Illusory changes in the perceived speed of motion derived from proprioception and touch

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Abstract: In vision, the perceived velocity of a moving stimulus differs depending on whether we pursue it with the eyes or not: A stimulus moving across the retina with the eyes stationary is perceived as being faster compared with a stimulus of the same physical speed that the observer pursues with the eyes, while its retinal motion is zero. This effect is known as the Aubert-Fleischl phenomenon. Here, we describe an analog phenomenon in touch. We asked participants to estimate the speed of a moving stimulus either from tactile motion only (i.e. motion across the skin), while keeping the hand world-stationary, or from kinesthesia only by tracking the stimulus with a guided arm movement, such that the tactile motion on the finger was zero (i.e. only finger motion but no movement across the skin). Participants overestimated the velocity of the stimulus determined from tactile motion compared with kinesthesia in analogy with the visual Aubert-Fleischl phenomenon. In two follow-up experiments, we manipulated the stimulus noise by changing the texture of the touched surface. Similarly to the visual phenomenon, this significantly affected the strength of the illusion. This study supports the hypothesis of shared computations for motion processing between vision and touch.

Key Words: Aubert-Fleischl phenomenon, touch, kinesthesia, spatial frequency, perceptual noise

New and Noteworthy: In vision, the perceived velocity of a moving stimulus is different depending on whether we pursue it with the eyes or not, an effect known as the Aubert-Fleischl phenomenon. We describe an analog phenomenon in touch. We asked participants to estimate the speed of a moving stimulus either from tactile motion, or by pursuing it with the hand. Participants overestimated the stimulus velocity measured from tactile motion compared with kinesthesia, in analogy with the visual Aubert-Fleischl phenomenon.

Introduction

In active vision involving eye movements, perceptual illusions provided an excellent test bench for computational models of motion processing (Palmer 1999). Two of the more famous illusions, the Aubert-Fleischl phenomenon and the Filehne illusion, showed that under certain circumstances the perceived velocity of a moving stimulus is different depending on whether the image moves across the retina, with the eyes stationary, or whether the observer moves the eyes to pursue the stimulus, such that the pursued stimulus is stationary on the retina (Fleischl 1882; Aubert 1886; Filehne 1922; Freeman et al. 2010). The retinal speed is generally overestimated compared to the pursued speed, although this may change depending on the experimental condition (Dichgans et al 1975, Freeman & Banks 1998).

Three main hypotheses have been suggested to explain this phenomenon: First, it may be the consequence of an intrinsic difference in speed measurement between the retinal and the extra-retinal signals. That is, the *gain* between the two signals is intrinsically non-unitary (Dichgans et al. 1969). According to the second hypothesis, the estimated speed provided by the retinal signal will change depending on the *spatial frequency* ξ of a textured stimulus moving across the retina, possibly leading to a mismatch between the retinal and the extra-retinal signals (Dichgans et al. 1975; Diener et al. 1976; Freeman and Banks 1998). In agreement with this hypothesis, the Aubert-Fleischl phenomenon and the Filehne illusion change in magnitude and even in sign depending on the spatial frequency of the stimulus (Dichgans et al. 1975; Freeman and Banks 1998). The Aubert-Fleischl phenomenon even disappears when a single edge is used as stimulus (Dichgans et al. 1975). The dependency of perceived retinal speed on stimulus frequency was explained by assuming a mechanism of motion encoding based on elementary motion detectors (EMDs) of the type of the Hassenstein-Reichardt detectors (Dichgans et al. 1975; Diener et al. 1976). Egelhaaf and Reichardt (1987) characterized the output of an array of motion detectors in response to moving sine-wave patterns having different spatial wavelength λ (with λ being equal to $1/\xi$). Crucially, the response of the array depended on λ, which may account for the dependency of the Aubert-Fleischl phenomenon on the spatial frequency of the texture. A third hypothesis has been suggested, which follows the Bayesian framework to perception: The two illusions would arise from a difference in *precision* between the retinal and extra-retinal signal estimates and thus their differential effects when combined with a prior for object motion (Freeman et al. 2010). According to this framework, it is assumed that the measurements from the two signals are combined with a prior assumption on the statistics of object movement before they are compared (Freeman et al. 2010, Stocker and Simoncelli, 2006: Ernst, 2010). In more detail, the Bayesian framework assumes the following process to generate the two illusions, Filehene and Aubert-Fleischl. First, the observer would measure independently the relative and the absolute object motion from the retinal and the extra-retinal motion signals, respectively. The estimates derived from each of the two measurements are combined with the prior assumption that—statistically speaking—inanimate objects are generally at rest (the “static prior”, sometimes also referred to as “slow motion prior”, Weiss et al., 2002). The noisy sensory estimates (corresponding to the likelihood distribution in the Bayesian framework) and the prior distributions are multiplied and the weighting between them depends on the relative variance of the distributions. The absolute (extra-retinal) and the relative (retinal) velocity estimates have different variance, i.e., different sensory noise, hence are differently affected by the prior. Therefore, the sum of the two will generally be different from zero and thus generate the illusions. Phenomena akin to the Aubert-Fleischl do not only occur in vision, but also in auditory tasks and during self-motion (Garzorz et al., 2016; Freeman et al., 2017; Senna et al., 2017). Here, we investigated whether an analog of the Aubert-Fleischl phenomenon exists also in the somatosensory system, which may indicate similar motion processing mechanisms throughout these different sensory modalities.

The contact of our fingertip with a moving object produces complex patterns of skin deformation, as well as vibrations far from the contact site (Delhaye et al. 2012; Adams et al., 2013; Dallmann et al., 2015; Shao et al. 2016). This is an important difference between touch and vision, where the luminance-stimulus recruits a more defined area of the retina. However, the spatial and temporal engagement of the sensory surfaces—the retina and the skin, respectively—plays an important role in motion encoding in both sensory channels (spatiotemporal cues). A further analogy between the two senses is that in order to achieve spatial constancy the observer needs to account for the movement of the sensor, either the skin or the retina, and the relative movement of the object with respect to them (Moscatelli et al. 2015; Dupin et al. 2017). This leads to hypothesize that the two senses, facing with analogous problems, use similar central mechanisms for the processing of motion. These common mechanisms are referred to as canonical computations (Pack and Bensmaia, 2015). In accordance with this hypothesis, the analog of the Filehne illusion was recently demonstrated in touch (Moscatelli et al. 2015). In order to investigate further the hypothesis of canonical computations, here we evaluated whether an analog of the Aubert-Fleischl phenomenon occurs also in touch. To this end, we asked participants to estimate the speed of a moving stimulus either from tactile motion, by keeping the hand world-stationary (i.e., only motion across the skin), or from kinesthesia by tracking the stimulus with a guided upper-limb movement (i.e., only finger motion but no motion across the skin). In accordance with Proske & Gandevia (2012), we refer to either “kinesthesia” or “proprioception” to indicate the representation of limb position and movement gathered from receptors in the musculoskeletal systems and the skin. If the phenomenon is the same in haptics as in vision, we expect participants to overestimate the speed of the surface as measured by touch compared with kinesthesia. Additionally, we evaluated whether the texture of the moving surface and the perceptual noise affected the strength of the phenomenon. Results showed that these two features of the stimulus modulate the bias, supporting the hypothesis of similar mechanisms of motion processing across the different sensory modalities.

Methods

Participants

Nine right-handed volunteers took part in Experiment 1 (eight females, age range: 19 - 29 years), twelve took part in Experiment 2 (six females, age range: 20 - 29 years), and eight took part in Experiment 3 (six females, age range: 21 - 25 years). All participants were naïve to the purpose of the experiment and had no somatosensory deficits upon self-report. 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 participants. Informed written consent was obtained from all participants involved in the study.

