The role of vibration in tactile speed perception

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ABSTRACT

The relative motion between the surface of an object and our fingers produces patterns of skin deformation like stretch, indentation, and vibrations. Here, we hypothesized that motion-induced vibrations are combined with other tactile cues for the discrimination of tactile speed. Specifically, we hypothesized that vibrations provide a critical cue to tactile speed on surfaces lacking individually detectable features like dots or ridges. Thus, masking vibrations unrelated to slip motion should impair the discriminability of tactile speed, and the effect should be surface-dependent. To test this hypothesis, we measured the precision of participants in discriminating the speed of moving surfaces having either a fine or a ridged texture, while adding masking vibratory noise in the working range of the fast-adapting afferents. Vibratory noise significantly reduced the precision of speed discrimination, and the effect was much stronger on the fine-textured than on the ridged surface. On both surfaces, masking vibrations at intermediate frequencies of 64 Hz (65 µm peak-to-peak amplitude) and 128 Hz (10 µm) had the strongest effect, followed by high frequency vibrations of 256 Hz (1 µm) and low frequency vibrations of 32 Hz (50 µm and 25 µm). These results are consistent with our hypothesis that slip-induced vibrations concur to the discrimination of tactile speed.

KEYWORDS

Tactile speed perception, speed discrimination, vibrotactile masking, mechanoreceptive afferents, psychophysics
INTRODUCTION

The relative motion between the surface of an object and our fingers produces patterns of mechanical deformation of the skin like stretch, indentation, and vibrations. Motion-related vibrations occur not only in the direct contact area but also propagate to the hand and the forearm (Delhaye et al. 2012). The vibration frequency spectrum depends on both the texture of the surface and the speed of the scanning movement (Adams et al. 2012; Bensmaia and Hollins 2003; Delhaye et al. 2012; Fagiani et al. 2010). For example, increasing the scanning speed produces an increase in both the frequency and the amplitude of vibrations (Fagiani et al. 2010).

Vibration and motion speed signals are not only tightly coupled in the physical domain but also produce an overlap in the neurophysiological responses of cutaneous mechanoreceptive afferents (Gardner and Kandel 2000). That is, vibrations and other tactile motion cues, such as the rate of skin stretch and indentation, recruit the same type of afferent fibers. Vibrations elicit responses particularly in the fast adapting afferents (Johansson et al. 1982), which are also highly sensitive to slip motion (Essick and Edin 1995). Low frequency vibrations are predominantly signaled by fast-adapting type I (RA) afferents, which are most sensitive at about 30 Hz, whereas high frequency vibrations are predominantly signaled by fast-adapting type II (PC) afferents, which are most sensitive at about 250 Hz (Johansson et al. 1982; Mountcastle et al. 1972; Talbot et al. 1968). The response of these afferents to vibratory stimuli seems to be consistent with their response to the speed of a patterned moving stimulus when both stimuli are coded with respect to their temporal frequency (Goodwin et al. 1989). Accordingly, PC afferents were found to respond preferentially to tactile motion of fine-textured surfaces, whereas RA afferents were most sensitive to motion of surfaces with individually detectable features, such as dots or ridges (Srinivasan et al. 2010).
In addition to fast adapting afferents, slowly adapting type I (SA-I) afferents respond preferentially to vibrations in the lower frequency range (Johansson et al. 1982). These afferents are generally less sensitive to motion than RA afferents (Freeman and Johnson 1982; Johansson and Vallbo 1979; LaMotte and Whitehouse 1986) and rather insensitive to changes in motion speed (Goodwin and Morely 1987; Lamb 1983).

When scanning an object, the somatosensory system faces the challenging task of decoding speed information from these multidimensional and correlated signals (Dépeault et al. 2013; Pei and Bensmaia 2014). Skin vibrations, whose frequency spectrum depends on both surface texture and scanning speed, may provide a cue for the observer to discriminate both features of the tactile stimulus. Indeed, vibrations were found to be critical for discriminating fine textures directly with the bare fingertip (Delhaye et al. 2012; Hollins et al. 2001; Weber et al. 2013) or indirectly via a tool (Klatzky and Lederman 1999). Their role in discriminating tactile speed, however, remains to be elucidated.

