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The discrimination of tactile speed in absence of texture elements: Role of deformation and vibratory cues

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Abstract

Motion encoding in touch relies on multiple cues, such as the pattern of skin indentation produced by raised texture elements, high-frequency vibrations while slipping, or fingertip deformation by shear force. We evaluated the role of deformation and vibration cues in tactile speed discrimination. To this end, we tested the discrimination of tactile speed using a smooth glass plate, with and without masking vibrations. Without masking vibrations, participants were surprisingly precise at this task, as assessed by the steep slope of the psychometric function. Even with the moving glass plate, which is expected to recruit mostly slowly adapting fibers, high-frequency vibrations impaired the ability of the participants in discriminating surface speed.

keywords: Speed Discrimination, Shear, Vibrations

Introduction

It has been argued that motion is as important to touch as light is to vision [20]. Tactile motion plays a central role in perceptual and motor tasks. It provides a feedback for guiding hand reaching towards a target goal while sliding the hand on a surface, and for the manipulation of handheld objects [16, 28, 4]. Likewise, the brain adjusts the grip force in grasping based on the small slips between the object and the skin [19]. Different cues contribute to the perception of motion in touch, including the spatiotemporal pattern of local deformation, as for example

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the one generated by the tip of a pencil moving across the skin, high-frequency skin vibrations occurring during slip motion, and the gross skin deformation, such as the stretch generated by a shear force applied to the fingertip [32, 11, 13, 18, 29, 1]. The role of the first two motion cues, local indentation and vibrations, was deeply investigated in recent studies [5, 9, 15, 31, 23, 8]. Here, we evaluate the role of shear deformation for the discrimination of speed. Before introducing our study, we will summarise recent findings about different cues in tactile motion perception.

The indentation produced by traceable surface elements, like moving raised dots or ridges, provide a salient motion cue in touch [32, 5, 15]. Recently, a model based on the spatiotemporal pattern of skin deformation reproduced the tactile afferent signals quite accurately [29]. A second type of cues are those based on the local and remote skin vibrations that are generated by sliding across or tapping against the surface of an object [14, 31, 8]. Vibrations play a role in tasks like motion detection, speed discrimination, and roughness discrimination from scanning [32, 3, 7]. Their importance as motion cue has been demonstrated mostly during slip motion on a plate with a fine texture, lacking traceable elements [32, 7]. A third type of motion cues are referred to as gross deformation cues, such as the tangential stretch of the skin caused by shear force (Figure 1A) and the transition from stick to slip between the skin and a surface [32, 1, 22]. A smooth glass plate, lacking fine and gross texture elements, is typically used to investigate deformation cues [32, 1]. It is debated whether humans are able to detect motion of a smooth plate only from skin deformation. For light touch, i.e., for a normal force equal to 0.2 N, the slip of a smooth glass plate is indistinguishable from simple skin stretch [32]. Instead, it is possible to detect slip and partial slip of a glass surface at higher values of normal force, ranging from 2 to 5 N [1]. These behavioural results complement electrophysiological recordings of the afferent fibers. A moving glass plate elicits only a weak response in fast adapting fibers during light touch [32], whereas, for a normal force up to 4 N, nearly all afferents respond to tangential strain, and their response is broadly tuned to a preferred direction of force [6].

Here, we aimed to further investigate the role of deformation cues for motion encoding in touch. To this end, we tested the discrimination of tactile speed on a smooth glass plate. The advantage of using a discrimination task is that, differently from a yes/no detection task, the response is less bias-prone, i.e., it does not depend on the decision criterion. The precision of the response will tell us to which extent participants were able to discriminate surface speed in absence of raised texture elements. For comparison with previous studies, the task was replicated using a surface with a homogeneous texture similar to the one used by [7, 30]. In both surface conditions, high-frequency vibrations were delivered synchronously with surface motion in half of the trials. The goal was to investigate the possible interplay between deformation and vibration cues. If these two cues were processed in separate channels, and speed discrimination on a smooth plate depended on deformation cues only, masking vibrations should affect the precision of the response on the textured but not on the smooth plate. Otherwise, this would speak in favour of an interplay between vibration

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and deformation cues, which may occur at a mechanical or at a neural level.