Apparatus

The experimental device (Figure 1) consisted of a motor driven rubber belt (75 x 533 mm), similar to an inverted belt sander. A metal plane was placed under the belt between two rollers to support the participants' finger. The device was actuated by a brushless DC servomotor (Faulhaber motion control system 3564K024B CS), geared to one of the rollers (recommended speed from 5 to 12000 rpm; the speed ranged from 500 to 3000 rpm during the experiment). The motion control system furthermore included a high-resolution encoder (resolution 3000 increments/turn), and a position and speed controller. The motion controller was linked to a PC using a RS232 interface. Custom-made Matlab code was used to operate the motion control system. An L-shaped handlebar was attached to the device, 60 mm away from the right roller to support the finger of the participants during tactile estimation (see below). A computer monitor provided the instructions to the participants.

The belt used in Experiment 1, subsequently named "high spatial-frequency" belt, had a uniformly spaced, ridged texture. The distance between ridges λ was 3 mm, corresponding to a spatial frequency $\xi = \frac{1}{\lambda} \approx 0.3\ cy\ mm^{-1}$ (in cycle per millimeter). Ridge height was 1 mm. Experiment 2 consisted the three experimental conditions. We used one of the following belts in each of the three conditions: (i) the "high spatial-frequency" belt (identical to the one used in Experiment 1), (ii) a "low spatial-frequency" belt which consisted of ridges with lower spatial frequency $\xi = 0.07\ cy\ mm^{-1}$ (ridge height: 1 mm), and (iii) a "smooth" belt, which was lacking any detectable elements such as ridges or dots. The smooth belt consisted of a polyethylene plastic film covering an Armaflex band. In Experiment 3, the polyethylene "smooth" belt was put side to side the ridged belt with high spatial frequency ($\xi = 0.25\ cy\ mm^{-1}$). The width of each of these two belts was 37 mm.

Stimulus and Procedure

Each trial consisted of two intervals during which the reference and the comparison stimuli were presented sequentially with an inter-stimulus interval (ISI) of 2.5 s. The ISI is defined as the time interval between the end of the first motion stimulus and the motion onset of the second stimulus. The order of presentation of the two stimuli was randomized across trials (reference first or comparison first). In each stimulus interval, the belt always rotated counterclockwise, producing a leftward linear motion with respect to the participant. The belt moved with a trapezoidal motion profile including a constant acceleration, a plateau, and a constant deceleration phase (linear acceleration and deceleration $\approx \pm 500\ mm\ s^{-2}$). The linear speed at the plateau was $60\ mm\ s^{-1}$ in the reference stimulus and it was pseudo-randomly chosen among seven possible values in the comparison, ranging from *16.7* to *103.2* $mm\ s^{-1}$. The path length was chosen randomly from four possible path lengths ranging from 140 to 264 mm. This was done to prevent participants from using motion duration as a cue.

The procedure was the following: Participants sat on an office chair in a dimly lit room. The experimental device was placed on a table, to the right of the participants. A black curtain hid the device from participants' sight. Throughout each experimental session, participants wore earplugs and headphones playing pink noise in order to block and mask external sounds. In three experiments, participants reported which of the two stimuli, the reference or the comparison, was moving faster.

[FIGURE 1 ABOUT HERE]

In Experiment 1, participants estimated the speed of the High-Frequency belt either from kinesthesia, by keeping the fingertip on a fixed spot of the belt and following it with a pursuit movement of the arm (kinesthetic "K" stimulus; labelled as K in Figure 1), or from tactile motion, by maintaining the hand stationary (tactile "T" stimulus; T in Figure 1). Participants contacted the belt with the right index finger, to the left side of the rigid handlebar in K intervals, or to the right side of the handlebar in T intervals. Since the belt was always moving leftwards, it kept the finger by the handlebar during T intervals and it pushed the finger away from the handlebar during K intervals. This way, the handlebar prevented finger motion during T intervals, allowing a full slippage of the surface on the skin. In K stimuli, participants performed an active movement of the arm to follow the lateral motion of the belt. We called this "guided movement" or "pursuit" to distinguish it from the self-paced movement studies elsewhere (Morasso, 1981). During each stimulus interval, a drawing on the computer monitor prompted the participant to pursue the belt (K) or to keep the hand world-stationary, and perceive the belt's speed from tactile slip (T). At the end of each trial, after both intervals were completed, participants reported which of the two stimuli moved faster: first or second. They did so by pressing the right or the left button of a standard computer mouse held in the left hand. No feedback was provided during the experiment. The combination of the two modalities, T and K, resulted in four possible experimental conditions: KK, TT, KT, TK where the letter in the first position denotes the modality used as the reference stimulus and the letter in the second position denotes the modality used as the comparison stimulus (irrespectively of the order of presentation). Each of the four conditions was tested in a separate block. The order of the blocks was counterbalanced across participants. Each experiment consisted of 560 trials (4 conditions x 7 speed x 20 replications). The whole experiment lasted approximately six hours. Participants performed the experiment in two days within the same week (two blocks per day).

To test whether spatial frequency modulated the Aubert-Fleishl phenomenon in touch, in Experiment 2, participants were divided into three groups of four participants each. Different groups performed the same task as in Experiment 1 using either the Smooth belt, the Low-Frequency belt, or the High-Frequency belt. This experimental design, known in statistical literature as *split-plot design* (Anderson and McLean, 1974), has the advantage of preventing that a previously tested condition affected participants' response (crossover effect). Additionally, due to the long duration of the experiment, we avoided a within-subject design that would likely have produced non-stationary data for e.g. due to fatigue.

We run a third experiment to test for biases in perceived speed across textures. In Experiment 3, participants performed a tactile speed discrimination task. The motion profile of the stimulus was the same as in Experiment 1 and 2. This time, during both stimulus intervals, the reference and the comparison, participants maintained the hand world-stationary and they estimated the speed of the belt from tactile motion. The order of presentation of the reference and the comparison stimulus was randomized across trials. In each stimulus interval, participants contacted either the ridged (R) or the smooth (S) part of the belt, resulting in four experimental conditions: RR, SS, RS, and SR. Each of the four conditions was tested in a separate block, the order of the block was counterbalanced across participants.

Analysis

In Experiment 1, we fitted the responses of each individual observer with psychometric functions of the form,

$$\Phi^{-1}[P(Y = 1)] = \beta_0 + \beta_1 \Delta v,$$

where Φ^{-1} is the probit link function (Agresti 2002). The response variable Y had the value 1 if the observer reported the belt was moving faster in the comparison than in the reference, and 0 otherwise. On the right side of the equation, $\Delta v = v_{comp} - v_{ref}$ is the difference in speed between the comparison and the reference stimulus and β_0, β_1 are the intercept and the slope of the linearized equation, respectively. We analyzed the data of all nine observers using a Generalized Linear Mixed Model (GLMM), a hierarchical model extending the psychometric function to the group level (Agresti 2002; Moscatelli et al. 2012).

We evaluated the accuracy of the response in KT and TK to address our main research question, whether the modality of exploration, tactile slip or hand pursuit, affected the perceived surface velocity. To this end, we computed the *point of subjective equality* $PSE = -\frac{\beta_0}{\beta_1}$ corresponding to the stimulus value yielding a response probability of 0.5. The PSE should not differ significantly from zero if responses were accurate. Instead, if the illusion was the same in haptics as in vision, tactile-measured speed should be overestimated with respect to kinesthetic-measured speed. Therefore, when the PSE is determined from the KT condition it should be lower than zero and vice versa for TK: $PSE_{KT} < 0 < PSE_{TK}$. From the conditions KK and TT, we estimated the perceptual noise from the *just noticeable difference* of the psychometric functions ($JND = \frac{0.675}{\beta_1}$, where 0.675 is the 75th percentile of a standard normal distribution). We estimated the two parameters (PSE and JND) and the related 95 confidence interval using a bootstrap method described in (Moscatelli et al., 2012).