We hypothesized that motion-induced vibrations provide an important cue for the discrimination of tactile speed, particularly on surfaces lacking individually detectable features such as dots or ridges. Hence, masking vibratory noise should impair speed discrimination. To test this hypothesis, we measured the precision of participants in discriminating tactile speeds of a moving fine-textured surface (Experiment 1a and Experiment 1b) and of a moving ridged surface (Experiment 2). To reduce the reliability of the vibration cue, we masked the “natural” vibrations produced by the slip motion of the surface by simultaneously presenting vibratory noise in the working range of the two fast-adapting afferent types. The effect of masking vibrations was expected to be stronger on the fine-textured surface, because other motion cues are less pronounced on this surface.
MATERIALS AND METHODS

Participants

Overall, we tested 23 naïve participants plus author CJD (18-55 years old, median age 23; 12/24 females; all right-handed) in the two experiments. The sample size was equal to \( N = 10 \) participants in Experiment 1a and Experiment 2, and \( N = 9 \) participants in Experiment 1b. Four participants took part in more than one experiment. The testing procedures were approved by the ethics committee of Bielefeld University, in accordance with the guidelines of the Declaration of Helsinki for research involving human subjects. Informed written consent was obtained from all participants involved in the study.

Apparatus

Motion devices: In Experiment 1, we used the device described in Fritschi et al. (2006) and Moscatelli et al. (2014) to deliver the motion stimuli. The device consisted of a rotating, sandblasted billiard ball (diameter: 6 cm) having a fine-textured surface lacking individually detectable features such as dots or ridges. The fingertip contacted the ball through a small circular aperture (diameter: 2 cm) in the metal cover plate of the device (Fig. 1A). In Experiment 2, the motion device consisted of a ridged rubber belt connected to two rotating cylinders and supported by a metal plate in between (Fig. 1B). The ridges of the belt were oriented perpendicularly to its long axis and, unlike the ball, constituted clearly detectable surface features (ridge width: 1 mm, ridge height: 1 mm, distance between ridges: 1 mm). Each of the two devices was actuated by a servomotor (Faulhaber DC-micromotor 2232UO24 combined with MCDC2805 Motion Controller; maximum slip speed: 39.3 cm/s). The motor was accessed via a serial RS-232 connection from the operating computer and
controlled by a custom written Matlab script (The MathWorks Inc., Natick, MA, USA). The rotational speed was controlled via an encoder in the driver module.

The slip motion of each of the two surfaces induced characteristic vibrations on the fingertip that we analyzed (Fig. 2) in order to provide comparative information about the two surface textures. Vibrations produced by the rotating ball (*Experiment 1*) increased in amplitude with increasing speed, but lacked a dominant frequency (Fig. 2A). To quantify the vibration amplitude, we computed the root mean square of the time series shown in Fig. 2 (acceleration signal). The peak-to-peak amplitude of vibration ranged from 0.07 to 0.29 cm/s² within the range of the tested slip motion speed. The moving belt (*Experiment 2*) induced vibrations in the fingertip that increased in amplitude with increasing speed, with dominant frequencies occurring at multiples of the spatial period of the belt (Fig. 2B). The peak-to-peak amplitude of vibration ranged from 0.10 - 1.52 cm/s² within the range of the tested slip motion speed. Thus, the amplitude ratio of the vibration generated by the two surfaces (ball:belt) ranged from 0.7 (slowest slip speed) to 0.2 (fastest slip speed).

**Vibration device:** The vibration device (BR-25, Monacor International, Bremen, Germany) delivered sinusoidal vibrations of different frequencies and amplitudes to excite predominantly one or multiple afferent types (below). Vibration amplitudes and frequencies were inferred from accelerometer recordings (ADXL335, Analog Devices, Norwood, MA, USA). We processed the recorded acceleration signal with a fast Fourier transform and estimated the amplitude of displacement by integrating the transformed signal twice, assuming a simple harmonic motion. Prior to experimentation, we attached the accelerometer directly to the pulp of the distal phalanx and confirmed that vibrations were transmitted from the device to the skin.
Stimulus and Procedure

Motion Stimulus: In all experiments, tactile motion stimuli were delivered to the tip of the right index finger (Fig. 1, A and B), which has the highest density of mechanoreceptive afferents (Vallbo and Johansson 1984). The direction of motion of the surface was proximal to distal relative to the finger. Each motion stimulus consisted of a trapezoidal motion profile with a steep acceleration/deceleration ($\pm 180$ cm/s$^2$). Using the motion encoder, we confirmed that target speeds (see Experimental Procedure) were always reached at the plateau. Since the acceleration/deceleration was kept constant across trials, the shear force on the fingertip was not informative about the motion speed. Instead, the duration of the acceleration/deceleration phase (6 - 88 ms) could in principle provide a cue to motion speed, if participants were able to discriminate the acceleration phase from the speed plateau. However, this additional cue would not account for a potential effect of masking vibrations because the acceleration/deceleration did not vary across experimental conditions.

