# Experimental changes in bodily self-consciousness are tuned to the frequency sensitivity of proprioceptive fibres

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**Several lines of evidence suggest an important implication of proprioceptive signals in bodily self-consciousness. By manipulating proprioceptive signals using muscle vibration, here, we investigated whether such effects depend on the vibration frequency by testing three different vibratory stimuli applied at the lower limbs (20, 40 and 80 Hz). We thus explored whether frequency-specific proprioceptive interference that has been reported in postural or motor tasks will also be found for measures of bodily self-consciousness. Self-identification (questionnaires) and visuotactile integration (asking participants to make tactile discriminations) were quantified during synchronous and asynchronous stroking conditions that are known to manipulate bodily self-consciousness. We found that even though muscle vibrations were applied at the same body location in all cases, 20 Hz vibrations did not alter the magnitude of self-identification and visuotactile integration, whereas 40 and 80 Hz vibrations did. These frequency-specific effects extend earlier vibration effects on motor and postural tasks to bodily self-consciousness. We suggest that the observed changes in bodily self-consciousness are due to altered proprioceptive signals from the lower limbs and that these changes depend on the tuning of Ia fibres to muscle vibration.** ***NeuroReport*** **00:000–000**


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## Introduction

Physiological, neurological and psychological data stress the importance of proprioceptive signals for body perception, and these have also been found to be important for illusory own-body perceptions related to body ownership. Thus, manipulation of proprioceptive cues (by muscle vibrations) has been shown to affect how participants experience the size, orientation and configuration of their body [1–4]. Concerning body ownership, the rubber hand illusion [5,6] and the full-body illusion [7–9] have been extensively used to manipulate bodily aspects of self-consciousness through multisensory conflicts. In these experiments, illusory body ownership, visuotactile integration [8,10,11] and an altered position estimation of a hand or a body are induced if the participant watches a fake rubber hand or a virtual body that is stroked in synchrony with his own hidden hand or body. These changes are absent or weaker if the stroking is not synchronous, a control object is seen or other factors are altered [12,13]. We recently showed that modified proprioceptive signals from the lower limbs (due to muscle vibration) are associated with changes in full-body ownership (or self-identification) as well as changes in visuotactile integration (measured through the crossmodal congruency effect, CCE). Thus, when 80 Hz vibrations were applied bilaterally at the tibial anterior and the triceps surae muscles, Palluel *et al.* [14] reported no stroking-dependent changes in illusory body ownership and visuotactile integration as measured by the CCE (which were observed in the absence of the application of muscle vibrations). These vibration-induced changes were absent when the upper limbs (wrists) were vibrated with the same intensity and frequency, indicating – compatible with clinical data [15] – that bodily self-consciousness depends, in addition to tactile cues from the back and visual own body signals, on proprioceptive cues from the legs, but not the arms.

The proprioceptive effects of muscle vibration show frequency tuning, with the largest sensitivity for ~80 Hz vibrations (applied to the ankle muscles) and progressively lessened responses to lower vibration frequencies [1,4,16]. Here, we exploited this sensitivity and tested whether experimentally induced changes in bodily self-consciousness (self-identification and visuotactile integration) would show comparable frequency tuning. For this, we investigated the effects of three different vibratory frequencies (20, 40 and 80 Hz) that were applied to the lower limbs. We predicted that effects should be maximal at 80 Hz vibrations and that 40 Hz vibrations and especially 20 Hz vibrations would have no (or significantly less) effects on bodily self-consciousness. Alternatively, the previously observed changes in bodily self-consciousness could have been simply due to the additional application of a somatosensory stimulus to the leg (in addition to the tactile back cues); in this case, we would expect to find similar effects across all tested muscle vibration frequencies.

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## Materials and methods

### Participants

A total of 36 healthy right-handed participants took part in three experiments: 11 (20 Hz frequency group: six men, mean age 23 years) in experiment 1, 14 different participants (40 Hz frequency group: seven men, mean age 22 years) in experiment 2 and 11 different participants (80 Hz frequency group: five men, mean age 23 years) in experiment 3. The participants from experiment 3 are the same as those already reported in Palluel *et al.* [14]. All participants had normal or corrected to normal vision and had no history of neurological or psychiatric conditions. 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 used a research protocol that has previously been used [8,14]. For the crossmodal congruency task, four vibrator–light pairs were attached to the backs of participants, who viewed their body from behind by a camera and a head-mounted display. The three-dimensional video camera was placed 2 m behind them. 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 (400 ms) added to the video (asynchronous condition). In the present experiments, vibrations were continuously applied at the tibial anterior and triceps surae muscles of the ankles at 20 Hz (experiment 1), 40 Hz (experiment 2) or 80 Hz (experiment 3). The device consisted of two mechanical vibrators (VIB 115; TechnoConcept, Mane, France). A no-vibration session was also included for all groups.

