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# Leg muscle vibration modulates bodily self-consciousness: integration of proprioceptive, visual, and tactile signals

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**Palluel E, Aspell JE, Blanke O.** Leg muscle vibration modulates bodily self-consciousness: integration of proprioceptive, visual, and tactile signals. *J Neurophysiol* 105: 2239–2247, 2011. First published March 2, 2011; doi:10.1152/jn.00744.2010.—Behavioral studies have used visuo-tactile conflicts between a participant's body and a visually presented fake or virtual body to investigate the importance of bodily perception for self-consciousness (bodily self-consciousness). Illusory self-identification with a fake body and changes in tactile processing—modulation of visuo-tactile cross-modal congruency effects (CCEs)—were reported in previous findings. Although proprioceptive signals are deemed important for bodily self-consciousness, their contribution to the representation of the full body has not been studied. Here we investigated whether and how self-identification and tactile processing (CCE magnitude) could be modified by altering proprioceptive signals with 80-Hz vibrations at the legs. Participants made elevation judgments of tactile cues (while ignoring nearby lights) during synchronous and asynchronous stroking of a seen fake body. We found that proprioceptive signals during vibrations altered the magnitude of self-identification and mislocalization of touch (CCE) in a synchrony-dependent fashion: we observed an increase of self-identification and CCE magnitude during asynchronous stroking. In a second control experiment we studied whether proprioceptive signals per se, or those from the lower limbs in particular, were essential for these changes. We applied vibrations at the upper limbs (which provide no information about the position of the participant's body in space) and in this case observed no modulation of bodily self-consciousness or tactile perception. These data link proprioceptive signals from the legs that are conveyed through the dorsal column-medial lemniscal pathway to bodily self-consciousness. We discuss their integration with bodily signals from vision and touch for full-body representations.

body; crossmodal congruency effect; visuotactile; somatosensory

HOW DOES THE HUMAN BRAIN INSTANTIATE self-consciousness? What are the involved brain mechanisms? Extending earlier data from neurological patients (Critchley and Lhermitte 1954; Gerstmann 1942; Head and Holmes 1911; Hécaen and de Ajuriaguerra 1952; Pözl 1925; Schilder 1935), more recent neurological theories stress the importance of bodily processing for the self and self-consciousness (bodily self-consciousness). These theories emphasize the importance of visual, tactile, proprioceptive, motor, vestibular, and interoceptive signals and their multisensory and sensorimotor integration for the representation of body and self (Aspell et al. 2009; Botvinick 2004; Botvinick and Cohen 1998; Craig 2002; Damasio 1998; Gallace and Spence 2008; Lenggenhager et al. 2007;

Lopez et al. 2010; Pavani et al. 2000). Bodily self-consciousness has been studied extensively using the so-called rubber hand illusion (Botvinick and Cohen 1998). In this illusion the participant watches a fake rubber hand on a table being stroked in synchrony with his corresponding (left or right) hidden hand. After about 1 min this visuo-tactile manipulation leads in many participants (Ehrsson et al. 2005; Lloyd 2007) to the illusory feeling that the rubber hand “feels like my own hand” (i.e., illusory hand ownership). This does not happen when the stroking is applied asynchronously, suggesting that visuo-tactile integration is crucial for hand ownership (Botvinick and Cohen 1998). This phenomenological experience of illusory hand ownership is accompanied by a change or recalibration of where participants localize their real stroked hand (Botvinick and Cohen 1998; Ehrsson et al. 2004; Tsakiris and Haggard 2005).

Despite the significance of these findings, these data do not indicate how such sensory integration results in the generation of key subjective states of bodily self-consciousness related to the centerdness of consciousness (such as self-identification, i.e., the experience that my body belongs to me) (Metzinger 2000) that refer to a person's full body. It has recently been shown that such key subjective states can be studied experimentally using video-projection and by inducing various visuo-tactile conflicts for a person's full body (Blanke and Metzinger 2009). Thus several researchers exposed participants to various visuo-tactile conflicts and were able to experimentally manipulate self-identification (Aspell et al. 2009; Blanke and Metzinger 2009; Ehrsson 2007; Lenggenhager et al. 2009; Lenggenhager et al. 2007; Petkova and Ehrsson 2008, 2009; Slater et al. 2010). For example, Lenggenhager et al. (2007) demonstrated that self-identification could be disrupted by multisensory (visuo-tactile) bodily conflicts. In their protocol, the participants viewed their own body from behind (a virtual body seen from the back) via a head-mounted display. They were stroked on the back and saw the stroking on their virtual body either in real time (synchronous condition) or with a short delay added to the video (asynchronous condition). When the felt stroking on the back of the body was synchronous with the seen stroking on the virtual body, participants self-identified with the virtual body. More recently, Aspell et al. (2009) employed cross-modal congruency effects (CCE) (Spence et al. 2004) to make online measurements of such changes in bodily self-consciousness. They found a systematic mislocalization of touch toward the virtual body in conditions leading to illusory self-identification, providing behavioral corroboration for the importance of tactile and visual cues for bodily self-consciousness.