Vibratory Stimulus: Vibrations were delivered to the ventral side of the distal phalanx of the right index finger, few millimeters proximal to the skin area contacting the moving surface (Fig. 1, A and B). The pulp of the distal phalanx rested on a metal rod (diameter: 1 mm), which was rigidly attached to the vibration device above the finger. In different experimental conditions, the device delivered vibrations of 32 Hz, 64 Hz, 128 Hz, and 256 Hz. Peak-to-peak amplitudes were 50 $\mu$m, 65 $\mu$m, 10 $\mu$m, and 1 $\mu$m, respectively. In the control condition, the vibration device was in place but produced no vibrations. Amplitudes and frequencies of vibration were chosen according to the tuning function of the different afferent fiber types (Fig. 1C). Specifically, vibration amplitudes and frequencies were designed to predominantly
target RA afferents (32 Hz), RA and PC afferents (64 Hz), or predominantly PC afferents (128 Hz and 256 Hz) (Johansson et al. 1982; Mountcastle et al. 1972). As illustrated in Figure 1C, the tuning curves of RA and PC afferents largely overlap in the lower frequency range. To further address their contribution to the participants’ response, we additionally tested—on the fine-textured surface only—the effect of small-amplitude (25 µm), low frequency (32 Hz) masking vibrations (Experiment 1b). Prior to each experiment, participants confirmed that they could clearly detect all masking vibrations.

Experimental Procedure: Participants were comfortably seated in front of the setup table, with the right forearm and hand supported on a padded board. They kept the right finger stationary during the entire experimental session, in contact with the motion device. An opaque plane between the right and the left arm occluded the vision of the motion device. In addition, room light was limited to the indirect light of a computer screen displaying experimental instructions. Pink auditory noise was delivered to the participants via earphones throughout each experimental session in order to mask external sounds from the motion and the vibration device.

Using a forced-choice procedure, we assessed the ability of participants to discriminate the speed of the fine-textured and ridged surface under different vibratory noise conditions. In each test trial, we successively presented two motion stimuli (the standard and the comparison, in pseudorandom order), and simultaneously applied the masking vibrations (Fig. 1D). Participants then reported whether they had perceived the second motion stimulus to be faster or slower than the first one by pressing either the up (faster) or down (slower) button on a standard keyboard with their left hand. Each motion stimulus lasted 1 s with an inter stimulus interval (ISI) of 1 s. The vibration stimulus started 0.1 s before the motion
stimulus and ended 0.1 s after the motion stopped. The speed of the standard stimulus was always 8.5 cm/s. In each vibratory noise condition, the standard was presented first in 50% of the trials. The speed of the comparison stimulus was pseudorandomly chosen among seven speeds: 1, 3.5, 6, 8.5, 11, 13.5, or 16 cm/s. Tested speeds were within the recommended maximum speed of the servomotor (39.3 cm/s). In Experiment 1a and 2, each comparison stimulus was presented 20 times per vibratory noise condition, resulting in a total of 700 trials per experiment. In Experiment 1b, we presented each comparison stimulus 40 times per condition, resulting in a total of 560 trials. Participants completed all trials within 1 h. To keep concentration levels high, participants took a 5-minute break after completion of half of the trials.

Data analysis

We modeled the responses of all participants by means of a Generalized Linear Mixed Model (GLMM). GLMMs are conditional models designed for the analysis of clustered data (Agresti 2002; Moscatelli et al. 2012). In our case, a cluster is the collection of repeated responses from a given participant. In the GLMM framework, the observed response is modeled as a linear combination of the systematic effect of the experimental variables (the surface speed and the vibratory noise), the random variability between participants, and the residual error within participants (the latter arising from the binomial process in the forced-choice procedure). The GLMM accounts separately for the experimental effects and the variability between participants by means of random- and fixed-effect parameters, respectively (Moscatelli et al. 2012). By combining both parameters, we obtained the model predictions at the level of single participants, which are highly valuable for evaluating the model fit to the data (Fig. 3A, 4A, and 5A).
In Experiment 1a, random-effect parameters were denoted with the lowercase letter $u_{i,j}$ and fixed-effect parameters with the Greek letter $\theta_{1,\ldots,9}$. The model equation was the following:

$$\Phi^{-1}[P(Y_{ij} = 1| u_{i})] = (\theta_0 + u_{0i}) + (\theta_1 + u_{1i})s_{ij} + \theta_2 C_{32ij} + \theta_3 (s_{ij} C_{32ij}) + \theta_4 C_{64ij} + \theta_5 (s_{ij} C_{64ij}) + \theta_6 C_{128ij} + \theta_7 (s_{ij} C_{128ij}) + \theta_8 C_{256ij} + \theta_9 (s_{ij} C_{256ij}).$$

This model was chosen among several nested GLMMs based on the Akaike Information Criterion (AIC). The left side of the equation is the probability that participant $i$ in trial $j$ reported that the comparison was moving faster than the standard, in symbols $P(Y_{ij} = 1| u_{i})$, with $\Phi^{-1}[]$ being the probit transform of this probability (i.e., the inverse of the cumulative Gaussian function). The right side of the equation is a linear combination of the fixed and random effect predictors. Specifically, $s_{ij}$ is the speed of the comparison stimulus and $C_{32ij}, \ldots, C_{256ij}$ are the categorical predictors coding for the vibratory noise condition. We used a dummy coding for the vibratory noise condition; therefore the control condition (without vibratory noise) is the baseline in this model. The fixed-effect parameters $\theta_0, \ldots, \theta_9$ estimate the effect of the experimental variables (i.e., surface speed and vibratory noise), common to all participants. The fixed-effect parameters $\theta_0$ and $\theta_1$ correspond to the intercept and the slope of the response function in the control condition, respectively.

The slope provides an estimate of the discriminability of the stimulus: the higher the slope, the higher the discriminability. The fixed-effect parameters $\theta_2, \theta_4, \theta_6, \theta_8$ test whether the slope in a given experimental condition was significantly different from the control, which was the main focus of the present study. The slope in a given condition “*” was equal to the algebraic sum of $\theta_1$ and $\theta_*$ for example, the slope in $C_{32}$ was $\theta_{1(C32)} = \theta_1 + \theta_3$. If the
discriminability of the stimulus was not significantly different from the control, then $\theta_{1(C32)}$ would be not significantly different from $\theta_1$, hence $\theta_3$ not significantly different from zero (the null hypothesis). The other fixed-effect parameters $\theta_3$, $\theta_5$, $\theta_7$, $\theta_9$ provided a minor adjustment to the intercept in each vibratory condition. The random-effect parameters $u_{0i}$ and $u_{1i}$ estimated the heterogeneity between participants. Using two random-effect parameters, the model allowed the intercept and the slope of the response to vary in a random fashion between participants. We applied an analogous model in Experiment 1b and Experiment 2. The fixed-effect parameters were denoted with the Greek letters $\beta$ and $\eta$, respectively.

In all experiments, the significance of the slope parameters of the GLMMs were tested using the Likelihood Ratio Test, as explained in Moscatelli et al. (2012). The $P$-values were adjusted for multiple comparisons using the Holm method (Holm 1979). For comparison with previous studies, we also estimated the Just Noticeable Difference (JND) in each condition, which is an inverse function of the slope. We estimated the parameter using the bootstrap method described in Moscatelli et al. (2012). All statistical analyses were carried out in R (R Core Team, www.R-project.com). We used the lme4 package to fit the GLMM and the MERpsychophysics package (http://mixedpsychophysics.wordpress.com) to estimate the JND.

RESULTS

Participants discriminated the speed of a fine-textured surface (Experiment 1a and 1b) and a ridged surface (Experiment 2) moving across the stationary fingertip. Our leading hypothesis was that motion-induced vibrations provide a cue for discriminating tactile speeds. If so, vibratory noise would mask the cue and impair speed discrimination. Therefore, we expected the slope parameter of the GLMM (which estimates the discriminability of the stimulus; see
Material and Methods) to be smaller if vibratory noise was presented simultaneously with the motion stimulus. A systematic error (a shift of the response curve) was not expected, because vibratory noise was delivered with both the standard and the comparison motion stimulus.

