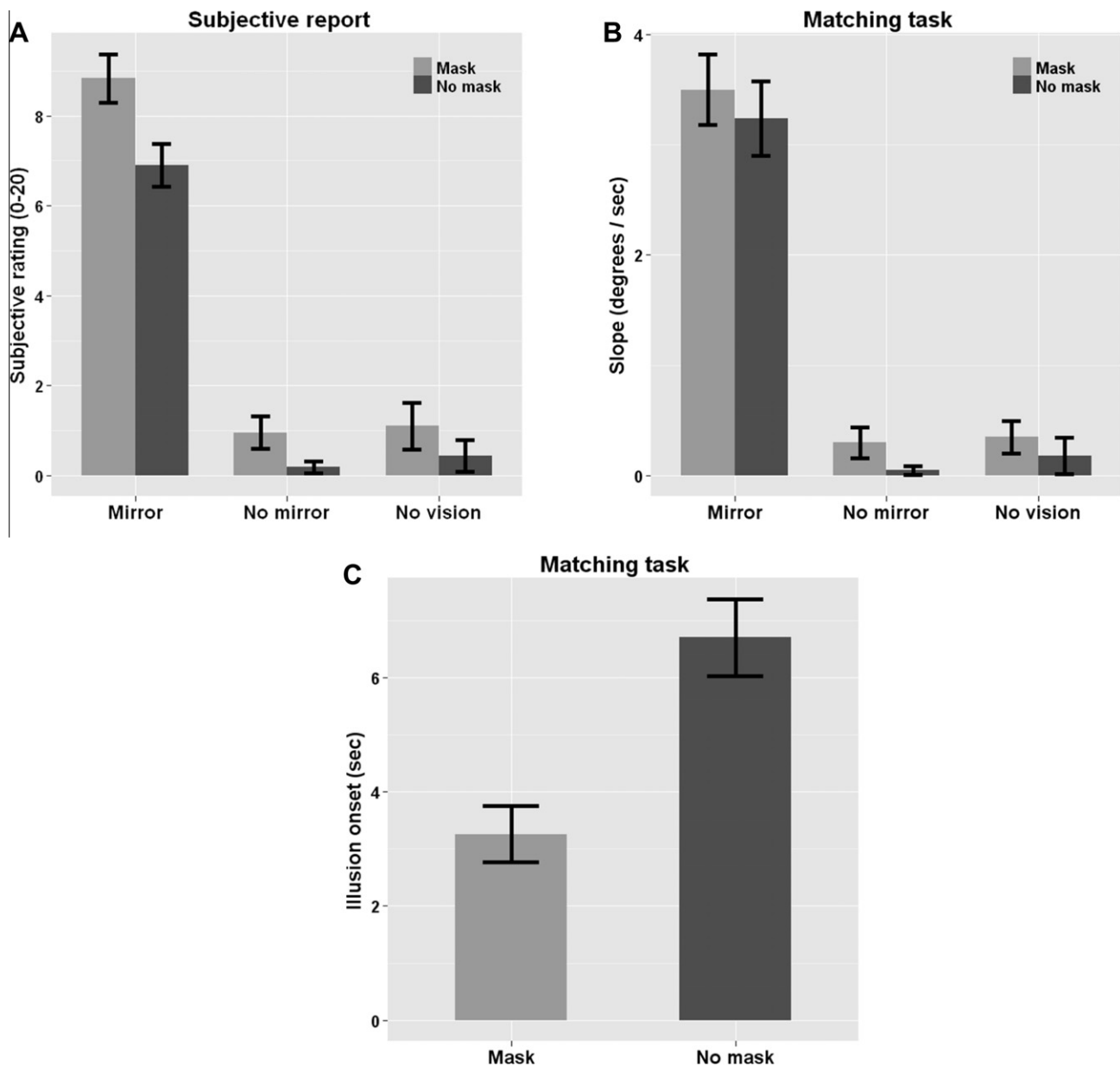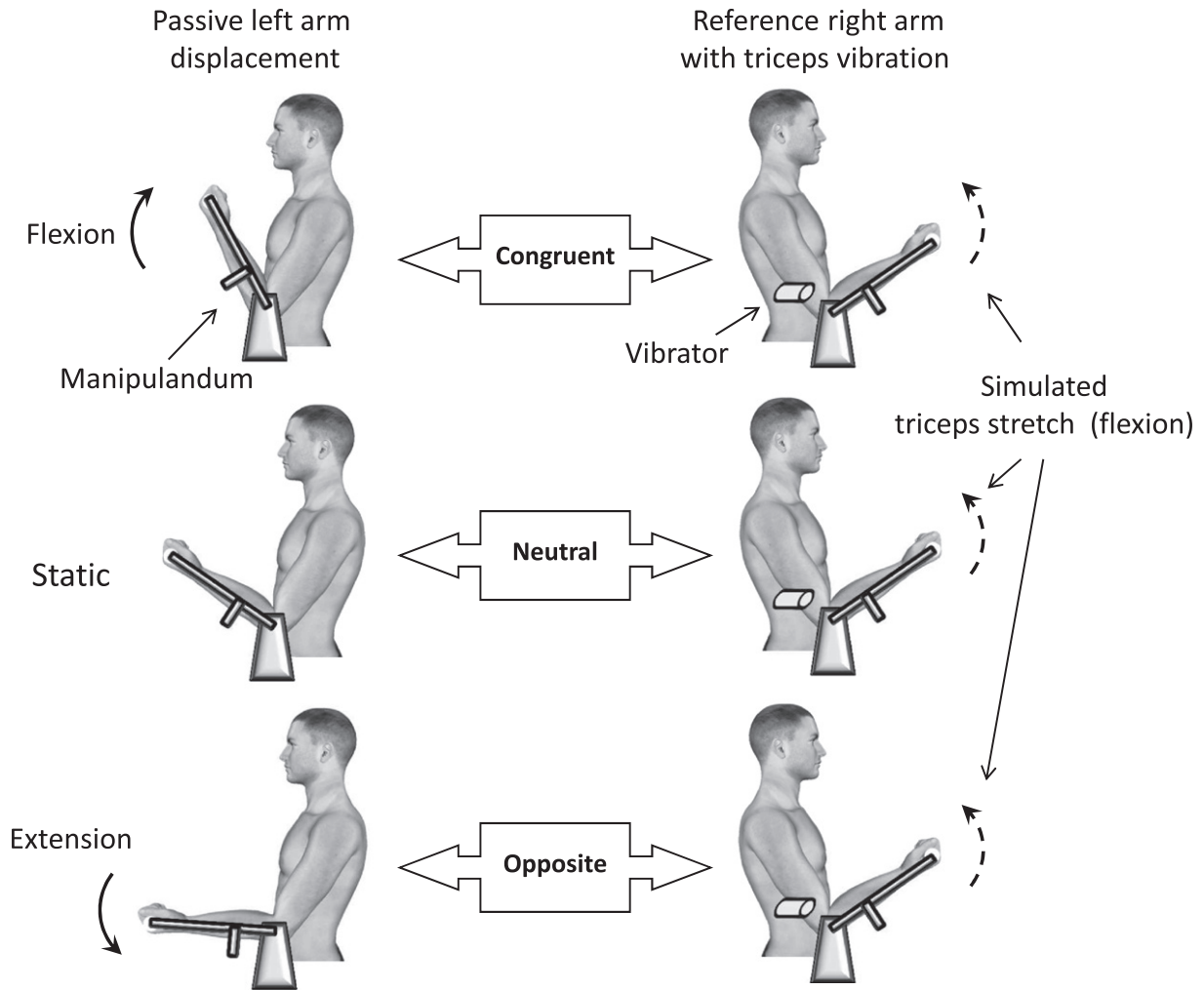
Fig. 2. Mean and standard error of movement illusion speed in the subjective task (A) and the foot matching task (B), in condition of mirror vision, no mirror or no vision, with either proprioceptive masking (light grey bars) or no masking (dark grey bars). Positive values indicated that the kinesthetic illusion was in the direction of the passively moved left arm. (C) Mean and standard error of illusion onset (in seconds) in the mirror condition (the passive displacement of the left arm reflected in the mirror) with either proprioceptive masking (light grey bars) or no masking (dark grey bars).

