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Research report

Path integration in tactile perception of shapes

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HIGHLIGHTS

- We studied path integration in the tactile system.
- Participants estimated the path of a moving tactile stimulus.
- Similar response pattern as in navigation studies involving locomotion.
- Direction bias that we explained the as a motion aftereffect.

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ABSTRACT

Whenever we move the hand across a surface, tactile signals provide information about the relative velocity between the skin and the surface. If the system were able to integrate the tactile velocity information over time, cutaneous touch may provide an estimate of the relative displacement between the hand and the surface. Here, we asked whether humans are able to form a reliable representation of the motion path from tactile cues only, integrating motion information over time. In order to address this issue, we conducted three experiments using tactile motion and asked participants (1) to estimate the length of a simulated triangle, (2) to reproduce the shape of a simulated triangular path, and (3) to estimate the angle between two-line segments. Participants were able to accurately indicate the length of the path, whereas the perceived direction was affected by a direction bias (inward bias). The response pattern was thus qualitatively similar to the ones reported in classical path integration studies involving locomotion. However, we explain the directional biases as the result of a tactile motion aftereffect.

1. Introduction

Whenever we move the hand across a surface, proprioceptive signals provide information about the velocity and the position of the hand with respect to the body. At the same time, tactile signals provide information about the relative velocity between the skin and the surface. If the system were able to integrate tactile velocity over time, cutaneous touch may also provide an estimate of the relative displacement between the hand and the surface. Here, we asked whether humans are able to form a reliable representation of a motion path from tactile cues only, integrating cutaneous motion information over time.

Humans are sensitive to tactile motion cues, which do not require temporal integration, such as the orientation, the direction, and the speed of motion [1–3]. To form a global motion percept, the tactile system spatially integrates the local motion signals provided by primary afferents across the skin [4]. Accordingly, Pei and colleagues showed that the perceived direction of motion of a plaid surface (i.e., a surface formed by superimposing two gratings of different orientations) is the result of spatial integration of the different local motion components [5]. Conversely to decode the motion path of an object sliding over a fixed area of the skin, direction and speed information, which are directly available to the nervous system [6–9], would need to be integrated *over time*. However, it is still unknown whether the tactile system can actually integrate tactile motion information over time in order to from a spatial representation of the tactile path.

Here, we developed three experimental paradigms to address the issue of path integration in touch. These tasks may be considered as the tactile equivalent of a well-established locomotion

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Fig. 1. The device and the tangential motion of the ball in the transverse plane. In Experiments 1–3, tactile stimuli were generated by means of the Slip Force Device, which consists of a billiard ball driven by two servomotors and it provides slip forces in both lateral axes of the fingertip. The participants touched the ball through a small aperture of 2 cm diameter in the cover plate. For the purpose of our experiments, we considered the tangential motion of the ball in the transverse plane. The red path shows an example of path in the transverse plane.

task—the triangle completion task [10,11]. In the locomotion task, a blindfolded participant is guided along an L-shaped path and then asked to walk back to the starting position along the shortest path, that is, via the hypotenuse of the triangle. Since the participant cannot use absolute landmark cues from, e.g., vision or audition, she/he has to integrate the velocity information over time in order to find back to the starting position (supplementary video SV1). This skill, based on both vestibular and proprioceptive cues, is usually referred to as *path integration* [11,12]. We developed the putative analogue in touch of this locomotion task (supplementary video SV2). Using the tactile device described in [13] we rendered the displacement of a surface along different paths. We asked participants to keep their hand world-stationary during the presentation of the stimulus. Therefore, proprioceptive and kinaesthetic inputs were not informative about the path of motion. Participants touched the moving surface with the tip of the index finger, and reported the perceived path length of the hypotenuse of a triangle using a discrimination task (Experiment 1). This experiment provides insights into the capabilities of humans to integrate tactile motion signals to form a spatial representation and a distance estimate. The results show that participants are surprisingly accurate to estimate the length of the hypotenuse. In order to further assess participants' ability to form a spatial representation of shape, in the second experiment participants had to reproduced a triangular-shaped path by drawing (**Experiment** 2). Next to information about distance perception from tactile motion, this experiment provided insights into the perceived direction of motion and shape perception. The results indicate that the angles of the triangle were systematically underestimated. In order to provide further insights into this underestimation of angle, in Experiment 3 we assessed the role of a potential motion aftereffect in tactile path integration. Indeed Experiment 3 revealed that the biases on the perception of the angle between two line segments were consistent with the interpretation of a tactile motion aftereffect distorting the orientation estimate of the second of two consecutively presented line segments. Taken together, the experiments reported below show that humans are surprisingly well able to integrate tactile motion information in order to form a spatial representation of shape.