We applied a similar model in Experiment 2 and 3. In addition, in Experiment 2 we applied a multivariable GLMM to test whether the spatial frequency of the stimulus modulated the perceptual illusion. The multivariable GLMM accounted for two continuous predictors, the difference in speed between reference and comparison, Δv, and the spatial frequency of the surface ξ. In line with previous studies (Dépeault et al. 2008), we assumed that the perceived velocity $\hat{v}_T$ is a linear combination of the physical velocity v and the spatial frequency ξ:

$$\hat{v}_T = \beta_1 v + \beta_2 \xi.$$

We set $\xi = 0\ cy\ mm^{-1}$ for the smooth surface with no detectable texture elements (zero cycle per mm). The model assumes that the perceived kinesthetic velocity of a given stimulus is a linear function of the physical velocity of the belt:

$$\hat{v}_K = \beta_1 v.$$

Accordingly, the perceived difference in speed $\Delta\hat{v}$ between the comparison and the reference stimulus is:

$$\hat{\Delta v} = \begin{cases} \hat{v}_T - \hat{v}_K = \beta_1 \Delta v + \beta_2 \xi & \text{if } KT, \\ \hat{v}_K - \hat{v}_T = \beta_1 \Delta v - \beta_2 \xi & \text{if } TK. \end{cases}$$

The probability that in a given trial j the comparison stimulus is perceived faster than the reference is given by the probability that $\Delta\hat{v} > 0$:

$$\begin{aligned} P(Y_j = 1) &= P(\hat{\Delta v} > 0) \\ &= \Phi(\hat{\Delta v} > 0) \\ &= \Phi(\beta_1 \Delta v \pm \beta_2 \xi), \end{aligned}$$

Providing the following response function for each participant i:

$$\Phi^{-1}[P(Y_i = 1)] = \beta_1 \Delta v \pm \beta_2 \xi.$$

Finally, using a mixed-model framework, we extended the model to the whole sample of participants.

$$\Phi^{-1}[P(Y_i = 1|u)] = \beta_1 \Delta v \pm \beta_2 \xi + Zu$$

The model accounted for the random variability between participants and blocks by means of the random-effect predictors Zu, where u is the normally distributed error term: $u \sim N(0, u)$ and Z is the label specifying the participant. In the model above, we tested whether the two parameters were significantly different from zero with the Likelihood Ratio (LR) test.

Results

Experiment 1: The Haptic Analog of the Visual Aubert-Fleischl Phenomenon

Participants compared the speed of the moving belt between a reference and a comparison stimulus. In different experimental conditions, participants estimated the speed in each stimulus interval from either kinesthesia (K), by tracking the belt with a guided upper-limb movement, or from tactile motion (T) by keeping the hand world-stationary (Figure 1). In the “kinesthetic-tactile” condition (KT), participants estimated the reference speed from kinesthesia and the comparison speed from tactile motion. In the “tactile-kinesthetic” condition (TK) the procedure was identical, except that this time participants estimated the reference stimulus from tactile motion and the comparison from kinesthesia. In case of an illusion, we expect to find a shift in the PSE in the opposite directions between the two conditions, KT and TK. In order to measure the perceptual noise involved in the K and T estimates, we additionally conducted two unimodal tasks, TT and KK. In each of the two, the reference and the comparison stimulus were estimated from the same sensory modality (tactile motion in TT and kinesthesia in KK). The order of the four experimental blocks was randomized across participants. In case of the Bayesian account for the illusion, we expect the illusion to scale with the difference in noise between the K and T conditions.

For each block and participant, we fit psychometric functions as described in the method section and determined the Point of Subjective Equality (PSE). The PSE would be larger than zero if the comparison was perceived as slower than the reference, and smaller than zero otherwise. If the modality of exploration (T or K) did not introduce any bias in the perceived speed, the PSE would be non-significantly different from zero. Figure 2 shows the psychometric functions for a representative observer (a) and the PSE estimates in the group data of all nine observers (b). The PSE was significantly smaller than zero in KT, $-7.2 \pm 1.9\ mm\ s^{-1}$ (estimate$\pm SE$) and significantly larger than zero in TK, $16.2 \pm$

1.8 $mm\ s^{-1}$ (Figure 2B). This means that the participants perceived the velocity of the surface as faster when they measured it from tactile motion, with the hand world-stationary, than when they measured it from kinesthesia. The slope of the GLMM was equal to 0.048 in KT and 0.039 in TK. This means that the task was slightly easier in KT as compared to TK (possibly due to the different level of motor noise in the two conditions, because in TK participants pursued a stimulus that varied in speed across trials).

In each unimodal condition, the Just Noticeable Difference (JND) provided an estimate for the discriminability of the stimulus. The JND was numerically similar across conditions. It was 11.8 $mm\ s^{-1}$ in TT (95% CI: 10.0– 14.0 $mm\ s^{-1}$) and 12.1 $mm\ s^{-1}$ in KK (95% CI: 10.3– 14.6 $mm\ s^{-1}$). This corresponds to a Weber fraction of 0.197 and 0.20, respectively. In both conditions, the discriminability of the stimulus was in agreement with the values reported in the literature (Lönn et al. 2001; Bensmaia et al. 2006; Dallmann et al., 2015).

Supplementary figures showing raw data and GLMM fit in Experiment 1-3 is available on Github at the following URL: https://github.com/moskante/Supplementary

[FIGURE 2 ABOUT HERE]

Experiment 2: Spatial Frequency and Perceptual Noise Modulates the Aubert-Fleischl Phenomenon

In vision, the spatial frequency of the stimulus modulated the Aubert-Fleishl phenomenon, such that with an increasing spatial frequency of the visual background, the retinal speed was increasingly perceived as being faster compared to the extra-retinal speed (Dichgans et al. 1975; Diener et al. 1976; Freeman and Banks 1998). The speed bias did not occur when a single edge stimulus moved across the visual field ($\xi = 0\ cy\ mm^{-1}$). If the mechanism generating the speed bias is the same in touch as in vision, we should be able to modulate the perceptual bias by changing the spatial frequency of the contact surface. Similarly, the speed bias should not occur if participant contacted a homogeneous surface, lacking any detectable element such as ridges or dots. To test this hypothesis, we replicated the same task as in Experiment 1, but varied the spatial frequency of the tactile stimulus. Twelve participants were randomly assigned to three groups of 4 each, and they performed the task using (1) the High-Frequency ($\xi = 0.3\ cy\ mm^{-1}$), (2) the Low-Frequency ($\xi = 0.07\ cy\ mm^{-1}$), or (3) the Smooth belt ($\xi = 0\ cy\ mm^{-1}$).

We fit the data with the multivariable GLMM, described in the method session. The probability of perceiving the comparison stimulus as faster than the reference increased with the difference in speed, Δv, and the spatial frequency of the belt, ξ. That is, both parameters β_1, β_2 were significantly different from zero, $\beta_1 = 0.04 \pm 0.004$ (LR test; $\chi_1 = 93.6$; p < 0.001) and $\beta_2 = 2.3 \pm 0.44$ ($\chi_1 = 27.9;\ p < 0.001$). This means that the higher was the spatial frequency of the surface, the faster was perceived motion stimulus. For a comparison with Experiment 1, we computed the PSE values in KT and TK separately for each of the three groups (Figure 3). With the Smooth belt, the PSE was equal to $2.9\ mm\ s^{-1}$in KT (95% CI from -2.5 to $8.8\ mm\ s^{-1}$) and $4.3\ mm\ s^{-1}$in TK (95% CI from 0.24 to $8.9\ mm\ s^{-1}$). With the Low-Frequency belt, the PSE was equal to $-9.5\ mm\ s^{-1}$ in KT (95% CI from -16.1 to $-3.5\ mm\ s^{-1}$) and $9.6\ mm\ s^{-1}$ in TK (95% CI from 5.0 to $14.6\ mm\ s^{-1}$). With the High-Frequency belt, the PSE was equal to $-10.4\ mm\ s^{-1}$ in KT (95% CI from -17.0 to $-4.7\ mm\ s^{-1}$) and $21.2\ mm\ s^{-1}$in TK (95% CI from 15.3 to $28.8\ mm\ s^{-1}$). Taking together the two analyses, multivariable GLMM and PSE estimates, we conclude that the tactilely sensed spatial frequency modulated the haptic version of the Aubert-Fleischl illusion, similarly as reported for vision. In the range tested here, results were consistent with a linear effect of the spatial frequency on perceived speed.