Vibratory noise impairs speed discrimination on the fine-textured surface (Experiment 1)

In Experiment 1 (fine-textured surface), all participants were able to discriminate tactile speeds in the control condition (Fig. 3A). The JND in control condition was 3.10 ± 0.23 cm/s (estimate ± SE) in Experiment 1a and 2.9 ± 0.19 cm/s in Experiment 1b. This corresponded to a Weber fraction of 0.36 and 0.34, respectively, with the Weber fraction being the ratio of the JND to the standard speed.

In accordance with our hypothesis, masking the motion stimuli with vibratory noise impaired speed discrimination significantly. In Experiment 1a, the slope of the response was significantly reduced in all experimental conditions compared to the control ($P < 0.001$; Table 1 and Fig. 3B). Vibrations of 64 Hz and 128 Hz had the strongest effect, followed by vibrations of 256 Hz and 32 Hz. That is, the slopes in the 64 Hz and 128 Hz condition were both significantly smaller than in the 256 Hz and 32 Hz condition ($P < 0.001$, except $P < 0.01$ when comparing 128 Hz and 32 Hz). Inspecting the raw data and the model fits, the effects appeared to be consistent across participants (Fig. 3A). The slope of the fitted response was 0.20 cm/s (0.17 - 0.23 cm/s; Bootstrap-based 95% confidence interval, unless stated otherwise) in the control condition. Instead, it was equal to 0.07 cm/s (0.04 - 0.10 cm/s) in the 64 Hz and 128 Hz condition, 0.09 cm/s (0.07 - 0.12 cm/s) in the 256 Hz condition and 0.14 cm/s (0.11 - 0.17 cm/s) in the 32 Hz condition (Fig. 3B).

In Experiment 1b, the slope of the response was also significantly smaller in the 32 Hz condition compared with the control condition ($P < 0.001$; Table 2 and Fig. 4). The effect
was consistent across participants. The slope of the fitted response was 0.23 cm/s (0.20 - 0.27 cm/s) in the control condition and 0.19 cm/s (0.16 - 0.22 cm/s) in the 32 Hz condition.

These results demonstrate that the discrimination of tactile speed is impaired by vibratory masking noise in a frequency- and amplitude-dependent manner.

Effects of vibratory noise are weaker on the ridged surface (Experiment 2)

In Experiment 2 (ridged surface), participants discriminated speeds with higher precision compared to the fine-textured surface (Fig. 5A). A better performance can readily be seen by comparing the responses of participants that took part in both experiments (“AK”, “CH”, “FA” and “MA”). The JND was 2.07 ± 0.20 cm/s (estimate ± SE), which is about one third smaller compared to the fine-textured surface. This corresponded to a Weber fraction of 0.24, which is comparable to the Weber fraction of 0.25 estimated in a previous study (Essick et al. 1988).

Masking the motion stimuli with vibratory noise also impaired speed discrimination on the ridged surface. However, the effects were much weaker compared to the fine-textured surface (Fig. 5A). The slope of the response was significantly reduced with respect to the control only with 64 Hz ($P < 0.001$) and 128 Hz ($P < 0.05$) vibrations (Table 3 and Fig. 5B), which also had the strongest effect on the fine-textured surface. The slopes in these two conditions were also significantly smaller compared to the 256 Hz (both $P < 0.05$) and 32 Hz condition (both $P < 0.001$). Vibratory noise at 32 Hz and 256 Hz, on the other hand, had no significant effect on the slope. The slope of the fitted response was 0.33 cm/s (0.27 - 0.38 cm/s) in the control condition. It declined to 0.26 cm/s (0.21 - 0.31 cm/s) with 64 Hz vibrations and 0.27 cm/s (0.22 - 0.32 cm/s) with 128 Hz vibrations. With 256 Hz and 32 Hz
vibrations, the slope decreased only to 0.30 cm/s (0.25 - 0.35 cm/s) and 0.32 cm/s (0.27 - 0.37 cm/s), respectively.

These results suggest that the effects of vibratory noise were overall weaker in the presence of clearly detectable surface features, as is the case with the ridged surface. Notably, however, the effects tended to be of similar relative strength to the fine-textured surface: 32 Hz vibrations had the weakest effect, followed by 256 Hz vibrations and vibrations of 64 Hz and 128 Hz.