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In addition to visual and tactile signals, proprioception also contributes to bodily self-consciousness. If in the rubber hand illusion the fake hand is in a different anatomical position (Pavani et al. 2000; Petkova and Ehrsson 2009) or at a distance of more than 30 cm from the participant's arm (Lloyd 2007), rubber hand ownership is reported to decrease or disappear. These data show that congruent proprioceptive signals (with respect to visual arm position signals) alter bodily self-consciousness by increasing illusory hand ownership, whereas incongruent proprioceptive signals decrease illusory hand ownership. The influence of proprioception on bodily perception has also been investigated by directly changing proprioceptive signals through the application of vibratory stimuli to different muscles (e.g., Pinocchio illusion) (Lackner 1988). A broad range of illusions induced by muscle vibration and affecting how participants experience the configuration, dimension, and orientation of their body has been reported. Participants may experience a waist-shrinking illusion when the hands are in contact with the waist and when both hand extensors are vibrated (Ehrsson et al. 2005). Proprioceptive conflict induced by vibrations at biceps and triceps muscles also leads to an alteration of body representation (Longo et al. 2009).

Muscle vibrations selectively activate muscle spindle Ia afferent fibres and generate peripheral signals of muscular stretch that are very similar to those perceived during natural movements. Tendon vibration gives rise to a succession of rapid lengthenings that are interpreted centrally as continuous stretches of the muscle. This has been confirmed electrophysiologically using microneurography. It has been shown that each muscle spindle responds to a specific range of movement directions and shows maximum sensitivity to a specific direction (Roll et al. 1989). Such vibration-induced proprioceptive signals project centrally through the dorsal root and the dorsal column-medial lemniscal pathway to brainstem, thalamus, and to primary and secondary somatosensory cortex as well as motor and premotor cortex (Fasold et al. 2008; McGlone et al. 2002; Romaiquere et al. 2003). Muscle spindle group II afferents are less sensitive to such vibrations, and tendon organ Ib afferents are generally insensitive to vibration (Burke et al. 1976; Cordo et al. 1995; Roll and Vedel 1982).

It has been known for several years that ~80-Hz vibrations applied to the ankle muscles can alter proprioceptive signals from the lower limbs and induce illusory perceptions concerning the participant's full body in extrapersonal space (Burke et al. 1976; Kavounoudias et al. 2001; Lackner 1988; Roll and Vedel 1982). For example, stimulation of both tibialis anterior muscles at 80 Hz generates the illusory perception of a backward tilt of the participants' body. When applied bilaterally and to two antagonistic lower leg muscles (i.e., tibialis anterior and triceps surae), 80-Hz vibrations give rise to conflicting proprioceptive signals (due to nonecological simultaneous signals of stretch in tibialis anterior and triceps surae) and thus induce well defined proprioceptive noise that may be associated with small body oscillations (Roll et al. 1989; Teasdale and Simoneau 2001). Microneurographic studies revealed that a constant vibration frequency leads generally to a constant frequency afferent discharge (Roll and Vedel 1982). Collectively, these data show that the representation of the full body in space depends on the integration of congruent visual and tactile signals, as well as their integration with proprioceptive signals (see also Schwabe and Blanke 2008). Whether this also

applies to associated aspects of bodily self-consciousness (i.e., self-identification) is not yet known.

Here we investigated the contribution of proprioceptive cues from the lower limbs to self-identification and the localization of touch (CCE) while simultaneously manipulating visuotactile bodily conflicts. Exploiting the research protocols of Lenggenhager et al. (2007) and Aspell et al. (2009) we determined whether the application of a bilateral and antagonistic vibratory stimuli at the ankles—inducing bilateral proprioceptive noise at the tibialis anterior and triceps surae muscles—would interfere with changes in self-identification and tactile processing. As the study of Aspell et al. (2009) indicated a systematic mislocalization of touch toward the virtual body during this illusion, we hypothesized that muscle vibrations at the ankles—applied in an experimental condition that is characterized by visual dominance over tactile cues (i.e., Lenggenhager et al. 2007; Lopez et al. 2010)—may lead to even stronger reliance on visual signals, resulting in greater visual capture reflected in stronger self-identification and mislocalization of touch (CCEs) during vibration trials. We hypothesized that proprioceptive signals from the upper limbs would not interfere (or interfere less) with self-identification and the CCE.

## MATERIALS AND METHODS

**Participants.** A total of 34 healthy right-handed participants took part in these experiments: 11 (5 males, mean age 23 years) in *study 1*, 12 different participants (5 males, mean age 27 years) in *study 2*, and 11 different participants (6 males, mean age 26 years) in *study 3*. All participants had normal or corrected to normal vision and had no history of neurological or psychiatric conditions.

**Ethics statement.** All participants gave written informed consent and were compensated for their participation. The study protocol was approved by the local ethics research committee La Commission d'Ethique de la Recherche Clinique de la Faculté de Biologie et de Médecine at the University of Lausanne, Switzerland, and was performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

**Materials.** We extended a research protocol that has previously been described in detail (see Materials section in Aspell et al. 2009). Only the major points and the changed aspects of the protocol will be described here. For the crossmodal congruency task, four vibrator-light pairs were attached to the backs of participants (2 at the inner edges of the shoulder and 29 cm below) who viewed their body from behind via a camera and a head-mounted display (HMD). The three-dimensional video camera was placed 2 meters behind them. A white noise sound was played over headphones to mask any noise from the vibrators, and participants wore a cloth hood over their heads to occlude vision of their surroundings. The experiment took place under artificial illumination. Stimulus timings were controlled by a program written with E-Prime software (Psychology Software Tools). Each trial consisted of a light flash [light-emitting diode (LED)] followed 233 ms later (233 ms stimulus onset asynchrony or SoA) by a vibro-tactile stimulus. The active LED and active vibrating motor were varied randomly and independently from trial to trial. There were 100 vibrator-light stimuli per block. After participants had responded with a button press there was a 1-s pause before the succeeding trial started. For each stroking condition, the backs of the participants were stroked about twice per second by the experimenter with a long wooden stick, and participants could view their bodies, the stroking, and the LEDs via the HMD. The stroking began 1 min before the first vibro-tactile stimulus and continued throughout the entire block. In the asynchronous condition, a spatiotemporal conflict was induced by a 400-ms delay so that the seen stroking and the felt