In our previous study, we computed the tactile gain g in the Filehne illusion as $g = 1 - (PSE/pursuit\ speed)$ which was equal to $g=0.4$ (Moscatelli et al., 2015). Likewise, it is possible to compute the tactile gain in the Aubert-Fleischl phenomenon as $g = 1 - (PSE/reference\ speed)$ in TK and $g = 1 + (PSE/reference\ speed)$ in KT. A gain smaller than one indicates that participants overestimated surface speed when measured from touch compared to proprioception. On average, this was the case. In TK, the tactile gain was equal to $g = 0.93$, 0.84 and 0.65 for the three texture with spatial frequencies 0.0, 0.07, and 0.3 cy mm^{-1}, respectively. In KT, it was *g = 1.05, 0.84* and *0.83* for the 3 textures, respectively. Like in vision, the gain changed with the spatial frequency of the surface: it was close to one for the smooth surface, and progressively smaller for higher frequencies.

With the high frequency belt, speed bias was numerically larger in TK than in KT. This can be observed either from the PSE or from the gain values. We hypothesized an explanation in Appendix.

[FIGURE 3 ABOUT HERE]

In vision, the Bayesian model introduced by Freeman et al. (2010) provides an explanation for the illusion alternative to the one based on spatial frequencies described by Dichgans et al. (1975). According to this model, the estimated retinal speed is a function of the perceptual noise, so that the noisier the retinal signal, the lower is the perceived speed. Here we tested this hypothesis, as follows: for each participant, we computed the Euclidean distance between the PSE in KT and the PSE in TK to summarize the perceptual bias across the two conditions (labelled as *Bias* in the equation below). In order to see whether the difference in JND between the tactile and the proprioceptive estimate was a predictor for the size of the illusion, we regressed the perceptual bias towards the difference in JND between the two unimodal discrimination tasks, $\Delta_{JND} = JND_{TT} - JND_{KK}$. The linear model was the following:

$$Bias \sim \alpha_0 + \alpha_1 \Delta_{JND} + \varepsilon,$$

where α_0 and α_1 are the intercept and the slope, respectively, and ε is the error term. The slope of the linear regression α_1 was significantly different from zero ($\alpha_1 = -1.5$, $p = 0.018$). We can therefore conclude that the difference in noise predicted the size of the bias and thus the magnitude of the illusion (Figure 4A).

The spatial frequency and the Bayesian model predict that the observer would perceive *from touch* the movement of smooth surfaces as being slower than the one of textured surface (Figure 4B). In the former, the dependency of the perceived tactile speed on the spatial frequency of the surface is a property of the array of the elementary motion detectors that encode surface motion. Instead, in the Bayesian framework, reducing the spatial frequency would increase the noise in tactile measurements and therefore the slow-motion prior would receive more weight such that it can introduce a larger bias.

We considered also a third explanation that the speed bias depend on kinesthesia rather than on touch. Since friction coefficient changed between the two ridged and the smooth belt, it may be more difficult pursuing the smooth than the ridged belt, and this may have generated the speed bias. To test this hypothesis, we used a GLMM and compared the responses in the KK blocks (i.e., hand pursuit only) across the three belt conditions. We coded *belt type* as factor, with *smooth belt* as baseline. The main effect of *belt type* and the interaction between *belt type* and *speed* were not statistically significant ($p > 0.1$). This means that while pursuing, the belt did not significantly affect the response.

In addition to the negative result in the analysis above, we run a third experiment to test directly the "tactile" explanation. If the modulation of the speed bias depended on touch, a moving textured surface would be perceived as faster than a smooth surface when both are measured from tactile sense. The frequency and the Bayesian model both predict this outcome. The Bayesian model also predicts that the two stimuli would be associated with a different perceptual noise: the one perceived as faster being associated with less perceptual noise.

[FIGURE 4 ABOUT HERE]

Experiment 3: Spatial Frequency Affects the Perceived Tactile Velocity

Previous studies reported that the frequency of periodic motion, for e.g., a moving sine-wave grating in vision or a sinusoidal amplitude-modulated signal in audition, affects its perceived speed (Diener et al., 1976; Senna et al., 2017). Likewise, Dépeault et al. (2008) showed that the spatial frequency of a touched surface affects its perceived tactile speed. When participants judged the perceived speed of moving surfaces with different textures (ξ ranging from 0.3 to 0.125 cy mm^{-1}) using a magnitude estimation task and assigning arbitrary numbers to perceived speed, they reported the textures with a higher spatial frequency as moving faster than those with a lower spatial frequency. In separate blocks, smooth surfaces were also tested. Unfortunately, however, the study was not designed for a direct comparison between textured and smooth surfaces because participants may have changed their rating scale across the two conditions.

Here we run a third experiment to compare directly the perceived tactile speed of textured versus smooth moving surfaces. We chose these two surfaces because they produces the largest speed bias (texture surface) and no speed bias (smooth surface) in Experiment 2. Participants performed a forced-choice, speed discrimination task. This time, they maintained the hand world-stationary for both the reference and the comparison stimulus, and they estimated the speed of motion from tactile measurement only. In each stimulus interval, participants contacted either the textured ($\xi = 0.25$ cy mm^{-1}) or the smooth part of the surface that were placed side-by-side on the band drive.

Figure 5 shows the group estimates of the PSEs and JNDs across all 8 observers. The JNDs in RR and SS provided an estimate for the discriminability of the two stimuli. The JND was $13.9\ mm\ s^{-1}$ in RR (95% CI: 12.0– 15.7 $mm\ s^{-1}$) and 17.6 $mm\ s^{-1}$ in SS (95% CI: 14.9– 20.3 $mm\ s^{-1}$); therefore, the speed of motion was easier to discriminate with the ridged compared to the smooth surface. The PSE was significantly larger than zero in RS, $28.5 \pm 3.5\ mm\ s^{-1}$ (estimate$\pm SE$) and significantly smaller than zero in SR, $-7.1 \pm 1.3\ mm\ s^{-1}$ (Figure 5B). This means that the ridged surface was perceived as moving faster than the smooth one. The difference in the discriminability of the stimulus and the bias on the perceived speed are consistent with the results obtained by Dépeault et al. (2008).

The effect size, estimated from the absolute shift between the PSE and the reference speed, was much larger in RS than in SR. To test whether this difference was statistically significant, we computed for each participant the absolute value of the PSE in each of the two conditions, RS and SR. This time we analyzed the data using non-parametric statistics because the distribution of the variable deviated markedly from normality. Absolute values of PSEs were significantly different between the two conditions (Wilcoxon signed rank test, $p < 0.01$, median difference = 18 $mm\ s^{-1}$). The effect was not due to an after-effect because order of presentation of the reference and comparison stimulus was counterbalanced across trials. Hence, the number of times the textured stimulus was presented first was the same between RS and SR. The only difference between the two conditions was the variability of the speed values. That is, in RS the speed of the smooth surface, but not the one of the textured surface varied across trials, and vice-versa in SR. Investigating this additional finding in more depth is beyond the purpose of this study. In Appendix, we suggest an explanatory model accounting for it.