Methods

Participants

Fifteen naïve, right-handed participants took part in the experiment (10/15 females, age ranging from 20 to 36 years). The testing procedures were approved by the ethics committee of the Santa Lucia Foundation, 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

A motion device displaced the contact surface up and down at the required speed (Figure 1B). The motion device consisted of two rollers with a rigid plane in between, rotating a plastic belt (270 mm length x 30 mm width). The two rollers were vertically aligned and the downward roller was connected with a metal shaft to a Faulhaber motion control system. This included a DC-Micromotor (Faulhaber 3242G024CR combined with 7:1 Gearheads 32A), a high-resolution encoder (Faulhaber IE3-512), and a position and speed controller (Faulhaber MCDC3006SRS). A rigid plastic box having a cuboid shape (75 x 20 x 20 mm) was attached to the belt. This way, the rotation of the motor produced a vertical displacement of the box. We assembled two boxes having a contact surface of different materials, glass and plastic. The base of each box was interlocking with a basement firmly attached to the belt, so that they could be easily changed between two experimental blocks. The contact surface was either a smooth microscope glass (75 x 25 x 1.5 mm) or a plastic plate (75 x 20 x 1.5 mm). The plastic plate was printed in Polylactic Acid (PLA) using a 0.4 mm diameter nozzle, which produced a fine homogeneous texture on its surface. To detect contact, a force resistive sensor was placed between the box and the contact surface (Interlink 402 force resistive sensor connected to a Arduino UNO microcontroller). Prior to the experiment, the contact sensor was calibrated by means of a set of calibration weights, ranging from 0.98 to 4.9 N. A vibromotor (Haptuator Mark II by TactileLabs, connected to MAX9744 audio amplifier by Adafruit) was placed in a small niche inside the box to generate masking vibrations. Vibration stimuli were generated by a standard PC audiocard (HDA Intel PCH). Masking vibrations were recorded with an accelerometer attached to the contact plate to measure the amplitude and frequency of the signal (Fig. 1C). A custom-made Matlab code controlled the vibration and the motion stimuli. A one degree of freedom finger holder was attached to the frame of the setup, supporting the participant's finger.

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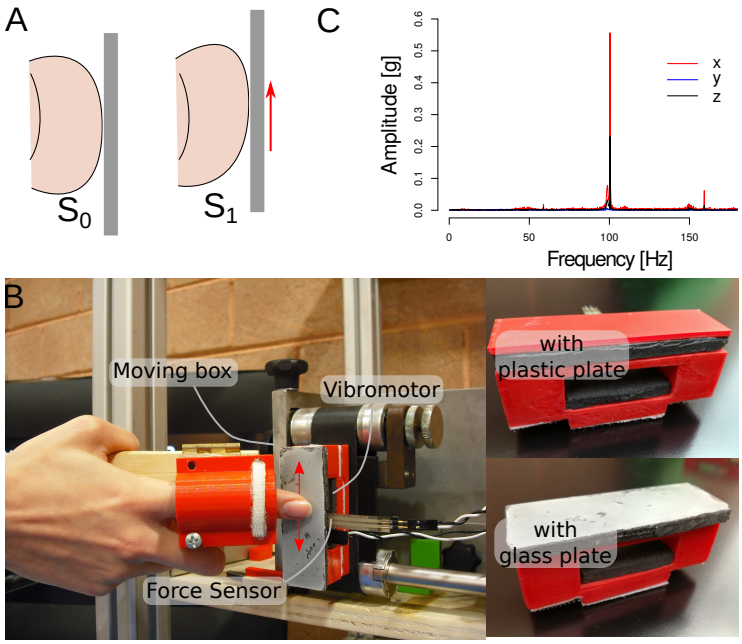

Figure 1: Rationale of the Experiment and Methods. A) The rate of skin stretch (i.e., the strain of the skin from the initial status S_0 to the final status S_1 in the unit of time) may provide a potential cue for the encoding of surface speed. B) The setup including the actuated box, the vibromotor and the force sensor. Two boxes having a glass or a plastic contact plate were used in two experimental blocks. C) Masking vibrations: x, y, and z acceleration component. Vibrations were recorded with an accelerometer (ADXL335 connected with an Arduino UNO microcontroller, sampling rate 360 Hz) attached to the contact plate, and processed with Fast Fourier Transform.