2. Materials and methods

2.1. Participants

In total 21 naïve participants plus author AM (average age ± SD: 25 ± 4 years; 10 males; two of them were left-handed) participated in the three experiments. None reported any sensorimotor deficits. The sample size was 8 in Experiment 1a and 6 in Experiment 1b, Experiment 2a, Experiment 2b and Experiment 3. Six of the participants performed more than one experiment. All experiments were approved by the Ethics Committee of the University Clinics Tübingen, Germany. Informed written consent was obtained from all participants involved in the study.

2.2. Apparatus

In all experiments the tactile stimuli were generated by means of a Slip Force Device (Fig. 1; [13]). The device consisted of a billiard ball (diameter 6.02 cm) driven by two servomotors (Faulhaber DC-micromotors 2232UO24 combined with MCDC2805 Motion Controller) and it provided slip forces in both lateral axes of the fingertip. The two servomotors were orthogonally arranged, each with a driving wheel attached to its output shaft. These wheels rotated the ball in the two lateral axes of motion, thus causing slip friction to the fingertip of the participant (maximum torque: 523 mNm; maximum slip speed: 39.3 cm/s). As a consequence of the orthogonal arrangement of the driving wheels, each of the two lateral axes could be actuated independently using one motor each. Using both motors in combination, any linear combination of the axes was possible.

Each motor driver module included a closed-loop position/velocity control accessed via a serial RS-232 connection from the operating PC (resolution of the encoder: 512 pulses per revolution). We used a custom-made Matlab code to send commands

Table 1
Stimulus values in Experiments 1a and 1b. The speed of motion was the same within the trial in Experiment 1a, while in Experiment 1b during the return path it was pseudo-randomly chosen from one of the three values reported in the table below.

Length of the return path [cm]	3.14, 4.71, 6.28, 9.42, 12.57, 14.13, 15.70
Angle with respect to *z*-side [°]	27, 34, 45, 56, 63
Speed of motion [cm/s]	1.91, 3.03, 4.71

to the servomotors. A metal plate with a small aperture (diameter 2.0 cm), positioned on top was covering the device. The participant touched the ball through the small circular aperture in the plate. The device is illustrated in the supplementary video SV2.

2.3. Stimuli

In all experiments, we defined the stimuli in terms of the tangential motion of the ball in the transverse plane (Fig. 1). We computed the tangential motion as $(\vartheta/360)\pi d$, where ϑ (in degrees) is the angle of rotation of the ball and $d = 6.02$ its diameter. We explained the task to the participant in terms of the linear motion of a flat surface; approximating the sphere to a flat surface is behaviourally reasonable, because of the large diameter of the ball and the small aperture on the cover plate [14].

2.4. Experiment 1: tactile triangle completion

2.4.1. Stimuli and procedure

In Experiment 1a, in separate blocks we tested two experimental conditions. In the *Triangle Condition*, we simulated the movement of the surface along a right-angle-triangular path (that is, a triangular path with 90° as the first angle). The surface moved in a transverse plane, first along the coronal axis (the *x*-axis) from the right to the left of the participant, then along the sagittal axis (the *z*-axis) towards the participant, and finally along the hypotenuse of the triangle, in the direction of the initial home position (Fig. 2a). In each trial, the actual length of this third displacement was either shorter or longer than the geometrical length of the hypotenuse. The geometrical length of the hypotenuse was held constant throughout the experiment and was equal to 9.42 cm. We varied both the speed of motion (which was constant within a trial) and the shape of the right-angled triangle across different trials. The length of the return-path, the angle, and the speed of motion are reported in Table 1.