[FIGURE 5 ABOUT HERE]

Discussion

In touch as in vision, the bodily surface that contains the sensory receptors is movable with respect to the other body parts. Estimating motion of external objects often requires taking into account movements of the sensor (eye or hand motion) and the relative motion of the object with respect the sensory surface (retinal or tactile slip). The two senses have weak spatial constancy, because combining relative and sensor motion leads to inaccurate estimates of object motion (Freeman and Banks 1998; Ziat et al. 2010; Wexler and Hayward 2011; Moscatelli et al. 2015). Accordingly, in a previous paper we showed a systematic error in the perceived direction of a movable texture in touch, akin to the Filehne illusion in vision (Moscatelli et al. 2015). We quantified the strength of the Filehne illusion in touch from the tactile gain that was equal to 0.4. This gain means that participants *implicitly* overestimated the tactile speed compared to hand speed. In the current study, participants overestimated the speed of the moving stimulus measured from touch compared with the one measured from proprioception, as measured *explicitly* in the speed discrimination task. We suggest that this novel phenomenon could be a putative analog of the

Aubert-Fleischl phenomenon in vision. In the current experiments, the tactile gain was always smaller than one, albeit larger than the one estimated in the Filehne illusion. In our previous study, we generated the tactile stimuli by means of a tactile display (Latero, Tactile Labs, Inc.); therefore, motion stimuli lacked net shear force (Moscatelli et al., 2015). This, and the other differences in the experimental protocol, may account for the difference in the tactile gain between the two studies.

In addition to biases in perceived object motion, combining motion signal between proprioception and touch may lead to illusory sensation of hand displacement and rotation (Blanchard & al 2011; Moscatelli et al., 2016; Bianchi et al., 2017, Moscatelli et al., 2019). In our previous, we hypothesized that also these proprioceptive illusions arise from the assumption from the observer that inanimate object around us are preferentially at rest, i.e., on the static prior studies (Moscatelli et al., 2016; Moscatelli et al., 2019). This way, when touching a moving object, the observer would attribute the relative motion felt on the skin to voluntary movement of the hand rather than surface motion, generating an illusory sensation of hand movement. In the current study, it is unlikely that participants integrated the information from proprioception and touch to estimate hand motion because participants were always aware that the belt was moving. Therefore, tactile information would not provide information on hand motion, which was prevented by the handlebar. Additionally, the task did not require simultaneous processing of tactile and kinesthetic motion (T and K intervals were presented sequentially).

Behavioral and imaging studies highlighted several analogies in motion processing between vision and touch (Hagen et al., 2002; Depeault et al., 2008; Bicchi et al., 2008; Moscatelli et al., 2015). For instance, both senses have weak spatial constancy, as explained above. Motion aftereffects transfer between vision and touch (Konkle et al., 2009). Analogies in motion perception may depend either on similar functional mechanisms, or on the partial overlap of the neural network between the two sensory modalities. Classical studies in physiology attributing to the primary somatosensory cortex a central role for motion processing in touch (Pei and Bensmaia, 2014). Additionally, other studies revealed that tactile motion also activates the human middle temporal/V5 (MT/V5) complex, which is also important for processing of visual motion (Hagen et al., 2002). These and other results led to the hypothesis of canonical computations, postulating that, despite the huge differences in stimulus encoding, the two senses may share common mechanisms of motion processing at a higher level of representation (Pack and Bensmaia 2015).

Due to such analogies between vision and touch, it is tempting to compare the strength of the Aubert-Fleischl phenomenon between the two senses. To this end, we compared the visual and tactile gain, as measured by Freeman and Banks (1997) with the one determined here. In (Freeman and Banks, 1997), participants were always required to pursue the reference stimulus, with a pursuing speed of 6.2 deg s^{-1}. This corresponds to KT condition in our study (hand-pursue of the reference stimulus). A second difference with our analysis, Freeman and Banks (1997) computed the PSE w.r.t. the speed of the comparison, whereas in our study we computed the PSE w.r.t. the difference between the speed of the reference and the speed of the comparison. To compare the results between the two studies, we computed the retinal gain as *g=1 + [(PSE – reference speed)/reference speed]*, and the tactile gain in KT as *g=1 + (PSE/reference speed).*

Like in touch, the Aubert-Fleischl phenomenon in vision scales with the spatial frequency the surface, expressed cycles per angular degree (Freeman and Banks, 1997). By inspecting Figure 3 of the original paper, for a frequency of 1 cy deg^{-1} the PSE was approximately 4 deg s^{-1}leading to a visual gain of 0.65. The tactile gain in KT in the two textured surfaces was slightly higher, about 0.8 (Result section). An important caveat when comparing the two senses is that spatial frequency in vision scales with distance, being expressed in cy deg^{-1}, unlike in touch where is expressed as $cy\ mm^{-1}$.

Dichgans et al. (1975) tested the Aubert-Fleischl phenomenon by using the method of the adjustment, and estimated the speed ratio between the speed perceived with eye pursuit and retinal slip. This was equal to one for a stimulus consisting of a moving edge (i.e., the phenomenon did not occur), and to 1.35 and 1.46 for the spatial period equal to 30 deg and 15 deg, respectively. We computed the speed ratio in our study as (|PSE| + reference speed)/ reference speed. This is approximately equal to one for the smooth surface, akin to the results with a single edge in vision. In TK, it was equal to 1.16 and 1.35 for the spatial frequency equal to 0.07, and 0.3 $cy\ mm^{-1}$, respectively. Conversely, in KT it was equal to 1.16 and 1.17 for the two spatial frequencies. In conclusion, we found qualitative agreement between vision and touch; however, the effect size was smaller in our study.

In vision, occasional slips between the retina and the target occur while pursuing (Freeman et al, 2010). In our protocol, we may expect partial slips along with the dynamic pattern of skin strain in response to the shear force by a moving surface (Delahye et al., 2016; Dzidek et al., 2017). Partial slips and shear strain may provide a cue for the detection of motion onset in both, K and T intervals. Instead, full slip between the belt and the fingertip is unlikely in K intervals, due to the slow belt velocity and the high coefficient of friction of rubber (Dzidek et al., 2017). Specifically, the peak velocity of the belt was much slower than the peak hand velocity in unrestricted movements—between 1.6 -10 cm/s in our stimuli, and typically above 60 cm/s in unrestricted hand movements (Morasso, 1981). This allowed pursuing the belt with the finger, without much effort from the participant.

Three hypotheses have been suggested to explain the Aubert-Fleischl phenomenon in vision. The first hypothesis postulates the existence of an intrinsic, fixed gain between retinal and extra-retinal signals (Dichgans et al. 1975). Alternatively, other studies hypothesized a mechanism of motion encoding which is sensitive to the spatial frequency of the stimulus, as for example an array of elementary motion detector, which (Dichgans et al. 1975; Freeman and Banks 1998). As a third hypothesis, Freeman et al. (2010) suggested a Bayesian process, where the interaction of a zero-centered prior (static prior) with the motion estimates from retinal slip and eye pursuit, each having a different amount of noise, generated the bias. Here, we showed that the perceived tactile speed changes with the spatial frequency of the textured stimulus, which goes along with different amounts of noise in the perceptual estimates. Hence, the tactile Aubert-Fleischl phenomenon is not consistent with the hypothesis of an intrinsic, fixed gain.

The spatial frequency of the stimulus and the perceptual noise in the speed discrimination task were highly correlated. Likewise, in vision the spatial frequency of the stimulus affected the perceptual noise in a speed discrimination task, as attested by the steeper slope of the psychometric functions for higher frequency stimuli (Diener et al. 1976). Because of to the correlation between the two experimental variables (texture and noise), it is not possible to establish whether the Auber-Fleischl phenomenon, and its putative analog in touch, depends on the spatial frequency or on the Bayesian prior (Figure 4B). In our previous study, we produced a similar illusion, the Filehne illusion, by means of a tactile display consisting on an array of vibrating pins (Moscatelli et al., 2015). This way, we were able to change the reliability of the tactile stimuli by changing the amplitude of pin vibrations, without modifying the spatial frequency of the rendered surface. This change in reliability significantly affected the strength of the illusion, the motion bias being smaller when the reliability of the tactile signal was reduced (low amplitude vibrations).