Stimuli and Procedure

Participants sat on an office chair in front of the apparatus, resting their right index finger on the finger holder. A panel hid the device from the participants' sight. Throughout each experimental session, participants wore earplugs and headphones playing pink noise in order to mask external sounds. Each experimental session consisted of 240 trials divided in two blocks. In each block, participants performed the experiment either with the smooth glass plate or with the textured plastic plate. The order of the two blocks was counterbalanced across participants.

The sequence of the stimuli in a trial is illustrated in Fig. 2 and Fig. 3. Each trial included a reference and a comparison stimulus. The order of the two was counterbalanced across trials. We instructed participants to push on the contact surface with their index finger to start the tactile stimulus. The servomotor and

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the vibromotor were actuated when the normal force (averaged across the last 20 ms) exceeded the threshold value of 1.5 N. The surface moved either upward or downward, with the motion direction of the second stimulus always being the opposite of first one. The motion speed was equal to 3.43 cm sec^{-1} in the reference stimulus, and it was pseudo-randomly chosen between five values ranging from 0.63 cm sec^{-1} and 6.42 cm sec^{-1} in the comparison. After each trial, participants reported whether the surface moved faster in the first or in the second stimulus interval. To prevent using motion duration as a cue, the path length of stimulus was pseudo-randomly chosen within a range of 10-14 mm. In half of the trials, masking vibrations consisting of a 100 Hz sinusoidal wave were delivered synchronously with the motion stimulus (Fig. 2).

Analysis

We analysed categorical responses by means of Generalized Linear Mixed Models (GLMM) [26], separately for each surface type, glass and plastic. We included the motion speed (S) and the presence/absence of vibration (V = 0 without vibration and V = 1 otherwise) as fixed-effect predictors.

$$\Phi^{-}1[P(Y=1)] = \beta_0 + \beta_1 S + \beta_2 V + \beta_3 SV + \vec{u}, \tag{1}$$

where $P(Y = 1)$ was the probability of reporting that the comparison was faster that the reference. Fixed-effect parameters were denoted with Greek letter $\eta_{1,\ldots,4}$ and random-effect parameter vector with the lowercase letter $\vec{u}$. The parameter β_1 (referred to as the model slope) estimates the reliability of the response in the control condition (without vibrations). With vibrations, the model slope was equal to $\beta_1 + \beta_3$. For comparison with previous studies, we computed the Just Noticeable Difference (JND $= 0.625/\beta_1$), the Weber Fraction (WF = JND/3.43, which is the value of the reference speed), and the related 95% Confidence Interval (CI) by means of the bootstrap method explained in [26]. Next, we applied the following model to compare the response between the two surface types:

$$\begin{aligned}\Phi^{-}1[P(Y=1)] =& \eta_0 + \eta_1 S + \eta_2 V + \eta_3 G + \eta_4 SV + \\ &+ \eta_5 SG + \vec{u},\end{aligned} \tag{2}$$

This corresponds to a 2x2 factorial design (2 surface types x 2 vibration conditions). Model (1) and (2) were selected among a pool of nested models based on the Akaike Information Criterion (AIC) and likelihood ratio test (LR test). The R packages *lme4* and *MixedPsy* were used to fit the GLMMs [2, 26].

Force signals were filtered using a second order, Butterworth low-pass filter (cutoff frequency equal to 10 Hz), as in our previous study[27]. In each trial, we saved the peak of the filtered signal for the descriptive statistics.