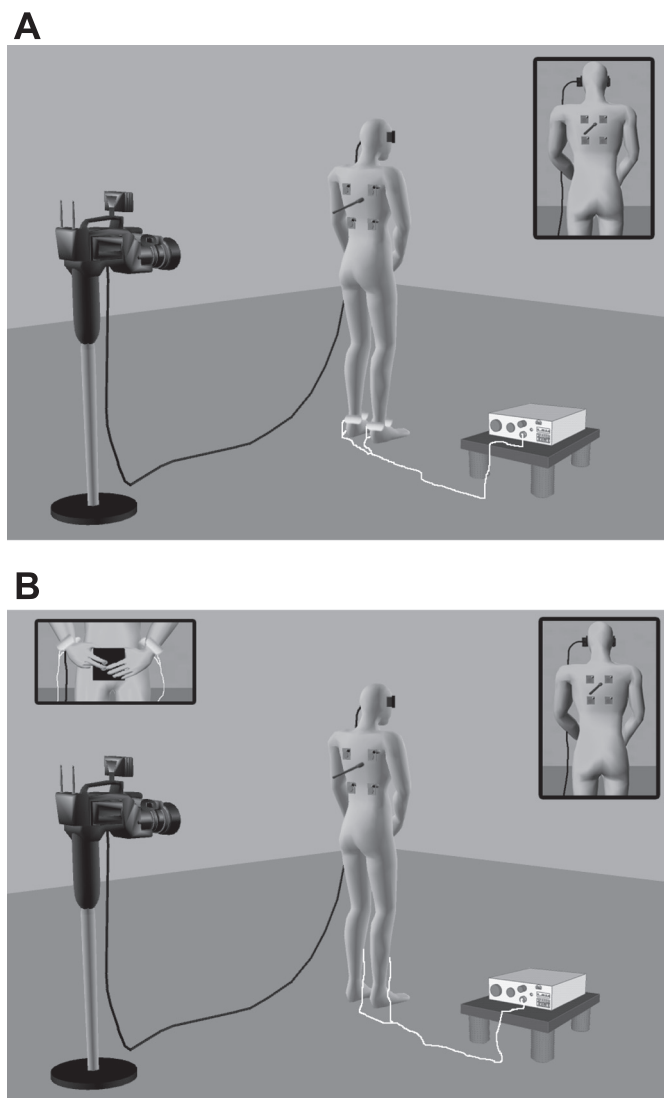


Fig. 1. *A*: experimental setup for *study 1*. Participants were standing with vibrators at the ankles. Four vibration devices were fixed to the participant's back, the upper 2 at the inner edges of the shoulder blades and the lower 2 9 cm below. A video camera filmed the participants from behind. The small inset window represents what the participants viewed via the camera and the head-mounted display (HMD). *B*: experimental setup for *study 2*. Participants were standing with vibrators at the wrists. Four vibration devices were fixed to the participant's back, the upper 2 at the inner edges of the shoulder blades and the lower 2 9 cm below. A video camera filmed the participants from behind. The small right inset window represents what the participants viewed via the camera and the HMD. The left inset shows how the vibrators were fixed to the wrists.

stroking did not occur concurrently. No delay was used in the synchronous condition. An adapted version of the CCE (Spence et al. 2004) task was used by Aspell et al. (2009), who revealed that conditions leading to changes in illusory self-identification (i.e., synchronous stroking) were also associated with changes in tactile processing (CCEs). These authors found that CCEs were larger during synchronous than during asynchronous stroking. Thus the distractor light interfered more with tactile processing during synchronous stroking (associated with changes in illusory self-identification), indicating a systematic mislocalization of touch toward the virtual body.

*Study 1.* In the present experiment, vibrations were continuously applied at the tibial anterior and triceps surae muscles of the ankles (study 1; Fig. 1*A*). The device consisted of two mechanical vibrators (VIB 115; Technoconcept, France) with a biaxial motor and eccentric

load. Each motor was embedded in a plastic cylinder (10 cm long, 3 cm in diameter). The vibrators were attached to the ankles with rubber bands. We chose the vibration frequency of 80 Hz because it induces the optimal proprioceptive perturbation (Burke et al. 1976; Roll and Vedel 1982). The amplitude of the signal was 1 mm (fixed amplitude of the device). The activation and deactivation of the vibrators were computer controlled. According to previous vibration data (Goodwin et al. 1972; Roll and Vedel 1982), such vibrations induce an alteration of proprioceptive inputs in the afferent peripheral nervous system.