### Procedures

The procedure was identical for all conditions (for details, see Palluel *et al.* [14]). Participants were asked to keep their eyes open and fixate a location in the middle of their backs. Vibrations at the ankles 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 or at the bottom of their backs (regardless of side), while trying to ignore the light flashes. These responses enabled us to measure the 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.* [7]). All participants completed a training session (without stroking) before the experimental conditions. The order of blocks was counterbalanced across participants. In each experiment, we used the following four conditions: synchronous stroking without vibrations, asynchronous stroking without vibrations, synchronous stroking with vibrations and asynchronous stroking with vibrations.

### Statistical analysis

For CCE analysis, trials with incorrect responses and trials in which participants failed to respond within 1500 ms were excluded from the RT analysis (following the method of Spence *et al.* [13]). The mean RTs were normally distributed (Kolmogorov–Smirnov test for normality) and were analysed using two-tailed repeated-measures analysis of variance with the between-participant factor frequency (20/40/80 Hz) and the within-participant factors stroking type (asynchronous/synchronous), vibration (without/with) and side (same/different).

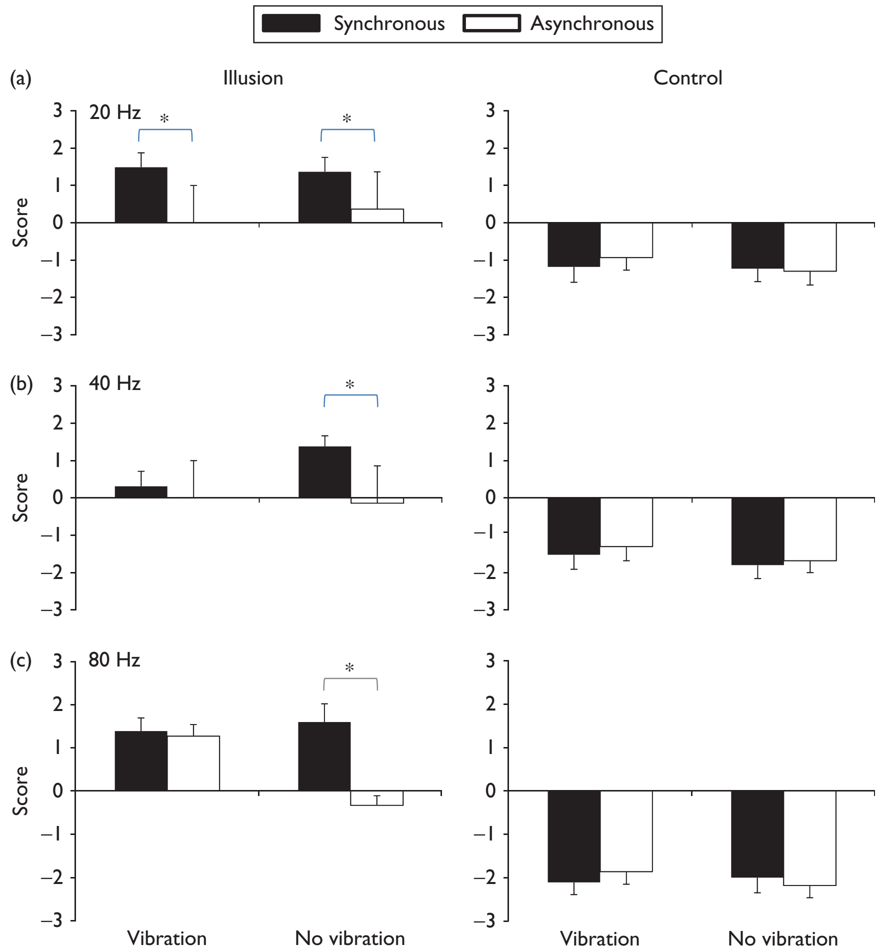
To analyse the illusion strength, we compared the ratings in the illusion questions (questions 1–3) with the ratings of the control questions (questions 4–7) in the four experimental conditions. For statistical analysis, we used an analysis of variance with the between-participant factor frequency (20/40/80 Hz) and the within-participant factors stroking type (asynchronous/synchronous), vibration (without/with) and question type (illusion/control) (i.e. Palluel *et al.* [14] and Slater *et al.* [17]). The significance ($\alpha$) level used was 0.05.