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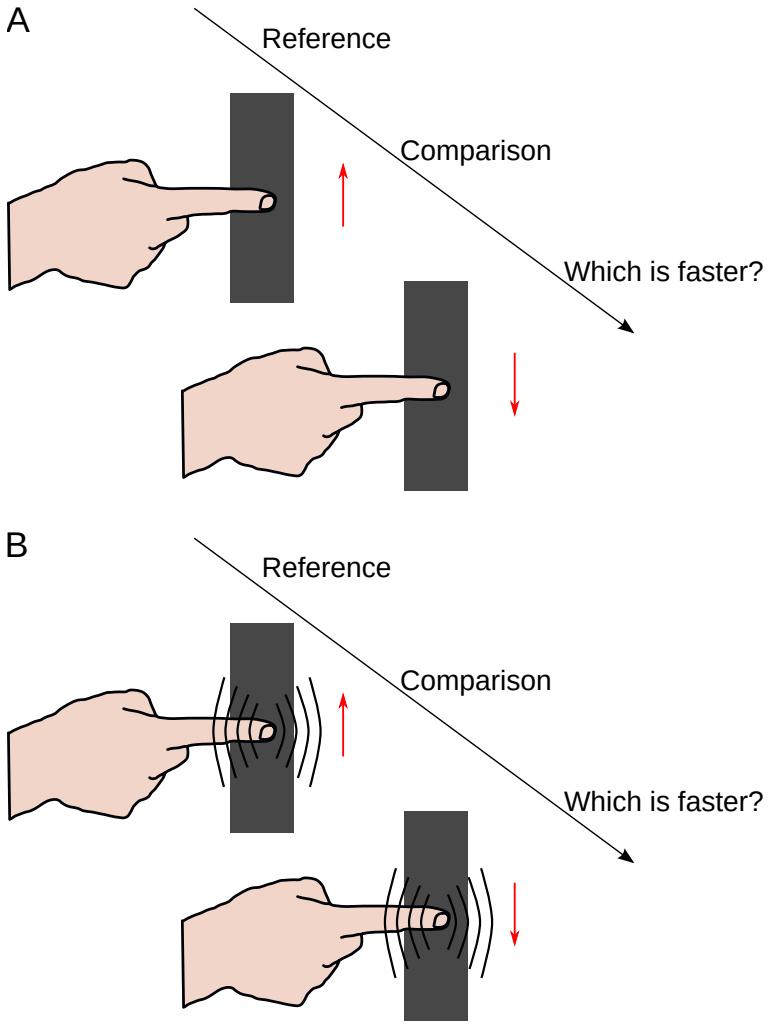

Figure 2: Experimental procedure. A) Control condition B) Masking vibration condition

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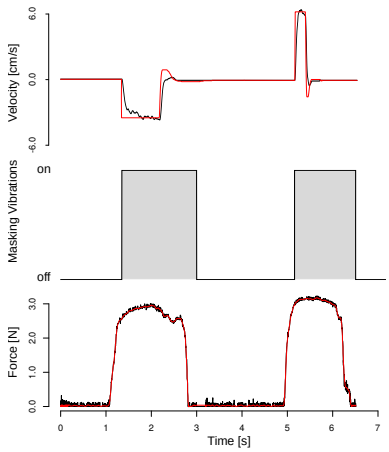

Figure 3: Motion, vibration and force profile in a single trial. In the upper panel, positive values of velocity correspond to downward motion and negative values to upward motion. Measured and target values are represented in black and in red, respectively. To prevent using motion duration as a cue, path length was randomized across trials. Middle panel: In half of the trials, high-frequency vibrations were presented while the participant contacted the plate (vibration condition). Vibration amplitude was set to zero in the other half of the trials (control condition). Vibration onset and offset was synchronised with the initiation and the cessation of contact. The lower panel shows the contact force. Raw and filtered data are represented in red and in black, respectively

Power Analysis

We performed the power calculation by using the R package *simr* [17]. We assumed a sample size equal to 15 participants, 60 trials each (corresponding to trial repetitions in each experimental condition), and effect size equal to 0.40 (slope of the model, or β_2). With these parameters, statistical power of the GLMM would be above 80%. This sample size is in accordance with the one reported in similar studies in the literature [7, 1, 25].

Results

The first aim of this study was to test whether participants were able to discriminate the motion speed of the smooth glass surface, with the fine plastic surface serving as control. As illustrated in Figure 4, participants were able to perform the task with either of the two types of surface. Without masking vibrations, the parameter of slope in Eq. (1) was significantly larger than zero with the smooth glass plate ($p < 0.001$; 0.65 ± 0.079, $\beta_{1(glass)} \pm$ Std. Error) and with the homogeneous-textured plastic plate ($p < 0.001$; 0.75 ± 0.10, $\beta_{1(plastic)} \pm$ Std. Error). This means that, differently from previous studies on the detection of