In the *Control Condition*, the surface moved back-and-forth along a straight line in the transverse plane (Fig. 2b). In each trial, the length of the backward displacement was either shorter or longer than the length of the forward displacement. The Triangle and the Control condition were matched with respect to the other motion parameters: The speed of motion was the same in the control and the triangle condition; the orientation and length of the return path in the control condition matched the orientation and length of the return path in the triangle condition, respectively.

The experimental procedure was the following: Participants were blindfolded and sat on an office chair in front of the device. In all the experiments, auditory white noise was delivered to the participants via earphones in order to mask any sound from the device. Participants gently touched the ball with the fingertip of their left index finger. They were aware that the displacement would follow a right-angle-triangular path with unknown size and orientation in the *Triangle Condition* and a straight back and forth path in the *Control Condition*. In a forced-choice discrimination task, participants indicated if the final position of the surface was stopped before or past its initial position (home position). Participants gave their response with the right hand by pressing one of the two answer buttons of the computer mouse. No feedback was provided. The *Triangle Condition* and the *Control Condition* were tested in two different blocks, each consisting of 105 trials. The order of the blocks was counterbalanced between participants.

Experiment 1b was nearly the same as Experiment 1a, with the only difference being that the speed of motion now changed within the trial. Here the speed of motion was equal to 3.03 cm/s in the outward path (i.e., the two catheti in the *Triangle Condition* and the forward path in the *Control Condition*) while it was pseudo-randomly chosen between three different values (1.91, 3.03, 4.71 cm/s) in the backward path.

2.4.2. Data analysis

Data analysis of all experiments was performed in R (R Project for Statistical Computing, [15]). In Experiments 1a and 1b, we modelled the response of each single participant and of the whole population by means of a psychometric function and a general linear mixed model (GLMM), respectively. The latter provides an extension to the fitting of psychometric functions (and of other general linear models) to clustered categorical data as in this case the repeated responses of all participants are considered jointly [16–18]. Please refer to the supplementary materials for further information on GLMM.

The psychometric function applied to the response of a single participant is defined as:

$$\Phi^{-1}[P(Y_j = 1)] = \beta_0 + \beta_1 x_j \tag{1}$$

where Φ^{-1} is the probit link function (i.e., the inverse function of the Cumulative Gaussian distribution), $P(Yj = 1)$ is the probability that in a given trial j the return path has been judged as longer than the implicit or explicit reference and x_j is the actual length of the return path. We applied the model separately to each participant and experimental condition. From the parameters of the psychometric function we estimated the point of subjective equality (PSE) and the just noticeable difference (JND). The PSE is given by:

$$\text{PSE} = -\frac{\beta_0}{\beta_1} \tag{2}$$

The PSE corresponds to the stimulus value leading to a response probability of 0.5 and it estimates the accuracy of the percept (i.e., its bias). The slope parameter β_1 in Eq. (1) provides an estimate for the precision of the percept (hence, the JND, as an inverse function of the slope, estimates the noise of the perceptual response).

We performed the group analysis by means of a generalized linear mixed model (GLMM). For this, we fitted the two experimental conditions simultaneously. The model is the following:

$$\phi^{-1}[P(Y_{ij} = 1)] = \beta_0 + u_i^0 + x_{ij}(\beta_1 + u_i^1) + d_{ij}\beta_2 + (x_{ij}d_{ij})\beta_3 \tag{3}$$

where $\phi^{-1}[P(Y_{ij} = 1)]$ is the probit transform of the probability of "longer" responses in participant *i* and trial *j*, x_{ij} is the actual length of the return path. d_{ij} is the dummy variable coding the experimental condition (either 0 for the *Control Condition* or 1 for the *Triangle Condition*), $\beta_0, \ldots, \beta_3$ are the fixed-effect parameters, and u_i^0, u_i^1 are the random-effect parameters. By introducing two random parameters in the model, we assumed that for each participant *i*, the intercept and the slopes of the response curve vary in a random fashion. In the GLMM, we estimated the PSE and JND using the bootstrap method suggested in [17].