*Study 2.* In the control experiment (*study 2*) we applied vibrations at the wrists. Vibrations were also continuously applied, but at the flexor and extensor muscles of the wrists (Fig. 1*B*). We chose this site for control vibrations, because the upper extremity does not interface the body directly with the ground in the present experiments (nor under most everyday conditions). Therefore it does not provide spatial and temporal information about the support surface properties, nor about the variations of pressure under the feet, nor about the position of the body in extrapersonal space (Kavounoudias et al. 2001).

*Study 3: perceived intensity of vibration at wrists and ankles.* We performed an additional study to determine the perceived intensity of 80-Hz vibration at the wrists and at the ankles. We asked the participants to rate the intensity of applied muscle vibrations at the ankles or at the wrists using the same intensity as used during our experiments on the bodily self. They were asked to rate the intensity between 0 (i.e., low) and 10 (i.e., strong) and received 1 min of muscle vibration with eyes open (no HMD).

*Procedures.* The procedure was identical for all conditions. Participants were asked to keep their eyes open and fixate a location in the middle of their backs. Vibrations at the ankles (*study 1*) or at the wrists (control experiment, *study 2*) were applied during the entire block. For the first minute of each condition no vibrotactile or LED stimuli were presented and participants had to wait quietly for the first stimulus. When the CCE trials began, participants had to signal with their right hand, pressing one of two buttons as fast as possible, whether they felt a vibration at the top (an upper device) or at the bottom (a lower device) of their backs (regardless of side), while trying to ignore the light flashes. These responses enabled us to measure reaction times (RTs) to calculate the CCE magnitude (RT incongruent-RT congruent). Illusion strength and several control questions were assessed at the end of each block by a questionnaire (score between -3 and 3; adapted from Lenggenhager et al. 2007; see Table 1). Participants took a short break before the subsequent block started. All participants completed a training session (without stroking) before the experimental conditions. There were 100 trials per block and therefore 25 trials for the same side congruent trials, same side incongruent trials, different side congruent trials, and different side incongruent trials in each study. The order of blocks was counterbalanced across participants in *study 1* and *study 2*.

Table 1. *Self-identification questionnaire*

During the Experiment There Were Times When	
Question Number	Question
1	It seemed as if I was feeling the touch of the stick in the location where I saw the virtual body being touched.
2	It seemed as though the touch I felt was caused by the stick touching the virtual body.
3	I felt as if the virtual body was my body.
4	It felt as if my (real) body was drifting toward the front (toward the virtual body).
5	It seemed as if I might have more than one body.
6	It seemed as if the touch I was feeling came from somewhere between my own body and the virtual body.
7	It appeared (visually) as if the virtual body was drifting backward (toward my body).

In *study 1* (and *study 2*) the four experimental conditions were synchronous stroking without vibrations at the ankles (wrists), asynchronous stroking without vibrations at the ankles (wrists), synchronous stroking with 80-Hz vibrations at the ankles (wrists), and asynchronous stroking with 80-Hz vibrations at the ankles (wrists).

**Statistical analysis.** For CCE analysis, trials with incorrect responses, and trials in which participants failed to respond within 1,500 ms were discarded from the RT analysis (following the method of Spence et al. 2004). As a result an average of 6.1% of trials per subject was discarded. The mean RTs were normally distributed (Kolmogorov-Smirnov test for normality) and were analyzed using two-tailed repeated measures ANOVA. We focus on the RT data rather than inverse efficiency data, as previous authors did (Aspell et al. 2009; Pavani et al. 2000; Spence et al. 2004). The significance ( $\alpha$ ) level used was 0.05.

To analyze the illusion strength we compared the ratings in the illusion questions (questions 1–3) with the ratings of the control questions (questions 4–7) in the four experimental conditions. For statistical analysis, we used an ANOVA with the factors stroking type (asynchronous/synchronous), vibration (without/with), and question type (illusion/control) (i.e., Petkova and Ehrsson 2009; Slater et al. 2008). The significance ( $\alpha$ ) level used was 0.05.

## RESULTS

**Study 1: ankle vibrations.** As shown in Fig. 2, *A* and *B*, we found that 80-Hz vibrations at the ankles modulate questionnaire ratings and CCE magnitude. For the questionnaire data, statistical analysis revealed a three-way interaction of stroking type  $\times$  vibration  $\times$  question type ( $F_{1,10} = 5.99$ ;  $P = 0.034$ ). Planned comparisons indicated that the rating scores for the illusion questions were significantly greater than for the control questions ( $P < 0.01$ ) and importantly that synchronous strok-

ing (but only for trials without vibration) was associated with greater rating scores ( $P < 0.001$ ). Thus self-identification was the same in the synchronous and in the asynchronous conditions with vibrations at the ankles (scores  $\pm$  SE:  $1.4 \pm 0.3$  and  $1.3 \pm 0.3$ , respectively;  $P = 0.99$ ), whereas self-identification without vibrations was only positively rated in the synchronous condition ( $1.6 \pm 0.4$ ) and was significantly greater than in the asynchronous condition ( $-0.3 \pm 0.2$ ;  $P < 0.001$ ). Ratings for the control questions were much lower (range:  $-2.2 \pm 0.3$  and  $-1.9 \pm 0.3$ ). These results extend previous data (Aspell et al. 2009; Ehrsson 2007; Ehrsson et al. 2008; Lenggenhager et al. 2007; Petkova and Ehrsson 2009) by showing greater self-identification during synchronous versus asynchronous stroking, but only when proprioceptive signals are not perturbed. We note that during vibration trials, self-identification was elevated for synchronous as well as asynchronous stroking and did not differ (see Fig. 2*A*). There were also significant main effects of stroking type ( $F_{1,10} = 10.11$ ;  $P = 0.009$ ), vibration ( $F_{1,10} = 9.44$ ;  $P = 0.012$ ), and question type ( $F_{1,10} = 69.16$ ;  $P < 0.001$ ) as well as significant two-way interactions: stroking type  $\times$  vibration ( $F_{1,10} = 25.20$ ;  $P = 0.001$ ), stroking type  $\times$  question type ( $F_{1,10} = 8.85$ ;  $P = 0.014$ ), and vibration  $\times$  question type ( $F_{1,10} = 9.15$ ;  $P = 0.013$ ). There were no other significant main effects or interactions.