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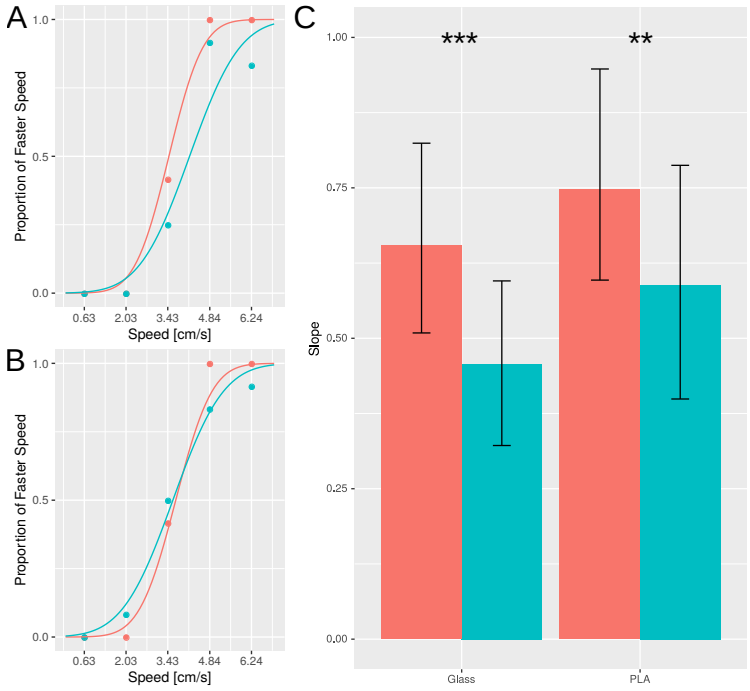

Figure 4: Results. A) Psychometric functions in a representative participant, raw data and GLMM fit (glass surface). Control condition and masking vibrations condition are represented in orange and azure, respectively. B) Psychometric functions in a representative participant, raw data and GLMM fit (pla surface) C) The bar plot shows the estimated slopes in the control and masking vibration conditions, separately for the glass and pla surface (GLMM estimates to 14 participants). The error bar represents the 95% confidence interval estimated with the bootstrap method.

slip motion, participants discriminated the motion speed of the smooth glass plate, well-above chance level.

With the glass plate, tactile speed discrimination was impaired by high-frequency vibrations. Accordingly, the slope was significantly smaller with masking vibrations compared to control ($p < 0.001$; -0.20 ± 0.048, $\beta_{3(glass)}\pm$ Std. Error). The same effect of masking vibrations was observed with the plastic surface ($p = 0.002$; -0.16 ± 0.05, $\beta_{3(plastic)}\pm$ Std. Error). Results are illustrated in Figure 4A-B, in a representative participant, and in Figure 4C for the whole population. We evaluated the difference between the two surface conditions by means of the GLMM in Eq. (2). The precision of the response, although higher with the plastic interface, was not significantly different between the two surfaces ($p = 0.06$; 0.057 ± 0.031, $\eta_5\pm$ Std. Error).[1]

[1]The estimated values of η_5 is slightly smaller than the difference between $\beta_{1(glass)}$ and

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For comparison with previous studies, the values of JND and WF in the four experimental conditions are reported in Table 1, along with the related 95% CI. With the fine plastic surface and in absence of vibrations, the value of Weber Fraction (0.26) is close to the ones reported in previous studies where the skin was stimulated either with a sandblasted surface or with a brush [12, 30, 7]. The precision of the response decreased with the glass plate, and in both surface types with masking vibrations—as assessed by the larger values of JND and WF.

Estimate	Inferior	Superior	Parameter	Vibration	Surface
1.03	0.82	1.33	JND	no	Glass
1.48	1.13	2.10	JND	yes	Glass
0.30	0.24	0.39	WF	no	Glass
0.43	0.33	0.61	WF	yes	Glass
0.90	0.71	1.13	JND	no	Plastic
1.15	0.86	1.69	JND	yes	Plastic
0.26	0.21	0.33	WF	no	Plastic
0.33	0.25	0.49	WF	yes	Plastic

Table 1: Values of Just Noticeable Difference (JND) and Weber Fraction (WF) in the four experimental conditions. Estimates and 95% CI estimated with the bootstrap methods.