2.5. Experiment 2: the drawing experiment

2.5.1. Stimuli and procedure

In Experiment 2a, the surface moved along a right-angle-triangular path. This time however, the movement of the surface corresponded to a closed triangular figure. We generated five different triangles with the constraint $\sqrt{x^2 + z^2} = 9.4$ cm. This implies

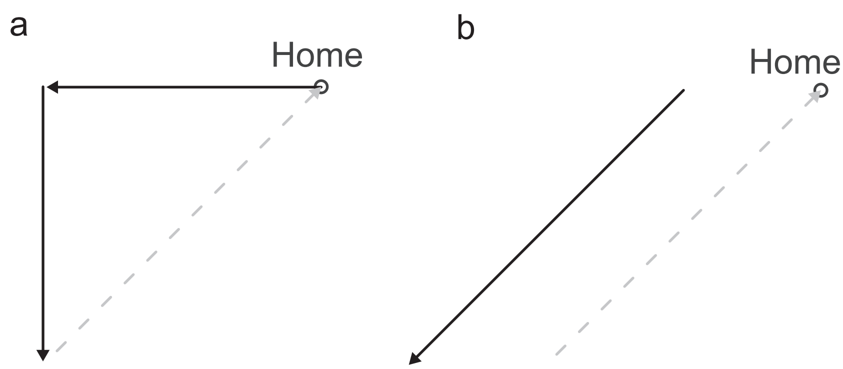

Fig. 2. Experiment 1, Stimuli. In the *Triangle Condition* (a), the surface moved along a triangular path lying on the transverse plane of the participant: first in the x-direction from the right to the left (x-cathetus), then in z-direction towards the participant (z-cathetus), and finally along the hypotenuse, in the direction of the initial home position. In the *Control Condition* (b) the surface moved back-and-forth in a straight path. In each trial, the participant indicated if the return path (indicated in grey) stopped before or past the initial home position.

that the angle between the hypotenuse and the second cathetus, as well as the perimeter of the triangle, varied (Table 2).

The experimental task was the following: Participants touched the surface of the device with their dominant hand; as in Experiment 1, they were aware that the surface would move along a right-angle-triangular path. The experiment consisted of 15 trials (5 different triangles, each repeated 3 times in a pseudo-random fashion). Participants neither received information about the size of the triangle nor on the relative cathetus length characterizing the triangle. During each trial, we first required the participants to image a movement of the finger consistent with the cutaneous stimulus (Fig. 4a). After the stimulus finished, they slid the index of the dominant hand on a 21 cm × 21 cm square sheet of paper so as to reproduce the cutaneous stimulus. Finally, they drew the perceived triangle on the paper sheet with a pencil. They were required to draw the triangle in the same size and orientation as the tactile stimulus. In a training session at the beginning of the experiment participants practised the task for 5 trials using the same stimuli as in the experimental session. No feedback was provided during the training or the experimental session.

In the Experiment 2b we replicated the same task using the mirror images of the triangles used in the previous experiment. The rationale of this was to evaluate the role of a motion aftereffect (i.e., of the direction of motion along the x-axis) in the reproduced drawings. For the same purpose, we also varied the inter-stimulus-interval between the three sides of the motion path. We mirrored the motion path along the sagittal axis, i.e. the surface moved first along the coronal axis (the x-axis), this time from left to right, then along the sagittal axis (the z-axis) towards the participant, and finally along the hypotenuse of the triangle, in the direction of the initial home position. The inter-stimulus-interval (ISI) between the x-, the z- and the hypotenuse-path varied among different trials (ISI equal to 0.1, 0.5 or 0.8 s). Each experiment consisted of 45 trials (5 shapes × 3 ISIs × 3 repetitions).