not significantly affect the movement illusion speed induced by vibration. When passive displacement of the left arm was incongruent ("*neutral*" and "*opposite*" conditions) with the simulated stretch of the reference arm, movement illusion speed was significantly higher without vision than with mirror vision ($p < .05$) (Fig. 4a).

The foot matching task. Analysis of foot displacement velocity provided results similar to subjective reports with significant main effects of both the "visual" ($F(1,9) = 51.2$, $p < .01$) and "congruency" factors ($F(2,18) = 14$, $p < .01$) and a significant interaction between them ($F(2,18) = 17.6$, $p < .01$).

Simulated stretch in the absence of vision. In the absence of vision, participants reported a kinesthetic illusion (through foot matching adjustments) in response to muscle vibration whose direction was related to the vibrated muscle. Post-hoc pairwise comparisons indicated that in the absence of vision, passive displacement of the left arm had no effect ($p > .05$) on such kinesthetic illusion (Fig. 4b).

Simulated stretch with mirror vision. With mirror vision, a significant kinesthetic illusion occurred only in the *congruent* condition, that is, when the passive displacement of the left arm was in the same direction

Fig. 3. Examples of experimental conditions being either congruent, neutral or opposite. The left panel represents the passive displacement of the left arm (flexion, static, extension) while the right panel represent vibration (90 Hz) applied on the triceps of the right reference arm.
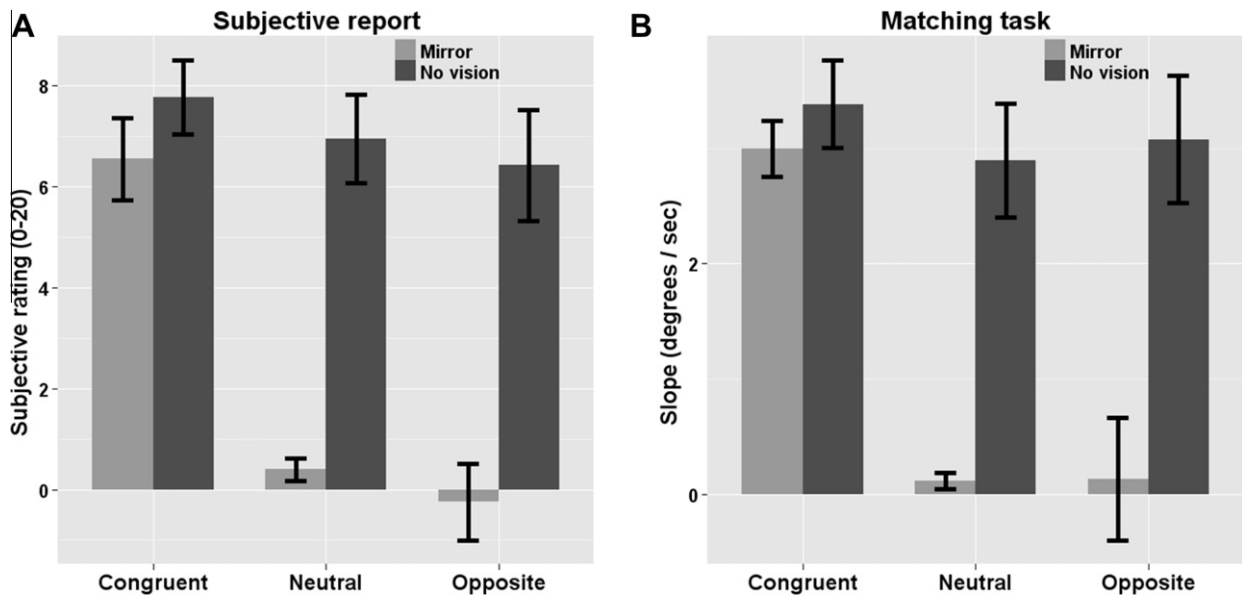
Fig. 4. Mean and standard error of movement illusion speed in the subjective task (A) and the foot matching task (B), in condition of congruent, opposite and neutral conditions with either mirror vision (light gray bars) or no vision (dark gray bars).
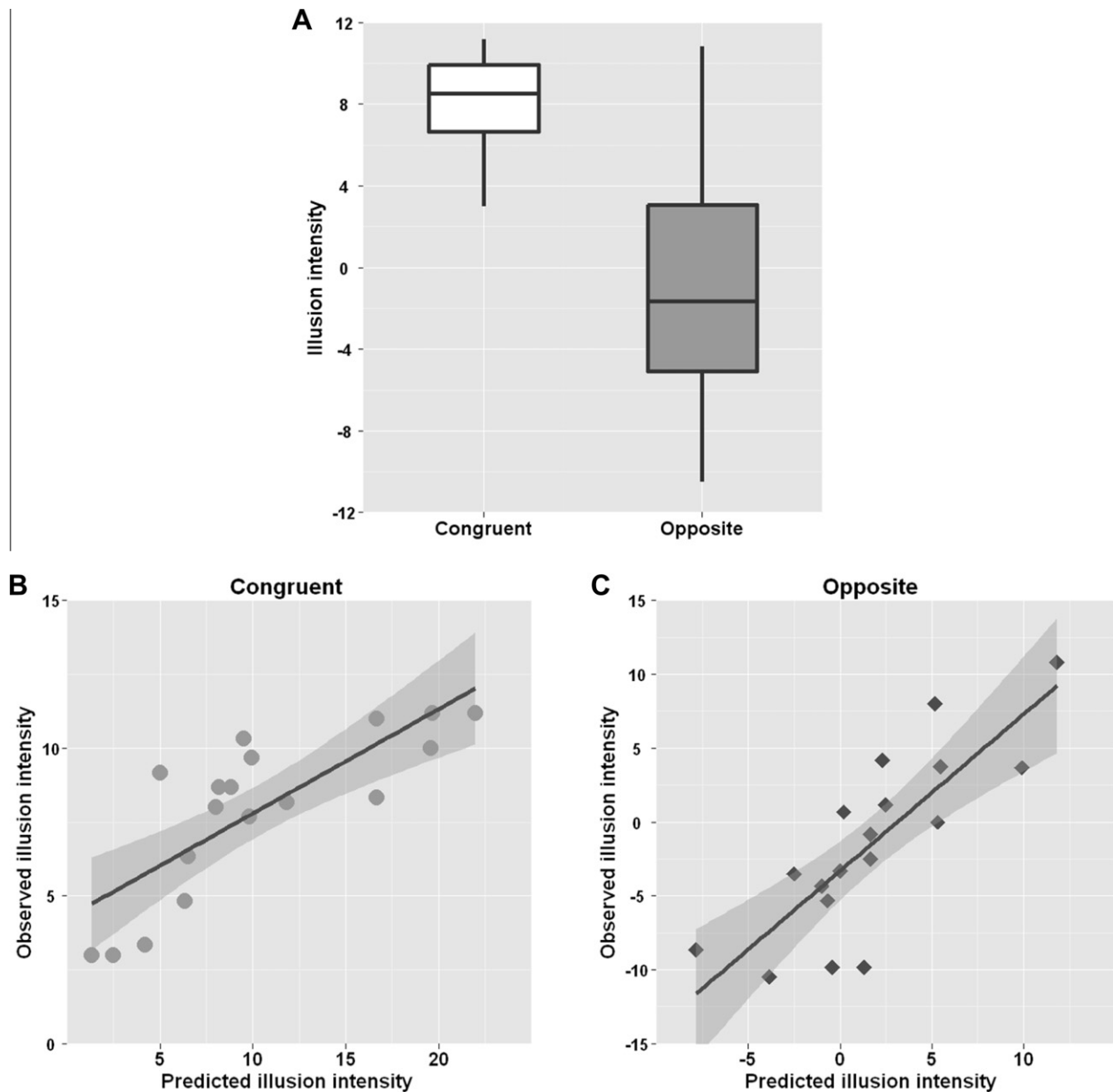
Fig. 5. (A) Intensity of the illusion in the congruent and opposite condition. Each box summarizes the distribution of responses of all subjects, the central line corresponding to the median, the box defining the inter-quartile range (IQR, between first and third quartile) and the whiskers corresponding to $\pm 1.5 * \text{IQR}$. Positive values indicate a felt displacement of the right arm in the direction of simulated muscle stretch whereas negative values indicate a felt displacement in the opposite direction. (B, C) Relationship between predicted illusion (calculated on the basis of addition/subtraction of scores obtained in isolated stimulation conditions) and illusion reported in combined conditions, either congruent (B) or opposite (C). The shaded area represents the 95% confidence interval of the regression line.