Measurements of CCE magnitude extended these questionnaire data. As reported previously, CCE magnitude was modulated by stroking (Aspell et al. 2009), but only without any application of vibrations. During vibrations, we recorded CCEs of normal magnitude during synchronous as well as asynchronous stroking, but importantly the CCE magnitude did not

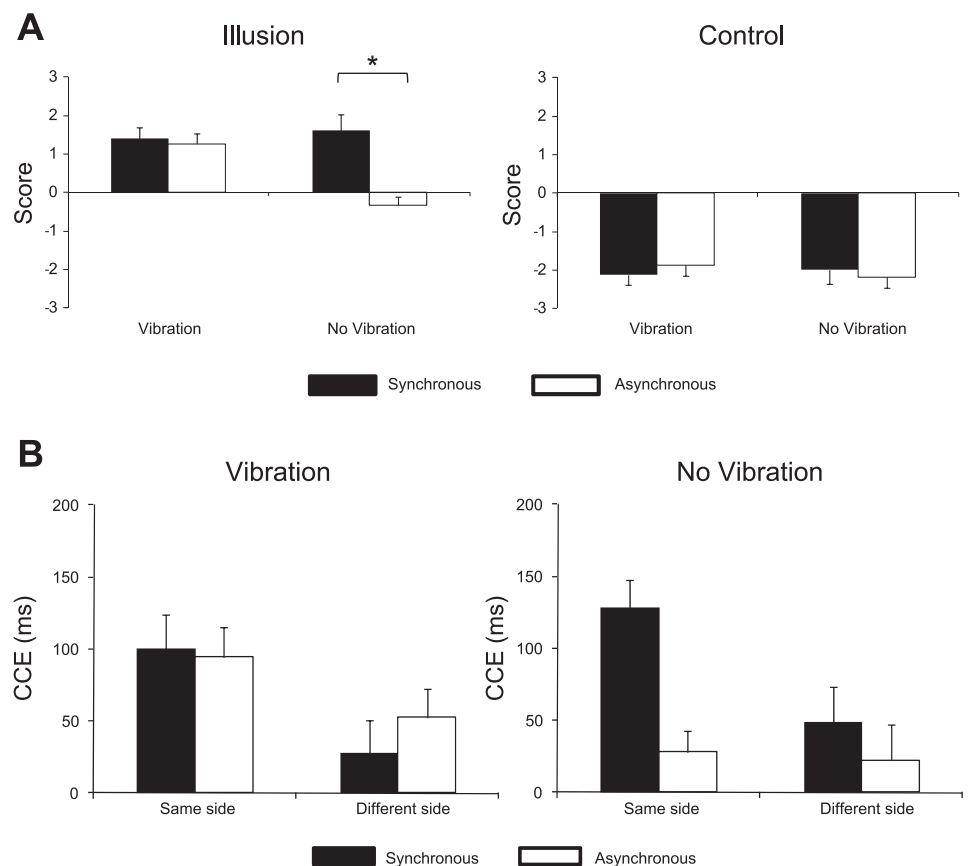


Fig. 2. *A*: questionnaire scores in *study 1*. *B*: cross-modal congruency effects (CCE) in *study 1*—synchronous and asynchronous stroking conditions without vibration and with 80-Hz vibrations at the ankles. Mean congruency effects in reaction time in milliseconds RT (RT in incongruent trials minus RT in congruent trials). Statistical analysis revealed a significant 2-way interaction between stroking type and vibration ( $F_{1,10} = 6.64$ ;  $P = 0.028$ ) and a significant main effect of side ( $F_{1,10} = 4.99$ ;  $P = 0.049$ ), with greater RTs in the same side condition.  $*P < 0.05$ .

differ between synchronous and asynchronous stroking. Statistical analysis revealed a significant two-way interaction between stroking type and vibration ( $F_{1,10} = 6.64$ ;  $P = 0.028$ ) and planned comparisons on the CCE values revealed that the CCE was significantly larger during synchronous than during asynchronous stroking, when no vibrations were applied ( $P < 0.05$ ). CCEs did not significantly differ when vibrations were applied ( $P = 0.86$ ). We note that during vibration trials CCE magnitude was elevated for synchronous as well as asynchronous stroking and was comparable with CCE magnitude during synchronous stroking without vibrations. This suggests that mislocalization of touch with respect to the virtual body (as reflected in CCE magnitude) is affected by proprioceptive signals. CCE analysis also revealed a significant main effect of side ( $F_{1,10} = 4.99$ ;  $P = 0.049$ ), with greater RTs in the same side condition. Concerning error rates, analysis of the main effect of side revealed a trend toward significance ( $F_{1,10} = 4.54$ ;  $P = 0.059$ ). There were no other significant main effects or interactions.