2.5.2. Data analysis

We digitized the participants' drawings by connecting the vertices of the drawn triangle by straight lines both for the analysis and in Fig. 4. We independently analyzed the perceived length of the displacement, summarized by the perimeter of the triangles, and the perceived direction of motion, summarized by the deviation from the right angle of the stimulus. We used Linear Mixed Models (LMM; [19]) to perform the analysis, so as to take into account both, the variability between and within participants. First we applied the following LMM, which relates the length of the drawn path $\tilde{P}_{ij}$ to the actual displacement of the surface P_{ij}:

$$\tilde{P}_{ij} = u_i + \gamma P_{ij} + \varepsilon_{ij} \quad (4)$$

The model has a single fixed-effect parameter γ, accounting for the effect of the physical displacement of the surface on the perceptual response. The random intercept u_i accounts for the offset of each participant and ε_{ij} is the within-participant error term.

Then, we applied a second model to test if the bias in the perceived right angle was a function of the length of the x-cathetus $l_{(x)}$. We applied the following LMM to the dataset:

$$\Delta_{ij} = u_i + \eta l_{(x)ij} + \varepsilon_{ij} \quad (5a)$$

We estimated the bias Δ_{ij} as the difference between the angle drawn by the participants and that created by the physical stimulus (90°). The fixed parameter η is the slope of the linear model and it tests if the length of the x-cathetus $l_{(x)}$ has a biasing effect on the perceived angle. If the length of the cathetus would produce no bias, then the slope would be close to zero.

In Experiment 2b we applied a model similar to Eq. (5a). We tested the effect of both, path length and ISI on the bias of the perceived angle (Eq. 5b).

$$\Delta_{ij} = u_i + \eta_1 l_{(x)ij} + \eta_2 ISI_{ij} + \varepsilon_{ij} \quad (5b)$$

2.6. Experiment 3: tactile motion aftereffects

2.6.1. Stimuli and procedure

Experiment 3 directly assessed the role of a potential tactile motion aftereffect. We used the following convention: the angle of the path was equal to 0° for a stimulus moving leftward along the x-axis and angles increased clockwise (i.e., a stimulus moving away from the participant in the z-axis was coded as 90°).

Each trial included an adapting and a test stimulus. In the adapting stimulus, the surface moved along the x-axis, either leftward (0°) or rightward (180°) depending on the experimental block. Shortly after the adapting stimulus (ISI = 0.1 s), a test stimulus moved along a pseudo-randomly chosen direction. Its direction of motion was one of the following: 30°, 50°, 70°, 90°, 110°, 130°, and 150° (Fig. 6a). In agreement with the previous experiments, the velocity of motion and the length of the displacement of both the adapting and test stimuli were fixed and equal to 3.03 cm/s and 9.42 cm, respectively. The participant indicated if the

Table 2
Stimulus values in Experiment 2. In Experiment 2, the movement of the surface always formed a closed triangle.

Perimeter of the triangle [cm]	22.07, 22.49, 22.75
Angle with respect to z-side [°]	27, 34, 45, 56, 63
Speed of motion [cm/s]	3.03

orientation of the test stimulus was leftward or rightward rotated with respect to his/her sagittal plane (z-axis), that is, more or less than 90°. They gave their response by clicking the left or right button on a computer mouse indicating a left- or rightward-perceived orientation of the test stimulus. Participants used the right index finger to receive the stimulus and give the response, which should minimize potential crossover effects between trials due to, for example, motion adaptation. Each experimental session consisted of two blocks (one for leftward and the other for rightward adapting stimulus), each consisting of 105 trials. The order of the blocks was counterbalanced between participants.

2.6.2. Data analysis

As in Experiment 1, we modelled the response of each single participant and of the whole population, respectively, by means of a general linear model (GLM) and a GLMM. We estimated the PSE and the JND from the mixed model using a bootstrap method [17].

3. Results

3.1. Experiment 1: the tactile equivalent of the triangle completion task

In Experiment 1 we investigated if participants were able to integrate the local motion signals, conveyed by the mechanoreceptors, to form an accurate percept of the length of a triangular shaped path. The participant touched the moving surface of the Slip Force Device with the tip of the right index finger (Fig. 1). In the *Triangle Condition*, the simulated surface moved along a triangular path, mimicking right-angle triangles of different shapes (Fig. 2a). Depending on the trial, the length of displacement along the third segment was either shorter or longer than the geometrical length of the hypotenuse. Therefore, the final position of the path occurred either before or past the start position (home position). In the *Control Condition*, the path was a back and forth movement along a straight line (Fig. 2b). Similarly to the *Triangle Condition*, the length of the backward displacement was either shorter or longer than the length of the forward displacement. At the end of each stimulus, the participant reported, in a forced-choice paradigm, if the final position was perceived in front or behind the home position.