as the simulated stretch. Specifically, foot displacement velocity was larger in the *congruent* condition ($m = 2.99$ deg/s, SD = 0.76) than in the other two conditions (*neutral*: $m = 0.11$ deg/s, SD = 0.21; *opposite*: $m = 0.13$ deg/s, SD = 1.6; $p < .05$), the latter being not different from each other ($p > .05$). As reported for perceptual estimates, the inter-individual variability of foot matching adjustments was larger in the *opposite* condition than in the *neutral* one (Brown–Forsythe test, $p < .05$).

Unimodal versus bimodal stimulation (Experiment 3)

Unimodal stimulation. Mirror only: When participants experienced an illusory displacement of their right reference forearm, it was systematically in the direction of the passive displacement of the left forearm. The mean subjective report of right arm displacement was $m = 4.3$ (SD = 3.7) while the mean foot displacement velocity (matching task) was $m = 2.15$ deg/s (SD = 1.8).

Vibration only: Simulated stretch (vibration) in the absence of vision induced kinesthetic illusion whose

direction was a function of the vibrated muscle. The mean subjective report of right arm displacement was $m = 6.05$ (SD = 3.9) while the mean foot displacement velocity (matching task) was $m = 1.8$ deg/s (SD = 1.4).

No significant correlation between visual and proprioceptive sensitivity occurred when either subjective reports ($r = 0.15$, $p > .05$) or the foot-matching task ($r = 0.19$, $p > .05$) were considered.

Bimodal stimulation. Congruent visual and proprioceptive stimulation. When visual and proprioceptive stimulation were congruent, illusory displacement was consistent with the simulated stretch of the right arm which also corresponded with mirror reflection of the left arm. The mean subjective report of kinesthetic illusion in the congruent condition ($m = 7.9$, SD = 2.7) was significantly larger than that reported in both unimodal mirror ($t = 4.9$, $p < .01$) or vibration ($t = 2.7$, $p < .01$) stimulation conditions. Similar results were observed when the foot matching task was considered, with a mean foot displacement velocity of $m = 3.6$ deg/s (SD = 1.4) that differed significantly from that observed in both unimodal conditions ($p < .01$). The mean subjective report in the congruent condition was however smaller than what one would expect if a linear additive process were at work (mean expected illusion based on the sum of unimodal conditions $m = 10.36$, SD = 6.1; $p < .05$). As for Experiment 2, a ceiling effect might be at the origin of this difference. Indeed, as shown in Fig. 5b, for few subjects (who were highly sensitive to both proprioceptive and visual stimulation) predicted subjective scores were well above the real displacement of the left arm, which refers to a score of 10 on the subjective scale. The difference did not reach significance for the foot matching task ($p > .05$).

Correlation analysis revealed a strong and positive relationship between prediction based on an additive model (sum of illusion intensity measured in unimodal conditions) and illusion intensity reported in the congruent condition (subjective reports: $r = 0.81$, $p < .01$; foot-matching task: $r = 0.87$, $p < .01$). Therefore, the sum of illusion scores obtained in unimodal conditions is rather a good predictor of the illusion experienced when sensorial stimulations are congruent.

Opposite visual and proprioceptive stimulation. When proprioceptive and visual stimulation were oppositely directed, some participants reported illusory arm displacement (kinesthetic illusion) in the direction of the simulated stretch (proprioceptively driven) while others reported illusion in the direction of the seen moving arm (visually driven). These opposite illusions canceled each other when averaged (subjective report: $m = -1.5$, SD = 6.2; matching task: $m = -0.5$, SD = 2.6). However, as observed in the congruent condition, the mean subjective report in opposite condition was different from what one would expect if a linear additive process were at work (mean expected subjective illusion based on subtraction of unimodal stimulations $m = 1.7$, SD = 4.7; $p < .05$). The difference did not reach significance for the foot matching task, though ($p > .05$). As depicted

in Fig. 5c, a strong and positive relationship between prediction (subtraction between vibration and mirror illusions when evaluated independently) and kinesthetic illusion in the opposite condition was observed (subjective report: $r = 0.84$, $p < .01$; matching task $r = 0.64$, $p < .01$). Therefore, participants who showed a clear sensorial preference are those who experienced the greatest kinesthetic illusions (visually or proprioceptively driven) in the opposite condition. Those showing no clear sensorial preference in the two unimodal conditions (i.e., illusion of similar intensity, either high, low or medium) experienced little or no illusion in the opposite condition.

DISCUSSION

Mirror illusion attests of visual signal contribution to kinesthesia

When looking at the mirror reflection of their passively moved forearm in Experiments 1–3, participants most frequently reported illusory displacement of their other forearm. The occurrence and intensity of this kinesthetic illusion are particularly interesting considering that some authors did not report such an illusion in healthy subjects (Zampini et al., 2004). In these previous reports, passive displacements were performed by the experimenters themselves and when reported, displacement velocity was 3–4 times higher than here (Zampini et al., 2004; Izumizaki et al., 2010). Here, the smooth and slow angular velocity of passive movements (constant velocity of 3.8 deg/s) of the left forearm, achieved by the motorized manipulandum, likely favored the occurrence of the illusion. As reported by Hall and McCloskey (1983), the higher the angular velocity of passive forearm displacement, the more likely such movement would be detected. Although this should be validated by controlling velocity, amplitude and duration parameters factors which are confounded in the present experiments, one might expect that the higher the velocity of the passively moved forearm, the less likely its reflected image would evoke a mirror illusion.