A detailed analysis of the contact force is beyond the purpose of this study. The distribution of the peak force ranged approximately between 2 and 4 N, with marked differences between individual participants (Figure 5). The median value of peak force was equal to 3.4 N.

Discussion

We investigated the ability of human participants to discriminate the motion speed of a movable glass plate, lacking texture elements, using touch. Participants were surprisingly good at this: Their responses were only 13% less precise when compared to a control condition, where the motion stimuli were delivered with a plastic plate having a fine texture. This has important implication for models of motion encoding in touch, because it shows that rich perceptual information is provided even in absence of texture elements. Which type of motion cues may the tactile system use in this case? A recent study suggested that the brain uses a deformation-based mechanism for slip detection on smooth surfaces [1]. Fingertip shearing caused by a stroking glass plate is related to surface displacement, as long as the finger is not fully slipping against the plate. Additionally, the skin in contact with the plate undergoes deformations due to partial slips. The authors hypothesised that shearing and partial slip, both play a role in a putative slip detection mechanism based on fingertip deformations

$\beta_{1(plastic)}$. This is due to the choice of the random-effect parameters in Eq. (2).

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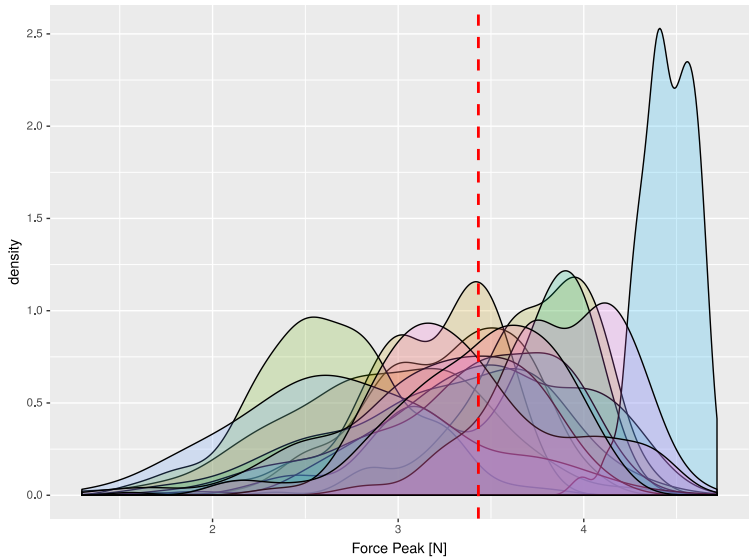

Figure 5: Distribution of the force peak. Values from different participants are illustrated each with a different colour. The dashed line is the median value, equal to 3.4 N.

[1]. Likewise, speed discrimination on smooth surfaces may be partially based on deformation-rate cues, such as fingertip shearing rate and the onset of the stick-to-slip transition.

High-frequency vibrations provide a second class of motion cues in touch. These play an important role in motion detection and for the discrimination of stimulus features like speed, roughness, and texture [32, 3, 23, 7]. Additionally, during tool use they allow us discriminating the texture of a surface sensed with a probe, and the position on the probe where it impacts with an object [21, 24]. In the current study, we showed that tactile discrimination was significantly impaired by the presence of high-frequency vibrations, on both surface types. Likewise, in a previous study we described a masking effect of vibrations by using either a sandblasted billiard ball or a surface with raised ridges to deliver the motion stimuli [7]. Perceptual impairment caused by masking vibrations may be explained either at a mechanical or at a neural level. According to the first hypothesis, the small slips between the surface and the skin revealed as skin vibration may provide auxiliary information on surface speed, and these would be masked by the high-frequency vibrations generated by the vibromotor. At a neural level, masking vibrations would recruit the afferent fibers, independently of surface speed. This would decrease the signal-to-noise ratio of the neural signal, leading to a noisier perceptual response.

The neural representation of motion in touch could be based on a within-fiber, intensity code [11, 13] and on a between-fiber spatiotemporal code [29].