## Results

As shown in Figs 1 and 2, 20 Hz did not reveal any significant differences in the strength of self-identification or CCE magnitude between conditions with and without vibrations. Both conditions (with vibration; without vibrations) were characterized by higher questionnaire ratings and larger CCE magnitude during synchronous stroking as reported in classical work on this topic [8]. At 40 and 80 Hz muscle vibrations, we found that self-identification and CCE magnitude did not differ between synchronous and asynchronous conditions with vibrations, whereas they were significantly greater in the synchronous than in the asynchronous conditions without any vibrations.

For the questionnaire data, statistical analysis revealed a significant four-way interaction between frequency, stroking type, vibration and question type ($F_{2,32} = 4.21$, $P = 0.024$). Planned comparisons indicated that the rating scores for the illusion questions were significantly greater than those for the control questions for the three tested frequencies ($P < 0.01$). Importantly, for the illusion questions, synchronous stroking was associated with greater rating scores than asynchronous stroking only in the 20 Hz group with and without vibrations (with vibrations: $P < 0.001$; without vibrations: $P = 0.007$). This was different for the 40 and 80 Hz conditions, where only

**Fig. 1**

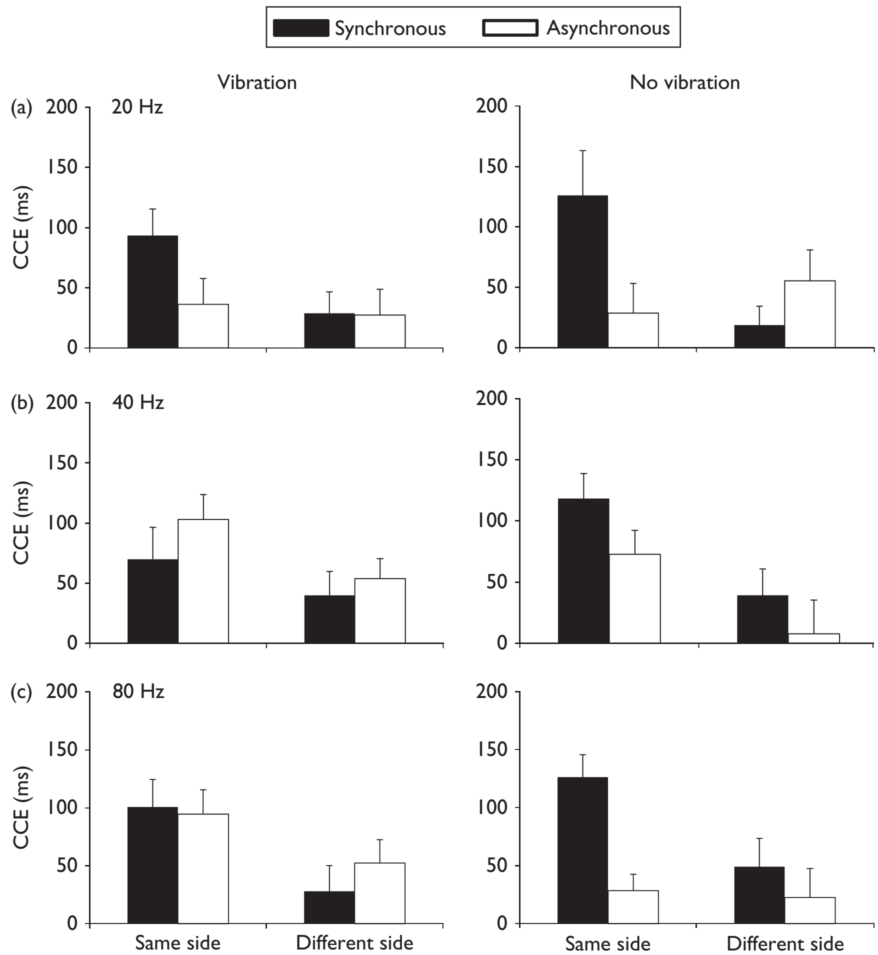



Questionnaire scores in the (a) 20 Hz group, (b) 40 Hz group and (c) 80 Hz group. *$P < 0.05$.