The illusory displacement evoked by muscle vibration in Experiments 2 and 3 corresponded to the simulated stretching of the vibrated muscle, inducing illusory flexion and extension when vibration was applied to the triceps and biceps, respectively. Several authors have already reported that vibration creates kinesthetic illusion provided that visual information about the body part is absent (Lackner and Levine, 1979; Lackner and Taublieb, 1984; Seizova-Cajic and Azzi, 2011). Our results show for the first time that vision of a static limb through the mirror, whose spatial position corresponded to the unseen vibrated limb, could also abolish the vibration illusion. In that particular condition, visual cues were clearly prioritized and proprioceptive flow evoked by muscle vibration largely ignored.

Integration of visual and proprioceptive signals in kinesthesia

Although vision is of great importance in the percept, Experiment 1 revealed that mirror illusion occurred

earlier (reduced latency) and with a greater intensity (the arm was perceived to move faster) when proprioceptive afferents were degraded (vibration mask). This is consistent with amputee's report (deprived of proprioceptive afferents), of astonishing illusions of reminiscent hand/arm kinesthesia when viewing their intact limb moving through a mirror (Ramachandran and Hirstein, 1998). It also indicates that proprioceptive cues (when not degraded) exerted an influence on spatial coding by limiting as well as delaying erroneous limb perception induced by visual manipulation.

The purpose of Experiment 3 was to further determine how visual and proprioceptive cues were combined to offer a coherent percept of arm movements when visual and proprioceptive channels convey either congruent or opposite information about arm movement. Kinesthetic illusions were measured in unimodal stimulation conditions (either mirror vision or vibration) and bimodal stimulation conditions (mirror vision and vibration) and predicted scores were computed on the basis of unimodal performance and were compared to the actual performance in bimodal conditions. Results revealed that illusions experienced in conditions of congruent combined signals were larger than those experienced in unimodal conditions (except in Experiment 2 in which a ceiling effect could be put forward) but did not perfectly fit with predictions based on a linear additive integration process. In the opposite bimodal condition, some participants reported kinesthetic illusions in the direction of the simulated stretch (proprioceptively driven) while others reported illusions in the opposite direction (visually driven). Of particular interest, predicted scores computed on the basis of those obtained in each unimodal condition correlated strongly with the kinesthetic illusion experienced in combined bimodal conditions. These results indicate that the different sensory signals are combined, although not in a linear additive way, to offer a coherent percept of arm movement.

As shown by Lackner and Taublieb (1984), interaction between visual and proprioceptive afferents depends on the exact condition of stimulation. In condition of direct vision of the arm in an illuminated environment, vibration illusion is abolished. When the arm was seen alone against a dark background, an illusion of arm displacement occurred. Therefore, the reliability of the visual cues appears of prime importance to determine the way the CNS constructs the kinesthetic percept; when vision provides unequivocal signals of a static arm (as in Experiment 2), not congruent with a simulated stretch, vision is clearly prioritized. This is compatible with multisensory integration processes in which the relative weight of each modality is proportional to its relative reliability (Ernst and Bülthoff, 2004; Bresciani et al., 2008). Accordingly, conditions in which vision "dominates" the percept would represent the extreme side of a continuum of cooperative integration processes in which percepts are obtained by "optimally" combining the contributions of all sensory available inputs (but also efferent signals what is beyond the scope of the present study; see Gandevia et al., 2006; Luu et al., 2011 for a discussion).

Findings suggest however, that two sensory sources are not systematically evaluated in a way that can improve perceptual experience and that the CNS can preferentially base perception on the most reliable or sensitive input available (Fitzpatrick and McCloskey, 1994). Although multimodal perceptual estimates tend to reduce the variance of the estimates (Ernst and Banks, 2002; Gepshtein and Banks, 2003) and enhance the detection of the stimuli (Gielen et al., 1983) it has been shown that the threshold for perception of body displacement was not lower with all sensory inputs (visual, proprioceptive and vestibular inputs) than when only the modality with the greatest sensitivity were available (Fitzpatrick and McCloskey, 1994).