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The latter is defined as the sequential activation of neighboring afferent fibers in response to a traceable feature of the surface, moving across their receptive field [32, 29]. An example of spatiotemporal code is the sequential activation of fast adapting fibers (FA)-I following the motion of a surface with a single raised dot [32]. In the model proposed in [29], tactile motion arises from the responses of the fibers to a moving pattern of skin indentation, based on a spatiotemporal code. This model does not incorporate lateral sliding and the concomitant shear forces. Scanning is mimicked by moving an "image" of the indentation pattern across the skin. The brain may use an intensity code to represent surface motion from the high-frequency vibrations and the gross deformation of the skin [32, 7]. In accordance with the hypothesis of the intensity code, a brush moving across the skin at different velocities produces a modulation in mean firing rate within the single afferent fiber [11, 13]. An intensity code could also account for motion encoding on a smooth surface. Instead, in this case a spatiotemporal code is unlikely for the lack of traceable elements.

Different motion cues and neural codes are not mutually exclusive. Alike in vision, where an observer is able to perceive the depth of a painting in absence of binocular cues, tactile system can encode and process surface motion also when the stimulus lacks one of the redundant motion cues. For instance, a moving pattern generated by a wave of vibrating pins provide a vivid sensation of a moving surface, even in absence of a net shear force [25, 10]. On the other hand, the results of the current study showed that deformation cues alone provide sufficient information to discriminate surface speed. This and previous results showed that touch is more than an "imager", because it is possible to discriminate motion features, such as direction and speed, even in absence of a moving pattern. The different cues—indentation wave, vibration, and deformation—provide redundant motion information; therefore, they could be integrated for an optimal estimated of tactile motion.

References

[1] Allan Barrea, Benoit P. Delhaye, Philippe Lefèvre, and Jean-Louis Thonnard. Perception of partial slips under tangential loading of the fingertip. *Scientific Reports*, 8(1):7032, 12 2018.

[2] Douglas Bates, Martin Mächler, Ben Bolker, and Steve Walker. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1):1–51, 6 2015.

[3] Sliman J Bensmaia and Mark Hollins. The vibrations of texture. *Somatosensory & motor research*, 20(1):33–43, 1 2003.

[4] Matteo Bianchi, Alessandro Moscatelli, Simone Ciotti, Gemma Carolina Bettelani, Federica Fioretti, Francesco Lacquaniti, and Antonio Bicchi. Tactile slip and hand displacement: Bending hand motion with tactile il-

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lusions. In *2017 IEEE World Haptics Conference (WHC)*, number June, pages 96–100. IEEE, 6 2017.

[5] Antonio Bicchi, Enzo P Scilingo, Emiliano Ricciardi, and Pietro Pietrini. Tactile flow explains haptic counterparts of common visual illusions. *Brain Research Bulletin*, 75(6):737–741, 4 2008.

[6] I Birznieks, P Jenmalm, a W Goodwin, and R S Johansson. Encoding of direction of fingertip forces by human tactile afferents. *The Journal of Neuroscience*, 21(20):8222–8237, 2001.

[7] Chris J. Dallmann, Marc O. Ernst, and Alessandro Moscatelli. The role of vibration in tactile speed perception. *Journal of Neurophysiology*, 114(6):3131–3139, 12 2015.

[8] Benoit Delhaye, Vincent Hayward, Philippe Lefèvre, and Jean-Louis Thonnard. Texture-induced vibrations in the forearm during tactile exploration. *Frontiers in behavioral neuroscience*, 6(July):37, 1 2012.

[9] Alexandra Dépeault, El-Mehdi Meftah, and C Elaine Chapman. Tactile speed scaling: contributions of time and space. *Journal of neurophysiology*, 99(3):1422–1434, 3 2008.

[10] Lucile Dupin, Vincent Hayward, and Mark Wexler. Direct coupling of haptic signals between hands. *Proceedings of the National Academy of Sciences*, 112(2):619–624, 1 2015.

[11] Benoni B Edin, Greg K Essick, M Trulsson, and K A Olsson. Receptor encoding of moving tactile stimuli in humans. I. Temporal pattern of discharge of individual low-threshold mechanoreceptors. *J Neurosci*, 15(1 Pt 2):830–847, 1995.

[12] G K Essick, O Franzen, and B L Whitsel. Discrimination and scaling of velocity of stimulus motion across the skin. *Somatosensory & motor research*, 6(1):21–40, 1988.