DISCUSSION

In this study, we showed that tactile speed discrimination is impaired when masking vibratory noise is presented simultaneously with slip motion. Low frequency vibrations of 32 Hz (50 µm amplitude) had the smallest effect, followed by high frequency vibrations of 256 Hz (1 µm) and intermediate vibrations of 64 Hz (65 µm) and 128 Hz (10 µm). Low frequency vibrations of 32 Hz with reduced amplitude (25 µm) also produced a small effect, which was statistically significant. The effects of vibratory noise were strong when discriminating speeds of a fine-textured surface (Fig. 3 and 4). A weaker, yet significant effect was found when discriminating speeds of a ridged surface with clearly detectable surface features (Fig. 5). In the two following paragraphs we present two alternative hypotheses on the functional mechanism of this masking effect.

PC-induced inhibition

Previous studies showed that high frequency masking vibrations impaired the detection of tactile vibrations (Ferrington et al. 1977) and finger movement (Weerakkody et al. 2007). These studies proposed that the impairment resulted from PC afferents inhibiting the input of
the other afferent types at synaptic relays of the sensory pathway. Given the vibration amplitudes in our experiments, PC afferents were likely activated by vibrations of 64 Hz, 128 Hz, and 256 Hz (Fig. 1C; Johansson et al. 1982; Mountcastle et al. 1972). Therefore, PC-induced inhibition could account for the drop in performance in this frequency range. It is less clear, however, to what extent PC-induced inhibition alone can explain the drop in performance in the lower frequency range. Given their high sensitivity, PC afferents could have been activated by the 32 Hz vibrations used in the present study, along with RA afferents and possibly slowly adapting afferents (Johansson et al. 1982; Mountcastle et al. 1972; Bolanowski et al. 1988). However, it is worth noting that in investigating PC-induced inhibition, Ferrington et al. (1977) and Weerakkody et al. (2007) found no effect of 30 Hz masking vibrations with rather high amplitudes (50 µm and 100 µm peak-to-peak amplitude, respectively). In contrast, 32 Hz vibrations significantly impaired speed discrimination in our experiments, even with lower vibration amplitudes (Experiment 1). Given the overlap of the response functions of the different afferent types in the low frequency range and their stochastic variation across individuals and trial repetitions, it is difficult to reliably predict afferent responses solely based on the behavioral data in the psychophysical task. Thus, further studies including afferent recordings might help to clarify if PC-induced inhibition alone can account for our results.

Vibrations as a cue to tactile speed

As an alternative explanation, we propose that the tactile system combines motion-induced vibrations with other time-varying cues for the discrimination of slip motion speed. According to this hypothesis, external vibrations masking the “natural” vibrations generated by the moving surfaces (Fig. 2) impaired speed discrimination in our experiments. That is,
external vibrations decreased the signal-to-noise ratio of the vibration cue to speed. The vibration cue could be integrated with other motion cues, like the indentation wave produced by the displacement of traceable surface features (such as ridges or dots) across the skin. Vibration cues might then be critical on fine-textured surfaces, lacking these traceable features.

Our results are consistent with this hypothesis. The difference in the reliability for the response between the fine-textured surface (Experiment 1) and the ridged surface (Experiment 2) was in accordance with an optimal integration of the different motion cues (Ernst and Banks 2002). That is, participants would have integrated multiple cues such as vibrations, feature tracking, and tangential skin stretch when estimating the speed of the ridged surface, resulting in a reliable response. In contrast, estimating the speed of the fine-textured surface resulted in a noisier response because of the lack of the feature-tracking cue. A better speed discrimination in the presence of individually detectable surface features also confirms previous findings (Dépeault et al. 2008).

A mechanism of speed discrimination based on motion-induced vibrations could rely on an intensive code (Dépeault et al. 2013; Essick and Edin 1995), which encodes higher relative speed as higher vibration amplitude. In our experiments, vibration amplitude increased with increasing speed on both the ridged and the fine-textured surface (Fig. 2), consistent with previous findings (Fagiani et al. 2010). On the fine-textured surface, the amplitude of vibrations (acceleration signal) increased approximately 4-fold within the tested range of slip motion speed (see Material and Methods and Fig. 2A). On the ridged surface, it increased approximately 15-fold (Fig. 2B). At the same tangential speed, the movement of the ridged surface induced vibrations of higher amplitude than the fine-textured surface. Hence, the signal-to-noise ratio (i.e., the ratio of slip-induced vibrations to masking vibrations) was
higher on the ridged surface compared to the fine-textured surface (Fig. 2), which can also account for the difference in the effect size between Experiment 1 and Experiment 2. Furthermore, if vibration amplitude were used as a motion cue, a rough or a ridged surface would be perceived as moving faster than a smooth surface moving at the same physical speed. A recent study demonstrates that this is indeed the case (Dépeault et al. 2008).