Difference signal calculated from the input coming from the two arms

Izumizaki and colleagues (2010) reported recently that in the absence of vision, passive displacement of one arm alters the speed of the vibration-evoked illusion on the other arm (~30%). They concluded that the movement sensation is not derived exclusively from the vibration-induced signal coming from the reference arm, but represents a difference of signal calculated from the input coming from the two arms. Here, in the absence of mirror vision (*no mirror/no vision* conditions in Experiment 1), occasional slight illusory displacements of the reference arm were reported when proprioceptive cues were degraded. Such illusory displacements did not occur when the left arm was static and, when present, were systematically in the direction of the moving left arm. Therefore, when facing degraded signals of the reference arm as in Experiment 1, the CNS might well integrate signals from the other arm to represent movement perception in the proprioceptively degraded arm.

However, Experiment 2 revealed that in the absence of vision, proprioceptive signals originating from the passively moved left arm (either in a congruent or opposite direction) did not affect the vibratory illusion evoked on the other arm. This result contrasts with the hypothesis that movement sensation represents a difference signal calculated from the input coming from the two arms (Izumizaki et al., 2010). Methodological aspects could account for such differences between studies. Indeed, in Izumizaki's experiment, subjects' arms were moved by the experimenter and at a velocity three times higher (~12 deg/s) than that used here (3.8 deg/s). Therefore, difference in spindle discharge rates between the two arms was far less important in their experiment (moved arm ~12 deg/s – vibration at 70–80 Hz) than in ours (moved arm ~3.8 deg/s – vibration at 90 Hz). If the CNS takes into account afferents originating from the two arms, one might expect to observe a greater effect of the moving arm in Izumizaki's experimental conditions than in ours. In contrast, when proprioceptive afferents of the reference arm is degraded, as in Experiment 1, the signal difference between the two arms would be beneficial to the passively moved one, possibly giving rise to

occasional illusions, as were reported here in the absence of vision.

CONCLUSION

The limited consciousness of proprioceptive afferent signals (Mon-Williams et al., 1997; Fourneret and Jeannerod, 1998) leads to large perceptual biases when visual cues, not congruent with the actual position of the body segment, are provided. Our results indicate, however, that kinesthesia is the product of cooperative integration processes in which the relative contribution of each channel to the final percept depends strongly on the experimental conditions and individual sensorial preferences. The observed changes in the relative contribution of each input across experimental conditions likely reflect reliability-dependent weights.

AUTHOR CONTRIBUTIONS

M.G., S.P., R.N., S.V., A.B. and J.P.B. participated in the conception, design and conduction of the studies. All the authors participated to the interpretation of the data. The original draft was prepared by M.G. but the six authors critically revised the manuscript before approving the final version.

REFERENCES

Bock O, Pipereit K, Mierau A (2007) A method to reversibly degrade proprioceptive feedback in research on human motor control. J Neurosci Methods 160:246–250.

Botvinick M, Cohen J (1998) Rubber hands 'feel' touch that eyes see. Nature 391:756.

Bresciani JP, Dammeier F, Ernst MO (2008) Tri-modal integration of visual, tactile and auditory signals for the perception of sequences of events. Brain Res Bull 75:753–760.

Burke D, Hagbarth KE, Lofstedt L, Wallin BG (1976) The responses of human muscle spindle endings to vibration of non-contracting muscles. J Physiol 261:673–693.

Caudron S, Boy F, Forestier N, Guerraz M (2008) Influence of expectation on postural disturbance evoked by proprioceptive stimulation. Exp Brain Res 184:53–59.

Caudron S, Nougier V, Guerraz M (2010) Postural challenge and adaptation to vibration-induced disturbances. Exp Brain Res 202:935–941.

Ceyte H, Cian C, Zory R, Barraud PA, Roux A, Guerraz M (2007) Effect of Achilles tendon vibration on postural orientation. Neurosci Lett 416:71–75.

Cordo P, Gurfinkel VS, Bevan L, Kerr GK (1995) Proprioceptive consequences of tendon vibration during movement. J Neurophysiol 74:1675–1688.

Dummer T, Picot-Annand A, Neal T, Moore C (2009) Movement and the rubber hand illusion. Perception 38:271–280.

Eklund G (1972) General features of vibration-induced effects on balance. Ups J Med Sci 77:112–124.

Ernst MO, Banks MS (2002) Humans integrate visual and haptic information in a statistically optimal fashion. Nature. 415:429–433.

Ernst MO, Bülthoff HH (2004) Merging the senses into a robust percept. Trends Cogn Sci 8:162–169.

Fourneret P, Jeannerod M (1998) Limited conscious monitoring of motor performance in normal subjects. Neuropsychologia 36:1133–1140.