**Study 2: wrist vibrations.** As shown in Fig. 3, A and B, study 2 did not reveal any significant differences in the strength of self-identification or the CCE between conditions with and without vibrations. In addition, both conditions (with vibration and without vibrations) were characterized by higher questionnaire ratings and larger CCE magnitude during synchronous stroking. Critically, for the questionnaire data, statistical analysis did not reveal the three-way interaction of stroking type  $\times$  vibration  $\times$  question type that we found in study 1 ( $F_{1,11} = 0.37$ ;  $P = 0.553$ ) (compare Fig. 2A and Fig. 3A). We only found a significant stroking type  $\times$  question type interaction ( $F_{1,11} = 13.55$ ;  $P = 0.004$ ) characterized by greater rating scores for the illusion than for the control questions

during synchronous stroking, independent of vibration ( $P = 0.001$ ). There were also main effects of stroking type ( $F_{1,11} = 4.81$ ;  $P = 0.005$ ) and question type ( $F_{1,11} = 6.84$ ;  $P = 0.024$ ). No other main effects or interactions were significant.

These questionnaire results were also reflected in a CCE magnitude that was similarly modulated by stroking with and without vibration. Thus there was no two-way interaction between stroking type and vibration ( $F_{1,11} = 0.023$ ;  $P = 0.88$ ) as found in study 1 (compare Fig. 2B and Fig. 3B) showing that the application of vibrations at the wrists did not modulate CCE magnitude. Moreover, neither the main effect nor the interaction involving vibration were significant ( $P < 0.06$ ). Statistical analysis revealed a significant main effect of stroking type ( $F_{1,11} = 9.52$ ;  $P = 0.010$ ), side ( $F_{1,11} = 18.58$ ;  $P = 0.001$ ), and a significant two-way interaction between stroking type and side ( $F_{1,11} = 4.86$ ;  $P = .049$ ). In the vibration and no vibration conditions, the CCE was larger during the synchronous stroking when the light appeared on the same side as the tactile stimulus compared with when it appeared on the different side ( $P = 0.002$ ), whereas the CCE during asynchronous stroking did not differ for same and different side light presentations ( $P = 0.25$ ). There were no other significant main effects or interactions. Neither main effect nor interactions were significant for the error rate. Differences between synchronous visuo-tactile stimulation (during ankle vibration) and synchronous visuo-tactile stimulation (during wrist vibration) (see Figs. 2B and 3B) were not found to be significant and are likely due to the different participants used in the two studies.

**Study 3: perceived intensity of vibration at wrists and ankles.** The data show that participants rated both types of muscle vibrations as having the same intensity ( $6.2 \pm 0.6$  for

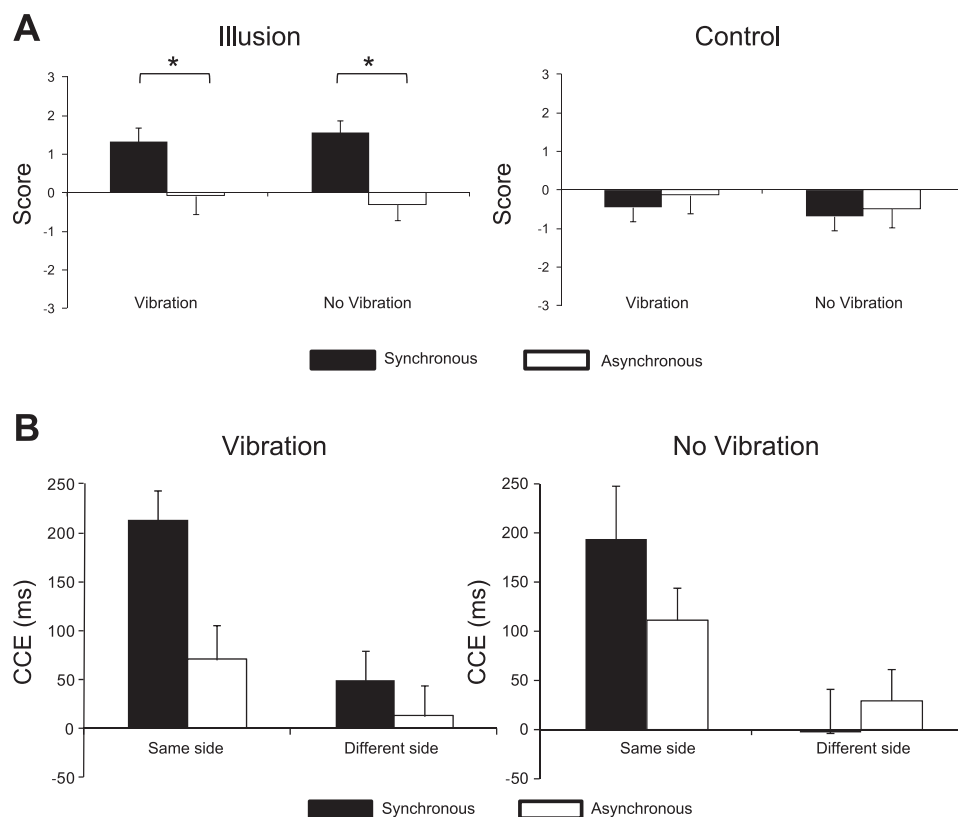


Fig. 3. A: questionnaire scores in study 2. B: CCE in study 2—synchronous and asynchronous stroking conditions without vibration and with 80-Hz vibrations at the wrists. Mean congruency effects in reaction time in milliseconds RT (RT in incongruent trials minus RT in congruent trials). Statistical analysis revealed a significant main effect of stroking type ( $F_{1,11} = 9.52$ ;  $P = 0.010$ ), side ( $F_{1,11} = 18.58$ ;  $P = 0.001$ ), and a significant 2-way interaction between stroking type and side ( $F_{1,11} = 4.86$ ;  $P = 0.049$ ).  $*P < 0.05$ .