conditions without vibration were associated with higher scores for the synchronous versus the asynchronous condition (40 Hz: $P < 0.001$; 80 Hz: $P < 0.001$). Other significant effects were a main effect of stroking type ($F_{1,32} = 21.46$, $P < 0.001$), question type ($F_{1,32} = 84.88$, $P < 0.001$) and a significant two-way interaction between stroking type and questionnaire ($F_{1,32} = 28.06$, $P < 0.001$), stroking type and vibration ($F_{1,32} = 12.83$, $P = 0.001$). We also found a three-way interaction between frequency, stroking type, vibration ($F_{1,32} = 4.55$, $P = 0.018$) and between frequency, vibration and question type ($F_{1,32} = 5.36$, $P = 0.01$). No other main effects or interactions were significant. Planned comparisons indicated that there was always a significant difference between synchronous and asynchronous stroking without vibrations for the three frequencies tested and only with vibrations in the 20 Hz group. Scores were always higher for the illusion than the control questions whatever the frequency ($P < 0.05$).

These questionnaire results were also reflected by CCE magnitude that was similarly modulated by stroking in a vibration frequency-dependent manner and thus affected by 20 Hz, but not by 40 and 80 Hz frequencies. Crucially, statistical analysis revealed a significant three-way interaction between frequency, stroking type and vibration ($F_{2,32} = 3.37$, $P = 0.047$). Planned comparisons showed that – as expected and reported previously – CCE values were significantly higher in the synchronous than in the asynchronous condition for all frequency conditions when no vibrations were applied (20 Hz: $P = 0.048$; 40 Hz: $P = 0.017$; 80 Hz: $P = 0.029$). Crucially, larger CCEs during synchronous versus asynchronous stroking depended on the frequency applied and were only significant for 20 Hz vibrations ($P = 0.009$; at 40 Hz: $P = 0.13$; at 80 Hz: $P = 0.61$). Statistical analysis also revealed a significant three-way interaction between frequency, stroking type and side ($F_{2,32} = 4.66$, $P = 0.017$). Planned comparisons indicated that the CCE values were higher for the same side than for the different sides during the synchronous stroking for all frequencies (all $P < 0.03$). No such differences were found for the asynchronous conditions at 20 Hz ($P = 0.99$) and 80 Hz ($P = 0.95$), but for 40 Hz, this

**Fig. 2**




Crossmodal congruency effect (CCE) in the (a) 20 Hz group, (b) 40 Hz group and (c) 80 Hz group – synchronous and asynchronous stroking conditions without vibration and with 20, 40 and 80 Hz vibrations at the ankles. Mean congruency effects in reaction time in milliseconds (RT in incongruent trials – RT in congruent trials).

difference was significant ($P = 0.027$). Statistical analysis also revealed a significant main effect of stroking type, with greater CCEs for synchronous conditions ($F_{1,32} = 5.15$, $P = 0.03$) and side ($F_{1,32} = 27.21$, $P < 0.001$), with greater CCEs in the same side condition. There were also two-way interactions between stroking type and vibration ($F_{1,32} = 5.3$, $P = 028$) and between stroking type and side ($F_{1,32} = 9.63$, $P = 0.004$). In terms of error rates, there was only a main effect of side ($F_{1,32} = 22.70$, $P < 0.001$). No other effects were significant.

## Discussion

The main purpose of this study was to further study the importance of proprioceptive signals for bodily self-consciousness. For this, we tested vibration frequencies that do not or only mildly alter the spontaneous firing of peripheral Ia fibres (20 Hz) with those that moderately (40 Hz) and strongly (80 Hz) alter the spontaneous firing rate of peripheral Ia fibres [18]. As predicted, we found that the changes in bodily self-consciousness observed during muscle vibrations applied at the ankles, which had been observed for 80 Hz vibrations [14], were not observed for 20 Hz, but were observed for 40 Hz vibrations. The present data show that even though muscle vibrations were applied at the same body location, 20 Hz vibrations did not alter the magnitude of subjective self-identification ratings and repeated measures of visuotactile integration, whereas 40 and 80 Hz vibrations did. Differences in self-identification and CCE magnitude that depend on the synchrony of visuotactile stroking and that are usually observed without vibrations are only present at the lowest frequency of vibrations (20 Hz) and are indistinguishable from conditions without any muscle vibrations. On the basis of the tuning of Ia fibres to muscle vibration, these data highlight the importance of proprioceptive signals for bodily self-consciousness.