[13] GK K Essick and BB B Edin. Receptor Encoding of Moving Tactile Stimuli in Humans. II. The Mean Response of Individual Low-Threshold Mechanoreceptors to Motion Across the Receptive Field. *The Journal of neuroscience*, 15(January):848–864, 1995.

[14] Ramona Fagiani, Francesco Massi, Eric Chatelet, Yves Berthier, and Adnan Akay. Tactile perception by friction induced vibrations. *Tribology International*, 44(10):1100–1110, 2011.

[15] Francesca Fardo, Brianna Beck, Tony Cheng, and Patrick Haggard. A mechanism for spatial perception on human skin. *Cognition*, 178:236–243, 9 2018.

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[16] J. Randall Flanagan, Miles C. Bowman, and Roland S. Johansson. Control strategies in object manipulation tasks. *Current Opinion in Neurobiology*, 16(6):650–659, 2006.

[17] Peter Green and Catriona J. MacLeod. SIMR: an R package for power analysis of generalized linear mixed models by simulation. *Methods in Ecology and Evolution*, 7(4):493–498, 4 2016.

[18] Vincent Hayward. Is there a 'plenhaptic' function? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 366(1581):3115–3122, 11 2011.

[19] RS S Johansson and G Westling. Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. *Experimental Brain Research*, pages 141–154, 1987.

[20] D Katz. *The World of Touch*. Lawrence Erlbaum Associates, Hillsdale, New Jersey, 1989.

[21] R L Klatzky and S J Lederman. Tactile roughness perception with a rigid link interposed between skin and surface. *Perception {&} psychophysics*, 61(4):591–607, 1999.

[22] Vincent Levesque and Vincent Hayward. Experimental evidence of lateral skin strain during tactile exploration. *Eurohaptics*, (July):261–275, 2003.

[23] Xavier Libouton, Olivier Barbier, Yorick Berger, Leon Plaghki, and Jean-Louis Thonnard. Tactile roughness discrimination of the finger pad relies primarily on vibration sensitive afferents not necessarily located in the hand. *Behavioural Brain Research*, 229(1):273–279, 4 2012.

[24] Luke E Miller, Luca Montroni, Eric Koun, Romeo Salemme, and Vincent Hayward. Sensing with tools extends information processing beyond the body. *Nature*, pages 1–29, 2018.

[25] Alessandro Moscatelli, Vincent Hayward, Mark Wexler, and Marc O. Ernst. Illusory Tactile Motion Perception: An Analog of the Visual Filehne Illusion. *Scientific Reports*, 5(1):14584, 11 2015.

[26] Alessandro Moscatelli, Maura Mezzetti, and Francesco Lacquaniti. Modeling psychophysical data at the population-level: The generalized linear mixed model. *Journal of Vision*, 12:26:1–17, 2012.

[27] Abdeldjallil Naceri, Alessandro Moscatelli, and Ryad Chellali. Depth discrimination of constant angular size stimuli in action space: role of accommodation and convergence cues. *Frontiers in Human Neuroscience*, 9(September):1–8, 9 2015.

[28] J. Andrew Pruszynski, Roland S. Johansson, and J. Randall Flanagan. A Rapid Tactile-Motor Reflex Automatically Guides Reaching toward Handheld Objects. *Current Biology*, 26(6):788–792, 2 2016.

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[29] Hannes P. Saal, Benoit P. Delhaye, Brandon C Rayhaun, and Sliman J. Bensmaia. Simulating tactile signals from the whole hand with millisecond precision. *Proceedings of the National Academy of Sciences*, (in press), 2017.

[30] Mark Salada, Peter Vishton, J.E. E Colgate, and E. Frankel. Two experiments on the perception of slip at the fingertip. In *12th International Symposium on Haptic Interfaces for Virtual Environment and Teleoperator Systems, 2004. HAPTICS '04. Proceedings.*, pages 146–153. IEEE, 2004.

[31] Yitian Shao, Vincent Hayward, and Yon Visell. Spatial patterns of cutaneous vibration during whole-hand haptic interactions. *Proceedings of the National Academy of Sciences of the United States of America*, 113(15):201520866, 2016.

[32] M. A. Srinivasan, J. M. Whitehouse, and R. H. LaMotte. Tactile detection of slip: surface microgeometry and peripheral neural codes. *Journal of neurophysiology*, 63:1323–1332, 1990.