the ankles and  $6.4 \pm 0.6$  for the wrists). There was no significant difference in rating strength ( $P = 0.76$ ). Despite this similarity in perceived intensity described in *study 3*, we cannot exclude in the behavioral study that there were differences in afferent signals between the wrist and ankle conditions [we note that this has not yet been studied by microneurographic recordings in humans (Aniss et al. 1990a; Aniss et al. 1990b; Burke and Eklund 1977) or animals (Banks and Stacey 1988)].

## DISCUSSION

The main purpose of this study was to determine whether altered proprioceptive signals from the lower extremities influence the strength of self-identification and the localization of touch (CCE) with respect to a virtual body in extrapersonal space that was stroked synchronously or not with the participant's own body. Our data show that altered proprioceptive signals due to 80-Hz vibrations change the magnitude of self-identification and CCE compared with conditions in which no vibration was applied. Differences in self-identification and CCE magnitude that depend on the synchrony of visuo-tactile stroking, which have been found in previous work (Aspell et al. 2009), were only present without vibrations and, critically, were absent when vibrations were delivered at the ankles. We observed an increase of self-identification and CCE magnitude in the asynchronous conditions in particular. Collectively, these data are compatible with our hypothesis of increased visual capture of touch and the integration of proprioceptive signals from the lower limbs with vision and touch for bodily self-consciousness.

*Proprioceptive mechanisms in visuo-tactile integration.* We found that an alteration of proprioceptive signals from the lower limbs leads to the disappearance of the difference that is usually found between the synchronous and the asynchronous conditions for body parts (Zopf et al. 2010) and for the full body (Aspell et al. 2009). In the present data this difference was observed only without vibrations: in the synchronous stroking condition the CCE was larger and the questionnaire ratings were higher. These results confirm that the synchrony of tactile and visual inputs generally affects the perceived location of touch and self-identification. In *study 1* and when vibrations were applied at the ankles, we found that there was no effect of stroking on self-identification and localization of touch. These data suggest that altered proprioceptive signals from the lower limbs may have affected the integration of the felt and the seen stroking because no difference in self-identification or in the mapping of tactile stimuli (CCE) between the synchronous and asynchronous conditions was observed. In the following we discuss several reasons that may account for this: changes in visuo-tactile integration, attentional mechanisms, and increased uncertainty about body position.

Self-identification and CCE magnitude may have been altered through a modification of the respective weightings of visual and tactile signals in the multisensory integration of these cues. The vibratory signal applied at the ankles deprived participants (at least partly) of the relevant proprioceptive information usually integrated online during body movements. The proprioceptive signals are combined with visual, vestibular, and plantar tactile inputs in the detection and the monitor-

ing of body position (Horak et al. 1990; Palluel et al. 2008b; Palluel et al. 2009; Peterka 2002). The brain continuously integrates and adapts the relative contributions of these different sensory inputs to postural control according to the sensory information available and the behavioral context (i.e., unstable support surface, suppression of vision). Intermodal compensation is generally observed when one or several sensory channels is altered (Carver et al. 2006; Nashner et al. 1982; Peterka 2002). Ankle vibrations may have led to higher reliance on visual information and thus to greater visual capture (see also Lopez et al. 2010). This is consistent with clinical data demonstrating that patients with proprioceptive loss usually rely more on visual information (Balslev et al. 2007; Boucher et al. 1995; Cole 2004; Ingram et al. 2000; Simoneau et al. 1994). Alternatively, proprioceptive stimulation may have interfered with visuo-tactile integration by causing decreased reliance on tactile signals (associated with a similar reliance on visual signals) during the vibration than during the no vibration condition. Visuo-tactile stroking manipulates the integration of spatial as well as temporal visuo-tactile cues. Thus the temporal matching between the seen stroking and the felt stroking may have been affected by vibration at the ankles. Vibrations have been reported to alter the perceived synchrony between tactile and proprioceptive stimuli (Kavounoudias et al. 2008).

In the present study we found that the perturbation of leg proprioception diminished the difference between the degree of visual capture in the synchronous and asynchronous conditions during the full body illusion. This observation of a vibration-induced relative increase in visual capture only in the asynchronous condition was found even though the stimulus onset asynchrony was large (i.e., 233 ms). Why was there no increase in visual capture during the synchronous condition? We propose two mechanisms that may account for this observation. The present vibration effect is specific to the asynchronous condition, perhaps because it rendered this condition less asynchronous through an alteration (increase) of the perceived synchrony between the visual and tactile signals so that signals that are asynchronous are perceived as (more) synchronous (Kavounoudias et al. 2008). Second, the level of visual capture may have already reached its maximum value during the synchronous condition. This is compatible with the reported CCE magnitudes during synchronous and asynchronous stimulation. Similar values of the CCE magnitude and the questionnaire scores have been reported in previous studies (Aspell et al. 2009; Lenggenhager et al. 2007). Ceiling effects for questionnaire scores and CCE may thus explain why they were similar in the no-vibration conditions and the vibration conditions during the synchronous stroking. We also note that although the asynchronous condition is often considered as a control condition, changes of own body perception such as the feeling of numbness have also been reported during the asynchronous stroking of the hand (Longo et al. 2008), suggesting that as in the present study asynchronous stroking is an interesting experimental condition to study bodily self-consciousness.