In principle, all vibrations-sensitive afferents could provide an intensive code. Given their high sensitivity and large receptive fields, PC afferents are likely to play a central role in conveying this cue (Vallbo and Johansson 1984; Srinivasan et al. 1990), although SA and RA afferents could contribute as well (Johansson et al. 1982; Talbot et al. 1968). According to recent studies (Dépeault et al. 2013, Harvey et al. 2013), the integration of multiple tactile cues could occur in the primary somatosensory cortex (S1). Neurons of S1 were found to be sensitive to moving tactile stimuli of the types used here (Dépeault et al. 2013). Moreover, they encoded vibration amplitude in the strength of their response and responded to a wide range of vibration frequencies, suggesting they receive input from PC and other afferents (Harvey et al. 2013).

In conclusion, we propose that skin vibrations are integrated with other motion cues for the discrimination of tactile speed, and that vibration cues are particularly important in the absence of clearly detectable surface features. Along a similar line of reasoning, Yao and Hayward (2006) showed that simulated vibrations produced the vivid sensation of a ball rolling inside a tube held in the hand. In their study, participants were able to estimate the length of the motion path of the object based on the simulated vibrations, which required inferring the motion kinematics. An integration of slip-induced vibrations with other tactile motion cues would further support the emerging view of submodality convergence in the tactile system (Saal and Bensmaia 2014; Jörntell et al. 2014).
ACKNOWLEDGMENTS

We thank Marian Rosenstengel, Alexandra Kassis, and Janina Röckner for laboratory assistance and Marieke Rohde for helpful comments on an earlier version of the manuscript. Current address of C. J. Dallmann: Department of Biological Cybernetics, Bielefeld University, Universitätsstraße 25, 33615 Bielefeld, Germany.

GRANTS

This study was supported by EU FP7/2007-2013 project 601165 WEARHAP (WEARable HAPtics for Humans and Robots) and the Cluster of Excellence Cognitive Interaction Technology ‘CITEC’ (EXC 277) funded by the German Research Foundation (DFG).

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

CJD, MOE, and AM conceived and designed experiments; CJD performed experiments; CJD and AM analyzed data; CJD, MOE, and AM interpreted results of experiments; CJD and AM prepared figures; CJD and AM drafted manuscript; CJD, MOE, and AM edited and revised manuscript; CJD, MOE, and AM approved final version of manuscript.

REFERENCES


**FIGURE LEGENDS**

Fig. 1. *A* and *B*: Schematic close-up side view of the experimental setup. The tip of the right index finger contacted either a fine-textured (*A, Experiment 1*) or a ridged (*B, Experiment 2*) surface, which was moved from proximal to distal (arrows pointing to the left). Vibrations were induced at the ventral side of the proximal phalanx (vertical arrows) via a metal rod that was rigidly attached to a vibration device above the finger. *C*: Frequencies and amplitudes of the masking vibrations used in the vibratory noise conditions and response ranges of rapidly adapting (RA and PC) afferents (the latter were estimated from Mountcastle et al. 1972). The open circle indicates the masking vibration used in *Experiment 1b*. *D*: Protocol of a single trial. The motion device delivered two tactile stimuli of 1 s each, with a 1 s interval in between. Tactile stimuli were masked with vibratory noise (see *C*). Participants reported whether they had perceived the second stimulus to be faster or slower than the first. The protocol was repeated 0.5 s after the response.
Fig. 2. Movement of the fine-textured (A) and the ridged (B) surface both induced vibrations in the right index fingertip that increased with increasing surface speed. Accelerations were measured in 1 s time windows during constant surface movement with an accelerometer attached to the fingernail. In contrast to the fine-textured surface, the ridged surface generated vibrations with dominant frequencies, which were reliably shifted toward higher frequencies with increasing speed. Arrows in B mark the dominant frequency for each speed.