The Bayesian hypothesis and the spatial frequency explanation are not mutually exclusive, as they represent on different levels the same phenomenon (the speed bias depending on the texture of the moving surface). The former one is about motion encoding, whereas the latter one about a higher computational mechanism involving the static prior. The Bayesian hypothesis has been deeply discussed elsewhere (Moscatelli et al. 2015). We discuss below the correlation detector hypothesis, which instead, to the best of our knowledge, has been overlooked in tactile literature.

Models based on elementary motion detectors (EMD; also known as Hassenstein-Reichardt detectors) provide a viable, neuronally plausible solution for motion encoding in vision (Reichardt, 1961; Borst and Egelhaaf 1989; Eichner et al., 2011) and have been proposed for other perceptual functions over the years (Parise and Ernst, 2016). Behavioral and neurophysiological studies in invertebrates and mammals, including humans provide evidences supporting this model (Bradley and Goyal, 2008). In its simplest form, a Hassenstein-Reichardt detector consists of two luminance sensors that are offset in space. The outputs of the two sensors are combined and multiplied to produce a response that is large when the sensors are triggered sequentially with a particular delay.

The response of individual EMDs depends on surface pattern: their response optima are shifted towards larger velocities for patterns with larger spatial wavelengths, λ (Reichardt 1987; Borst and Egelhaaf 1989, Egelhaaf and Reichardt 1987). Higher neurons in the visual system receive input by large arrays of individual EMD. Egelhaaf and Reichardt (1987) studied the response of an array of EMD and predicted its dependency on λ. In accordance with that, in human vision a textured surface with a high spatial frequency is perceived as moving faster than a second surface having lower frequency and moving at the same physical speed (Dichgans et al. 1975; Diener et al. 1976). Likewise, a possible explanation for the frequency bias observed in the current study is that motion encoding in touch relies (at least partially) on a mechanism akin to EMD in vision. Mechanoreceptors having small receptive fields, such as Meissner and Merkel type receptors, may be the neural substrate of tactile EMD, with the encoded speed depending on the delay in the activation of two neighbor receptors. The somatosensory system may integrate the outcome of the array of EMDs with the other motion cues described in previous studies (Dallmann et al., 2015; Barrea et al., 2018, Moscatelli et al, 2019). Further studies are necessary to address this hypothesis. These two explanations for the tactile Aubert-Fleischl phenomenon, postulating a tactile EMD or a central processing implying a stationarity prior, are not mutually exclusive, rather they address different levels of explanation (computation vs. neuronal implementation). Correlation detectors provide the system with an estimate of local motion. In the Bayesian model in vision, the global motion estimate is the convolution of the local estimates at different points of the surface and the static prior (Weiss et al., 2002). Likewise, in touch the correlation detectors and the Bayesian integration may represent two layers of motion processing, encoding local and surface (global) motion, respectively.

In conclusion, we showed a putative analog of the haptic Aubert-Fleischl phenomenon, which sheds light on the influence of noise and features of the textured surface on the tactile perception of motion. In this regard, such studies on perceptual illusions provide clear evidence of similarities in the motion processing between vision and touch, at a high level of representation.

Acknowledgments

This work was partially supported by the European Commission funded projects WEARHAP (project no. 601165) and the German Research Foundation DFG (CITEC). We thank Meike Scheller, Gabriele Joanna Kowalski and Sven Bergfeld for help with the setup and testing of participants, and Vincent Hayward and Irene Senna for inspiring discussions. Partial data from Experiment 1 (N = 6) have been presented at the Eurohaptics conference, 2014, Paris (Moscatelli et al., 2014).

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APPENDIX: INTEGRATION OF MOTION CUES IN TOUCH

In touch like in vision, features of the moving texture like the spatial frequency and the orientation of parallel ridges bias the perceived motion direction and speed (Diener et al. 1976; Bicchi et al., 2008; Depeault et al., 2008). This suggested that motion estimate in the two senses is partially based on *pattern-dependent cues,* i.e., on motion cues that are affected by the spatial frequency of the moving texture (Borst and Egelhaaf 1989). Pattern-dependent cues are relative motion cues, potentially providing information on the absolute surface velocity if specific features of the texture are known. For instance, a mechanism of motion encoding based on Hassenstein-Reichardt detectors would respond to the temporal frequency of a periodic motion, but it would account for the absolute surface velocity if the distance between its texture elements, λ, is known.

In agreement with previous studies, we found that the speed of a moving surface that was textured with parallel ridges was overestimated compared to a smooth surface moving at the same physical speed. However, in some conditions the bias was smaller than in others: In Experiments 1-2, the effect size (estimated from the absolute difference between the PSE and the reference speed) was significantly larger when the textured surface was in the reference stimulus, and the comparison speed was measured from proprioception (Exp. 1-2). Likewise, in Exp. 3 the effect size was significantly larger in RS than in SR, i.e. it was larger when the textured surface was in the reference stimulus. The order of presentation of the reference and comparison stimulus cannot explain this phenomenon because it was counterbalanced across trials: On average, the number of times the textured stimulus was presented first was the same for e.g. in RS and SR. Instead, in SR (but not in RS) the textured surface was explored across a variable range of motion speeds. This possibly enabled neural mechanisms for cue calibration that partially attenuated the bias.

The mechanism proposed here is similar to the one studied for depth cue combination in vision (Landy et al., 1995). This is a two-step algorithm, where an auxiliary cue is first calibrated by the interaction with absolute cues, a process referred to as *cue promotion*. For instance, in depth perception, motion parallax (absolute cue) and stereo disparity (relative cue) interact to specify the missing parameter of the viewing distance, and this interaction promotes the stereo cue. Next, the promoted cue is combined with other absolute cues to provide an optimal estimate of the stimulus feature, e.g. viewing depth. We will explain the hypothesis for Exp. 3; however, the same would apply to the other two experiments. We assumed that in the "R" stimulus interval in Exp. 3 (i.e., when contacting the textured surface), the observed is provided with at least two speed estimates, the one conveyed by the temporal frequency of the stimulus (the *relative or pattern-dependent cue*), and a second unbiased estimate, which was not affected by the surface texture. An example of unbiased speed estimate is the rate of tangential stretch that we investigated in a recent study (Moscatelli et al., 2019). The temporal frequency cue ($f = v/\lambda$) can be promoted to an absolute speed cue once the distance between texture elements λ is specified. We labelled the pattern-dependent and the unbiased estimates as $\hat{v}_{pd}$ and $\hat{v}_{un}$, respectively. In the tested range of speed, we assumed that $\hat{v}_{un}$ is a linear function the physical speed of the stimulus, v:

$$\hat{v}_{un} = v + \varepsilon_{un},$$

Where $\varepsilon_{un}$is the error term, Instead $\hat{v}_{pd}$ is a function of on the temporal frequency, f, and the unknown texture parameter, λ:

$$\hat{v}_{pd} = q(f, \lambda) + \varepsilon_{pd},$$

where ε_{pd} the error term and $q(\cdot)$is the computation to estimate the velocity from the two cues. As noticed in (Landy et al., 1995), when the a single stimulus value is available, for e.g. the R stimulus in RS, the observer can estimate the missing parameterλ by posing $\hat{v}_{un} = \hat{v}_{pd}$, and solving the equation for λ. Instead, when multiple speed samples were available (e.g., the R stimulus in SR), the observer can obtain a more stable estimate of λ, for e.g. using the value of $\hat{\lambda}$ that minimizes the least square distance between $\hat{v}_{pd}$ and $\hat{v}_{un}$. The larger is the variability of the speed sample, the better the estimate of λ (Landy et al., 1995). Finally, the fused estimate of motion speed, $\hat{v}$, can be assumed as a weighted average of the two cues:

$$\hat{v} = w_{un}\, \hat{v}_{un} + w_{pd}\, \hat{v}_{pd}.$$

In summary, the difference in the effect size for e.g. between RS and SR may possibly arise from a better calibration of the pattern dependent cue in SR, where the ridged surface was explored across a variable range of motion speeds, due to the more stable estimate of λ.