Do the observed vibration effects relate to potential attentional differences between our experimental conditions, in particular the asynchronous condition? We do not think so, because, first, the absence of a main effect of vibration type on CCE magnitude and error rates in *study 1* (and *study 2*) do not suggest that such major differences were present due to the application of the vibrations. Second, the CCE magnitude and

questionnaire ratings changed selectively, only in the asynchronous conditions when vibrations were applied and only during ankle vibration, not wrist vibration. Finally, if ankle vibrations made the asynchronous condition even more attentionally demanding thereby reducing the resources needed for performing the CCE task and to attend to the visuo-tactile stroking then we should have observed a weakening of the illusion measures. This is not what we observed, finding stronger (larger CCE and increased self-identification) values in the asynchronous condition versus no-vibration trials. These findings render an attentional mechanism not very likely. Finally, subjective reports at the end of testing did not reveal that our participants felt less stable and less concentrated during the asynchronous condition than during the synchronous one. Contrary with the study of Teasdale and Simoneau (2001) in which participants had to respond as fast as possible to an unpredictable auditory stimulus and were simultaneously asked to sway as little as possible, our participants were not asked to focus on their stance when vibrations were applied at both agonists and antagonists muscles of the ankles. Bilateral double vibrations of muscles anterior and posterior to the ankle muscles may have produced uncertainty about the location of the body in space (Horak et al. 1990; Palluel et al. 2008a; Peterka 2002). This may have affected the ability to bind vision and touch as visuo-tactile integration strongly relies on the representation of a common spatial source. Yet we do not think that our results are due to postural instability. Such vibration-induced mechanisms should have impaired visuo-tactile integration in the synchronous and the asynchronous conditions. Yet the CCE and the questionnaire ratings for the synchronous condition do not differ with and without vibrations (Fig. 2, A and B), and the vibration effect was found to be specific to the asynchronous condition. We also note that visual capture was somewhat higher in the wrist vibration condition, showing that visual capture was not stronger during ankle vibration than during wrist vibrations.

*Leg versus arm proprioceptive signals.* The results of study 2 suggest that these effects are specific to the application of vibrations at the lower limbs because CCE magnitude and questionnaire ratings were higher during the synchronous condition with or without vibrations applied at the wrists. Proprioceptive cues from the lower extremity signal foot contact with the ground as well as position in space (including the position of the trunk; Bloem et al. 2000). Proprioceptive signals from the wrists are much less relevant for detecting the position of the body and trunk (Allum et al. 1998). Alteration of lower limb inputs (*study 1*) may have rendered the integration of the multisensory stimuli (i.e., felt vs. seen body, felt vs. seen stroking, and vibrations vs. lights) more difficult than alteration of upper limb inputs. The results of *study 2* reveal that neither vibration per se nor proprioceptive signals per se, but only proprioceptive signals from the lower limbs, are associated with the changes described previously. Proprioceptive signals emanating from the upper extremity (not informative about the position of the participant's body in space) were altered in an identical fashion as those from the legs. However, they do not modulate bodily self-consciousness. This shows that proprioceptive signals from the upper extremity are not relevant for bodily self-consciousness (as tested in the present experiments).

Several studies have demonstrated that proprioceptive information provided by the upper extremities is important for bodily self-consciousness, but only with respect to the perceived position and representation of hands and arms. Our data show that with respect to mechanisms related to the representation of the trunk and the full body, proprioceptive arm signals are not relevant. This suggests that multisensory processes involved in the representation of body parts versus the trunk/full body as well as the related aspects of bodily self-consciousness differ, confirming clinical observations (Blanke and Mohr 2005; Hécaen and de Ajuriaguerra 1952; Heydrich et al. 2010), somatotopic brain representations in parietal cortex (Kaas et al. 1979; Penfield and Jasper 1954) and theoretical considerations (Blanke and Metzinger 2009). Although it is possible to adopt a position in which the arms provide information about the body's position (i.e., hand stand; push-up position), these are not commonly adopted body positions in everyday life. It is thus unlikely that participants would show similar effects on bodily self-consciousness based on arm muscle vibrations in such conditions. Conversely, if the participants were not standing, or positioned in a harness during the illusion, then it is conceivable that ankle vibrations would be less effective in decreasing the illusion and CCE magnitude; yet this was not tested in the present study.

### Conclusion

The present data suggest an implication of proprioceptive signals from the lower limbs in bodily self-consciousness. We suggest that changes in the perceived location of touch and self-identification during 80-Hz vibrations might be due to spatial and/or temporal changes in visuo-tactile integration and a ceiling effect in the synchronous condition. Attention and postural instability are unlikely to explain our results. Such changes were selectively found for vibrations at the ankles with an enhancement of visual capture during the asynchronous condition. Further research is needed to determine whether the modifications recorded with vibrations at the ankles are also observed in patients with polyneuropathy.

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### DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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