Ia muscle afferents have a spectrum of sensitivities to tendon vibration. Most primary endings fire in phase with a vibratory stimulus within the frequency range of 20–100 Hz and some of them may fire in a subharmonic manner at higher frequencies [16,18]. Moreover, stimulation of both tibialis anterior muscles at 80 Hz may generate the illusory perception of a backward tilt of the participants' body. The frequency of such vibrations has been shown to modulate the magnitude of the muscular and tilt responses [16,19]. Illusory movements have also been reported to be nearly absent at low frequencies of 10 and 20 Hz and to progressively increase until 80 Hz. Further vibration increases from 80 to 120 Hz lead again to decreases in illusory movement sensations [4,16]. Accordingly, it has been argued that these effects are caused by the frequency-related changes in the firing rate of Ia afferent fibres due to muscle vibrations. In terms of body movements, similar findings have been observed by Kavounoudias *et al.* [4]. These authors observed that 20, 40, 60–80 Hz vibration of the two tibialis anterior muscles all produced forward tilts of the body (n.b. we stimulated the anterior and the posterior muscles) that were associated with a constant increase in postural displacements between 20 and 80 Hz.

Our data suggest that bodily self-consciousness – evaluated through self-identification and CCE magnitude – was modulated by vibrations at the ankles, but depended on the frequency of the stimulation. Several studies have clearly demonstrated that self-identification and CCEs are powerful measures for bodily self-consciousness [8,10]. Here, we argue that 40 and 80 Hz vibrations interfered with bodily self-consciousness by interfering with the integration of the felt and the seen stroking. We did not observe such changes at 20 Hz because 20 Hz vibrations do not modulate (or result in less modulation of) the spontaneous discharge in peripheral Ia proprioceptive afferents. Transient reweighting of the sensory signals (i.e. visual, proprioceptive, plantar tactile, vestibular) is involved in the detection and monitoring of body position [20,21]. Only a few microneurographic studies on human muscle-spindle activity of the ankle muscles have been conducted during normal standing [22,23]. However, spontaneous activity of muscle spindles during standing approximates only a few Hz [16,19,22], with 20 Hz being very close to the spontaneous activity recorded in muscle spindles while standing. We suggest that the spontaneous firing rates of Ia muscle afferents during the 20 Hz vibrations trials of the present study protocol are thus similar to those without any vibration in all three participant groups, compatible with the unchanged magnitude of visuotactile integration and illusion strength at 20 Hz. This frequency-dependent modulation also shows that the changes in bodily self-consciousness are not simply due to the additional application of proprioceptive stimuli but that these changes are crucially related to the frequency of the stimulation and thus to the proprioceptive lower limb signal.

Our data suggest that 40 Hz muscle vibrations (which are less optimal in inducing illusory body movement and in altering the spontaneous firing rate of Ia muscle afferents) also interfere with self-identification and visuotactile integration. Thus, we find – as reported previously for 80 Hz vibrations [14] – that 40 Hz vibrations nullify the effects of stroking synchrony on self-identification and CCE magnitude. Vibration effects on motor tasks (such as reaching) showed that 40–60 Hz vibrations are also associated with altered perception of limb movement [24]. Our data suggest that 40 and 80 Hz vibrations affected bodily self-consciousness in a similar manner and resulted in higher reliance on visual information and therefore in greater visual capture (see also Lopez *et al.* [6] and Palluel *et al.* [14]). This is in line with clinical observations reporting that patients with proprioceptive alteration or loss generally rely more on visual inputs [25]. An interfering effect resulting in a decreased reliance on tactile signals and a similar reliance on visual signals may be an alternative explanation [6,14].

## Conclusion

Compatible with earlier muscle vibration effects on motor and postural tasks, here, we show that measures of bodily self-consciousness are affected in a similar frequency-dependent manner. Our data suggest that the altered proprioceptive signals modulate visuotactile integration and bodily self-consciousness. These data are specific for the lower limbs [14] and depend on the tuning of Ia fibres, revealing the importance of such proprioceptive signals for bodily self-consciousness.

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Author contributions: E.P., J.E.A. and O.B. conceived and designed the experiment. E.P. and T.L. performed the experiments. E.P. and T.L. analysed the data. E.P., J.E.A. and T.L. contributed reagents, materials and analysis tools. E.P., J.E.A. and O.B. wrote the paper.

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### Conflicts of interest

There are no conflicts of interest.

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