Figure Caption

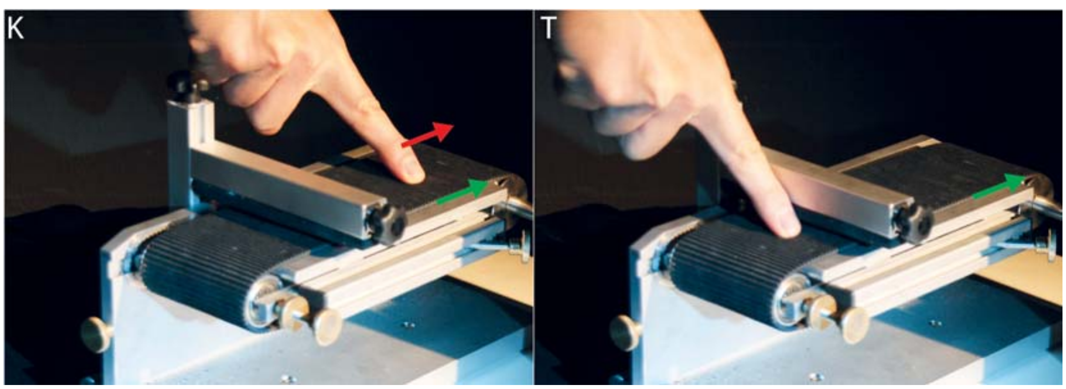
Fig. 1. *Experimental Procedure. Participants compared the speed of motion of the belt between a reference and a comparison stimulus. In each stimulus interval, they touched the belt and estimated its speed from kinesthesia, by moving the hand to second belt's motion (labelled as K) or from touch, by keeping the hand world-stationary (labelled as T).*

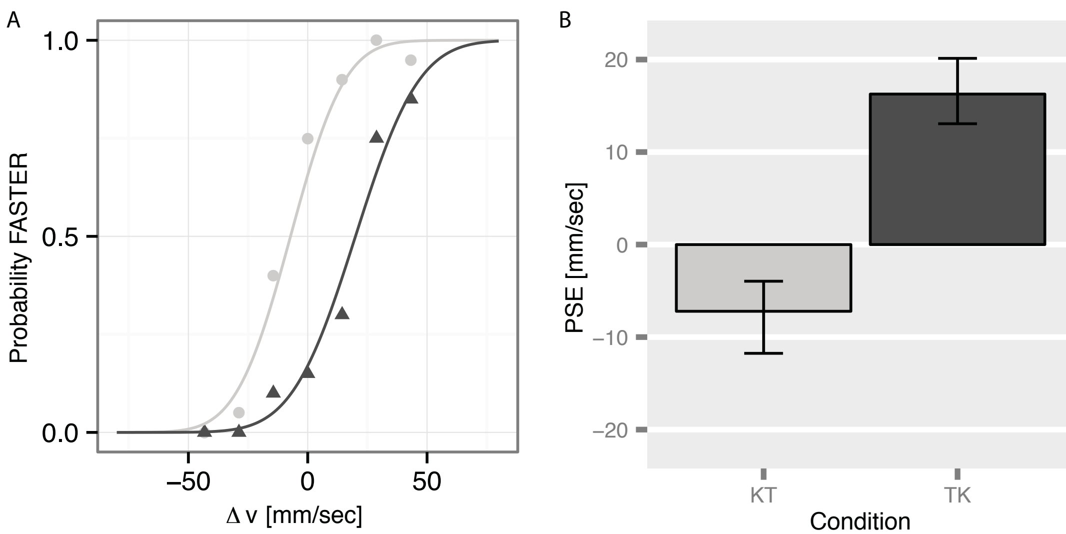
Fig. 2. *Results of Experiment 1. (A) The psychometric functions for a representative participant, in the two experimental conditions (gray: KT; black: TK). (B) The point of subjective equality (PSE) in the two experimental conditions (N = 9). The bootstrap-based 95% CIs ranged from* -11.8 *to* $-4.0\ mm\ s^{-1}$ *in KT and from 13.0 to* $20.1\ mm\ s^{-1}$ *in TK.*

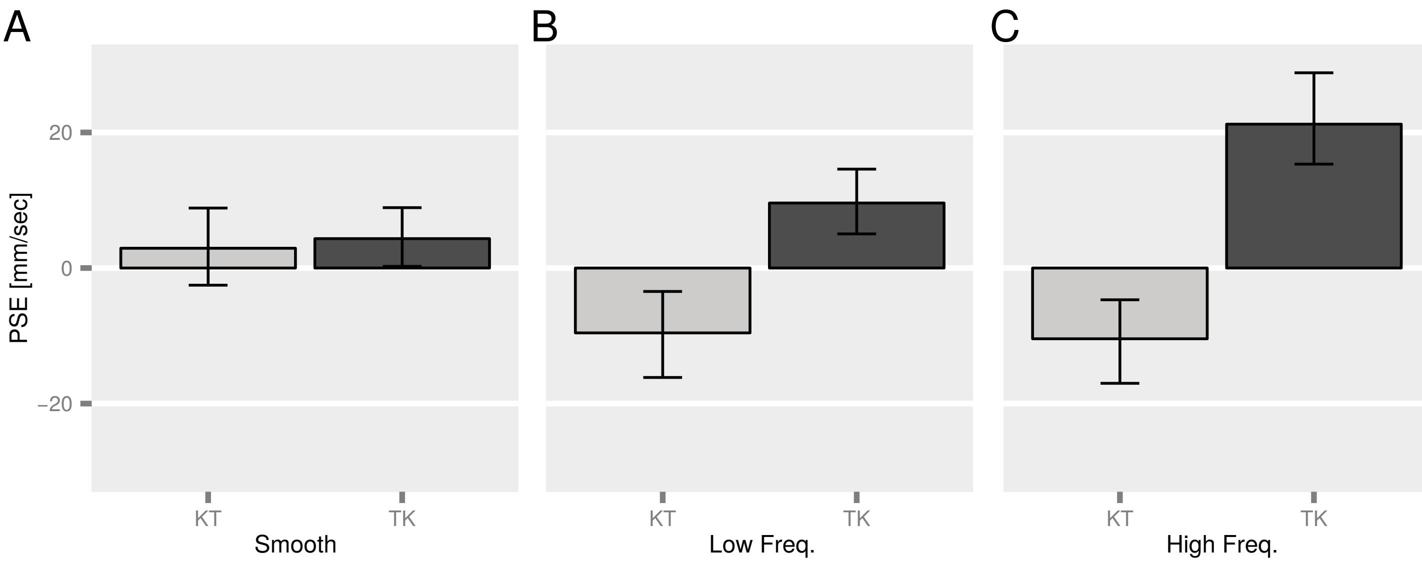
Fig. 3. *Results of Experiment 2. The phenomenon observed in the first experiment changed in size, depending on the texture of the contact surface. Estimated PSE and bootstrap-based 95% CIs. Results with (A) the smooth surface (B) the low frequency surface and (C) the high frequency surface.*