What are the possible outcomes that we may expect from this experiment? Our predictions are represented in Fig. 3a. We assumed that the response was unbiased in the Control condition [20]. Also, as the speed of motion was constant within the trial, it was possible to solve the control task using duration cues, in addition to motion cues to path-length. Therefore, the response in the *Control Condition* delimits the upper boundary in terms of precision. We considered three possible outcomes for the *Triangle Condition*. The response would be accurate, and nearly as precise as in control condition, if the participant were able to integrate the motion cues efficiently (path integration; p.i. in the figure). Alternatively, if the integration process were noisy, the response would be significantly noisier in the *Triangle* than in *Control Condition*. A third and fourth outcome might be that participants use a wrong explicit reference to solve the task (such as using only one of the two sides of the triangle or the sum of the two). In these two cases the responses would be biased one way or the other in *Triangle Condition* compared to the *Control Condition*.

Fig. 3b shows the response of a representative observer and the fitted psychometric function in the two conditions. In both cases, the response was quite accurate (PSE) and precise (JND), though slightly more precise in the *Control Condition*: for this example subject the JND was 1.4 ± 0.2 cm in control condition and 2.0 ± 0.3 cm in triangle condition, which corresponds to a Weber-Fraction of 14.9% and 21.2%. His PSE was 8.6 ± 0.5 cm in control condition and 8.3 ± 0.5 cm in triangle condition.

The population-level analysis confirmed these findings. The response was quite accurate in both experimental conditions: the PSE was 9.0 cm (95% CI: 7.9–10.2 cm) in the *Control Condition* and 8.9 cm (95% CI: 7.9–9.9 cm) in the *Triangle Condition* (Fig. 3c). Looking at the 95% confidence intervals of the PSEs, in both conditions the parameter was non-significantly different from the reference length of 9.42 cm. The response was slightly less noisy in the *Control* than in the *Triangle Condition*. The JND was 1.8 cm (95% CI: 1.4–2.3 cm) in the *Control Condition* and 2.2 cm (95% CI: 1.8–2.9 cm) in the *Triangle Condition*, respectively (Fig. 3d). This corresponds to a Weber Fraction of 19.1% and 23.3%. In summary, the differences between the two experimental conditions were quite small. Importantly, in both conditions participants were able to accurately represent the 2D-displacement of the simulated surface (see also Supplementary Figure SF1. Each participant is represented in a different box; the *Triangle* and *Control Conditions* are represented in the upward and downward lines, respectively).

The experimental procedure of this first task was designed in a way that the speed of motion was constant within each trial. In Experiment 1b we replicated almost the same task, with the only difference being that now the speed of motion changed within each trial. In the new procedure, the speed of motion was equal to 3.03 cm/s in the outward path (i.e., the first two segments of the triangle or the forward motion of the forward math in the *Control Condition*), while it was pseudo-randomly chosen between three different values (1.91, 3.03, 4.71 cm/s) in the backward path. This was designed to confirm that participants took into account both the stimulus duration and the speed to estimate the displacement, and thus that they truly have a spatial representation of the path displayed.

In order to test if this was the case, we fitted the data twice, first with a model that includes both the duration and the speed of motion as predictors, and second with a nested model that includes the duration but not the speed. We compared the two models using the Likelihood Ratio Test: the speed-and-duration model provides a better fit to the data ($p < 0.001$). This result seems to exclude that participants estimated path distance based on motion duration only. Further details on Experiment 1b are provided in the Supplementary Materials.

The result of the experiments above demonstrates that humans are surprisingly well able to integrate tactile velocity information provided to the tip of the finger over time. In the following experiments this finding is extended to more general cases, including the perception of the angles of the triangle.