Fitzpatrick R, McCloskey DL (1994) Proprioceptive, visual and vestibular thresholds for the perception of sway during standing in humans. J Physiol 478:173–186.

Gandevia SC, Smith JL, Crawford M, Proske U, Taylor JL (2006) Motor commands contribute to human position sense. J Physiol 571:703–710.

Gepshtein S, Banks MS (2003) Viewing geometry determines how vision and haptics combine in size perception. Curr Biol 13:483–488.

Gielen SC, Schmidt RA, Van den Heuvel PJ (1983) On the nature of intersensory facilitation of reaction time. Percept Psychophys 34:161–168.

Gilhodes JC, Roll JP, Tardy-Gervet MF (1986) Perceptual and motor effects of agonist–antagonist muscle vibration in man. Exp Brain Res 61:395–402.

Goodwin GM, McCloskey DI, Matthews PB (1972) The contribution of muscle afferents to kinaesthesia shown by vibration induced illusions of movement and by the effects of paralysing joint afferents. Brain 95:705–748.

Gregory JE, Morgan DL, Proske U (1988) Aftereffects in the responses of cat muscle spindles and errors of limb position sense in man. J Neurophysiol 59:1220–1230.

Hall LA, McCloskey DI (1983) Detections of movements imposed on finger, elbow and shoulder joints. J Physiol 335:519–533.

Izumizaki M, Tsuge M, Akai L, Proske U, Homma I (2010) The illusion of changed position and movement from vibrating one arm is altered by vision or movement of the other arm. J Physiol 588:2789–2800.

Kammers MP, de Vignemont F, Verhagen L, Dijkerman HC (2009) The rubber and illusion in action. Neuropsychologia 47:204–211.

Lackner JR, Levine MS (1979) Changes in apparent body orientation and sensory localization induced by vibration of postural muscles: vibratory myesthetic illusions. Aviat Space Environ Med 50:346–354.

Lackner JR, Taublieb AB (1984) Influence of vision on vibration-induced illusions of limb movement. Exp Neurol 85:97–106.

Luu BL, Day BL, Cole JD, Fitzpatrick RC (2011) The fusimotor and reafferent origin of the sense of force and weight. J Physiol 589:3135–3147.

Maravita A, Spence C, Driver J (2003) Multisensory integration and the body schema: close to hand and within reach. Curr Biol 13:R531–R539.

Mon-Williams M, Wann JP, Jenkinson M, Rushton K (1997) Synaesthesia in the normal limb. Proc Biol Sci 264:1007–1010.

Proske U (2006) Kinesthesia: the role of muscle receptors. Muscle Nerve 34:545–558.

Proske U, Morgan DL, Gregory JE (1993) Thixotropy in skeletal muscle and in muscle spindles: a review. Prog Neurobiol 41:705–721.

Ramachandran VS, Hirstein W (1998) The perception of phantom limbs. The D.O. Hebb lecture. Brain 121(Pt. 9):1603–1630.

Ribot E, Roll JP, Gauthier GM (1986) Comparative effects of whole-body vibration on sensorimotor performance achieved with a mini-stick and a macro-stick in force and position control modes. Aviat Space Environ Med 57:792–799.

Roll JP, Albert F, Thyrion C, Ribot-Ciscar E, Bergenheim M, Mattei B (2009) Inducing any virtual two-dimensional movement in humans by applying muscle tendon vibration. J Neurophysiol 101:816–823.

Roll JP, Roll R (1988) From eye to foot. A proprioceptive chain involved in postural control. In: Amblard B et al., editors. Posture and gait. Amsterdam: Elsevier. p. 155–164.

Roll JP, Vedel JP, Ribot E (1989) Alteration of proprioceptive messages induced by tendon vibration in man: a microneurographic study. Exp Brain Res 76:213–222.

Romaiguere P, Vedel JP, Azulay JP, Pagni S (1991) Differential activation of motor units in the wrist extensor muscles during the tonic vibration reflex in man. J Physiol 444:645–667.

Seizova-Cajic T, Azzi R (2011) Conflict with vision diminishes proprioceptive adaptation to muscle vibration. Exp Brain Res 211:169–175.

Teasdale N, Forget R, Bard C, Paillard J, Fleury M, Lamarre Y (1993) The role of proprioceptive information for the production of isometric forces and for handwriting tasks. Acta Psychol (Amst) 82:179–191.

Zampini M, Moro V, Aglioti SM (2004) Illusory movements of the contralesional hand in patients with body image disorders. J Neurol Neurosurg Psychiatry 75:1626–1628.