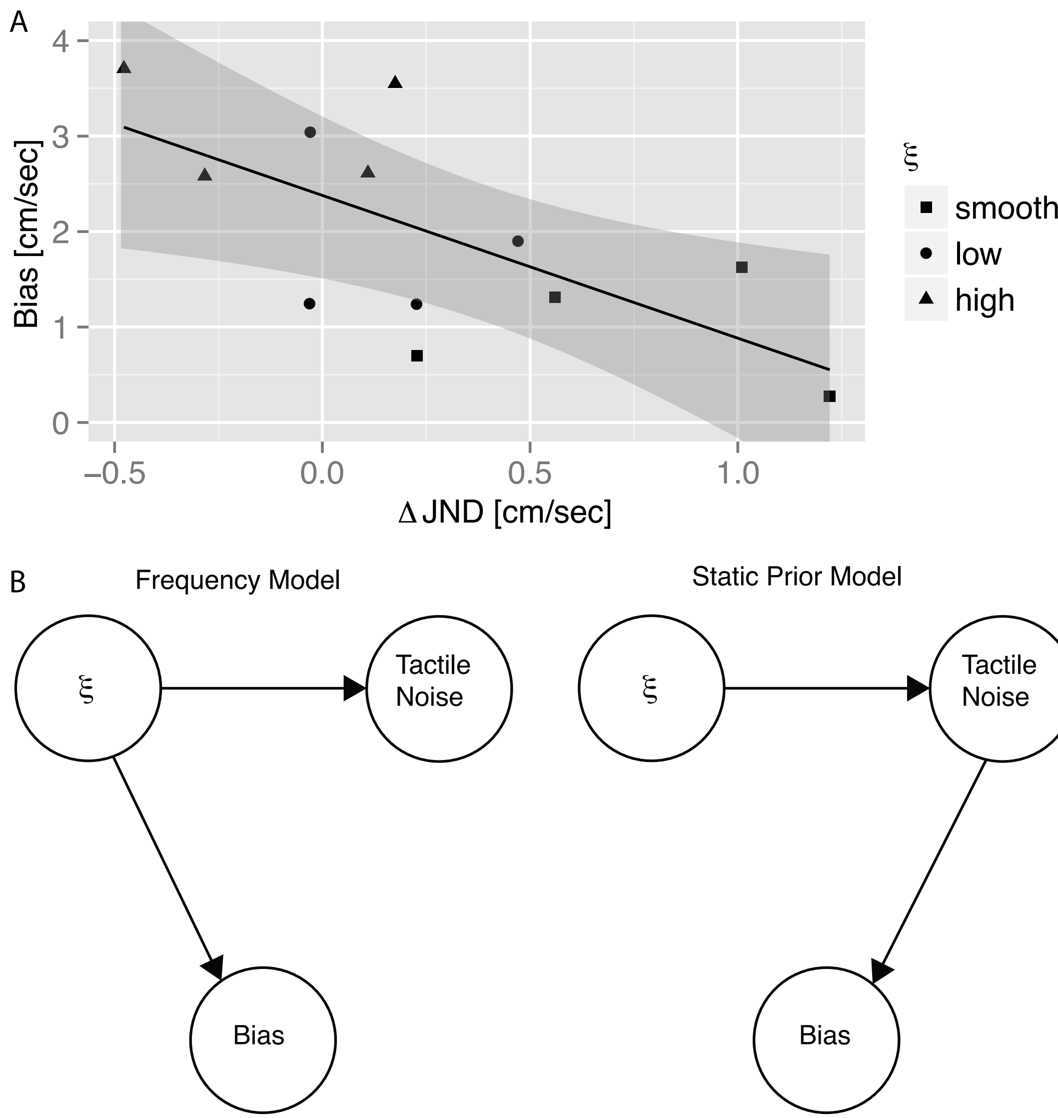
Fig. 4. *Explanatory Models. (A) Modulation of the illusion as a linear function of the perceptual noise; linear fit (black) and 95% confidence bands (dark gray). (B) According to a first explanatory model (left), the perceived speed depends on the outcome of an array of EMD, which is affected by the spatial frequency of the surface. In the Static Prior Model (right), the spatial frequency affects the perceptual noise, and this modulates the relative weight of the likelihood (tactile measurement) and the static prior.*

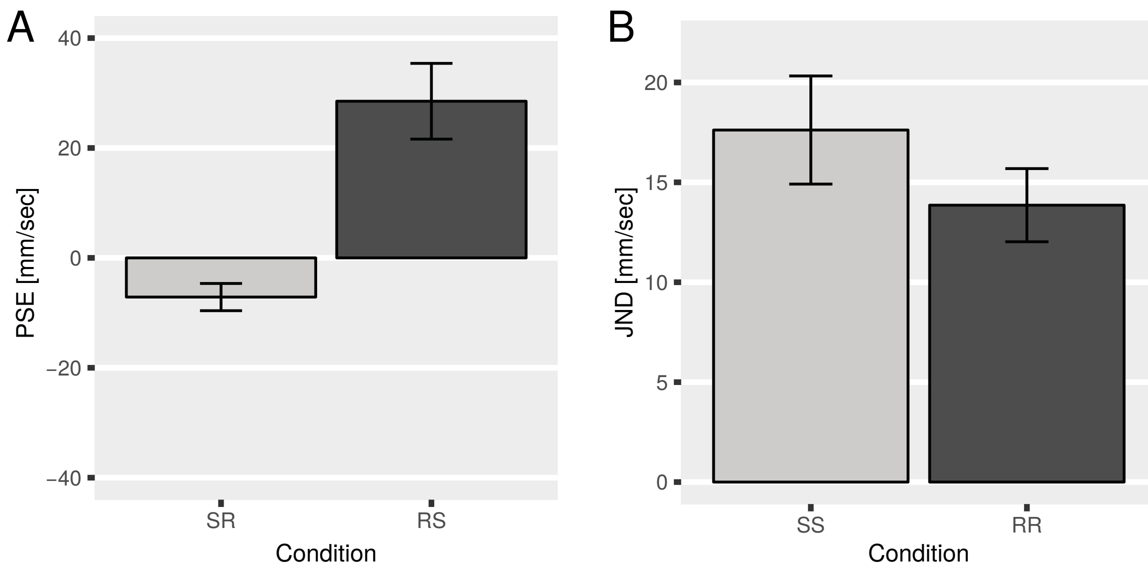
Fig. 5. *Results of Experiment 3. (A) The PSE in the RS and SR experimental conditions (N = 8). The bootstrap-based 95% CIs ranged from* -9.6 *to* $-4.6\ mm\ s^{-1}$ *in RS and from 21.6 to* $35.4\ mm\ s^{-1}$ *in SR. Results are consistent with speed bias depending on the spatial frequency of the belt. (B) The JND, the discrimination of the the motion speed is better for the ridged (smaller JND) compared to the smooth surface. The JND was* $13.9\ mm\ s^{-1}$ *in RR (*$95\%\ CI$: $12.0–15.7\ mm\ s^{-1}$*) and* $17.6\ mm\ s^{-1}$ *in SS (*$95\%\ CI$: $14.9–20.3\ mm\ s^{-1}$*).*


K
T


A
1.0
0.5
0.0
Probability FASTER
−50
0
50
Δ v [mm/sec]
B
20
10
0
−10
−20
PSE [mm/sec]
KT
TK
Condition


A
B
C
20
0
−20
PSE [mm/sec]
KT
TK
Smooth
KT
TK
Low Freq.
KT
TK
High Freq.


A
Bias [cm/sec]
4
3
2
1
0
–0.5
0.0
0.5
1.0
Δ JND [cm/sec]
ξ
smooth
low
high
B
Frequency Model
Static Prior Model
ξ
Tactile Noise
Bias
ξ
Tactile Noise
Bias


A
40
20
0
−20
−40
PSE [mm/sec]
SR
RS
Condition
B
20
15
10
5
0
JND [mm/sec]
SS
RR
Condition