Fig. 3. Results of the speed discrimination task on the fine-textured surface (Experiment 1a). A: Individual responses with GLMM fits. Vibratory noise reduced the precision (slope) of the response similarly in all participants. B: Vibratory noise of 64 Hz (dark blue) and 128 Hz (magenta) reduced the precision most strongly, followed by vibratory noise of 256 Hz (green) and 32 Hz (light blue). Vertical error bars show 95% confidence intervals.

Fig. 4. Results of the speed discrimination task on the fine-textured surface with 32 Hz masking vibrations of reduced amplitude (25 µm; Experiment 1b). A: Individual responses with GLMM fits. Vibratory noise reduced the precision (slope) of the response similarly in all participants. B: The effect of vibratory noise (light blue) was small but significant. Vertical error bars show 95% confidence intervals.

Fig. 5. Results of the speed discrimination task on the ridged surface (Experiment 2). A: Individual responses with GLMM fits. In contrast to the fine-textured surface, vibratory noise reduced the precision (slope) of the response only moderately on the ridged surface. B: Albeit much weaker, vibratory noise of 64 Hz (dark blue) and 128 Hz (magenta) had again the
strongest effect on the precision, followed by vibratory noise of 256 Hz (green) and 32 Hz (light blue). Vertical error bars show 95% confidence intervals.

**TABLES**

Table 1. Fixed-effect parameters of the GLMM for the fine-textured surface (*Experiment 1a*).

| Estimate | SE  | z-value | Pr(>|z|) |
|----------|-----|---------|---------|
| $\theta_0$ (intercept) | -1.77 | 0.16 | -11.07 | <0.001 |
| $\theta_1$ (speed) | 0.20 | 0.02 | 12.19 | <0.001 |
| $\theta_2$ (32 Hz) | 0.58 | 0.13 | 4.44 | <0.001 |
| $\theta_3$ (speed:32 Hz) | -0.06 | 0.01 | -4.29 | <0.001 |
| $\theta_4$ (64 Hz) | 1.28 | 0.13 | 10.2 | <0.001 |
| $\theta_5$ (speed:64 Hz) | -0.13 | 0.01 | -10.17 | <0.001 |
| $\theta_6$ (128 Hz) | 1.25 | 0.13 | 9.99 | <0.001 |
| $\theta_7$ (speed:128 Hz) | -0.13 | 0.01 | -10.09 | <0.001 |
| $\theta_8$ (256 Hz) | 1.04 | 0.13 | 8.22 | <0.001 |
| $\theta_9$ (speed:256 Hz) | -0.11 | 0.01 | -8.26 | <0.001 |

Table 2. Fixed-effect parameters of the GLMM for the control experiment with the fine-textured surface (*Experiment 1b*).

| Estimate | SE  | z-value | Pr(>|z|) |
|----------|-----|---------|---------|
| $\beta_0$ (intercept) | -2.02 | 0.14 | -14.38 | <0.001 |
| $\beta_1$ (speed) | 0.24 | 0.016 | 14.82 | <0.001 |
| $\beta_2$ (32 Hz) | 0.38 | 0.09 | 4.00 | <0.001 |
| $\beta_3$ (speed:32 Hz) | -0.04 | 0.01 | -4.10 | <0.001 |

Table 3. Fixed-effect parameters of the GLMM for the ridged surface (*Experiment 2*).
| Parameter                  | Estimate | SE  | z-value | Pr(>|z|) |
|---------------------------|----------|-----|---------|---------|
| $\eta_0$ (intercept)      | -2.88    | 0.26| -10.95  | <0.001  |
| $\eta_1$ (speed)          | 0.33     | 0.03| 10.42   | <0.001  |
| $\eta_2$ (32 Hz)          | -0.05    | 0.18| -0.29   | 0.77    |
| $\eta_3$ (speed:32 Hz)    | -0.01    | 0.02| -0.15   | 0.88    |
| $\eta_4$ (64 Hz)          | 0.48     | 0.16| 2.92    | <0.001  |
| $\eta_5$ (speed:64 Hz)    | -0.07    | 0.02| -3.93   | <0.001  |
| $\eta_6$ (128 Hz)         | 0.45     | 0.16| 2.75    | 0.01    |
| $\eta_7$ (speed:128 Hz)   | -0.06    | 0.02| -3.53   | 0.001   |
| $\eta_8$ (256 Hz)         | 0.20     | 0.17| 1.19    | 0.23    |
| $\eta_9$ (speed:256 Hz)   | -0.03    | 0.02| -1.59   | 0.22    |