3.2. Experiment 2: the drawing experiment

The previous experiment investigated the integration of surface motion for the perception of path length. In this second experiment, we now investigate the integration of surface motion with a focus on the perception of shape and angles between line segments. For this we now use an even more intuitive response mode, namely drawing of the perceived shape. As in Experiment 1, in Experiment 2a the simulated surface moved along a right-angle-triangular path, counter-clockwise from the x-cathetus to the hypotenuse. However, now the displacement of the simulated surface always formed a closed triangular figure, which was familiar to the participant. During the presentation of the stimulus, participants had to imagine the movement of the finger that matched the tactile sensation produced by the device (Fig. 4a). After the presentation, participants had to reproduce the movement of the finger on a squared sheet of paper (21 cm × 21 cm) and they had to draw it with a pencil. Since the response mode required a hand movement, we asked the participant to reproduce the imagined displacement of the hand (blue

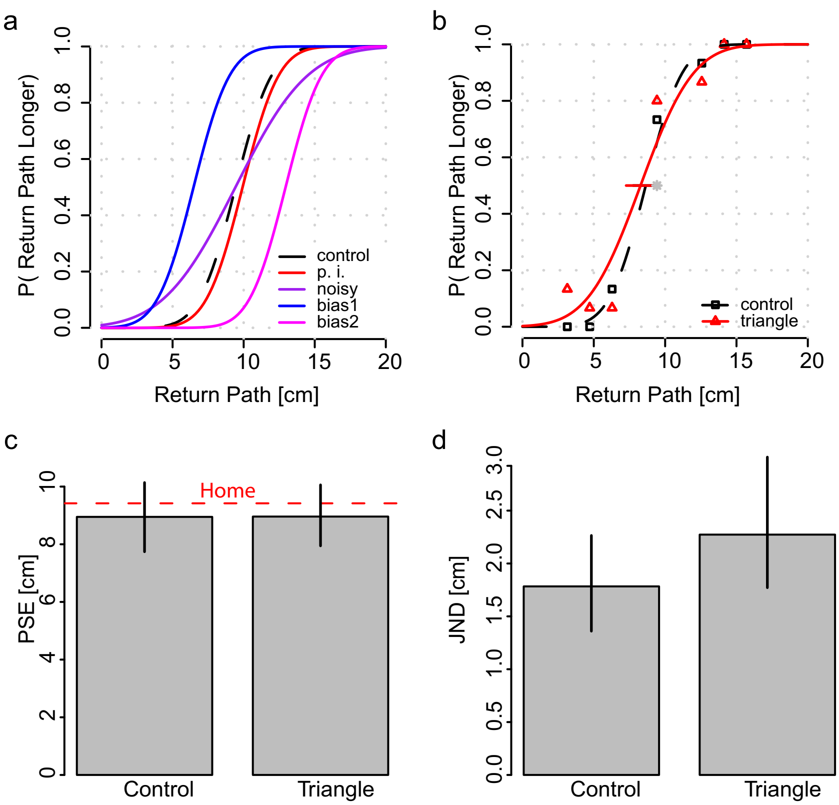

Fig. 3. Experiment 1a, Predictions and results. (a) Predictions. (b) Psychometric function in a representative participant. The veridical length of the standard is indicated with a grey asterisk. (c) PSE and 95% CI ($n = 8$). The red dashed line is the home position. (d) JND and 95% CI ($n = 8$).

path in Fig. 4a) rather than the displacement of the surface (red path in Fig. 4a), which are equal but opposite in sign. We asked participants to accurately reproduce the size, the shape, and the orientation of the simulated triangular path.

Fig. 4c provides some examples of the stimuli together with the figures drawn by the participants (the stimuli are represented by grey shapes and the responses of the participants by the red lines). We independently analyzed the perceived length of the displacement, summarized by the perimeter of the triangles, and the perceived direction of motion, summarized by the first angle. As in Experiment 1, the estimate of the length of the displacement was very accurate: the average of the extent of the simulated displacement was 22.4 cm and the grand mean of the perimeters drawn by participants was 21.9 cm. Thus, the accuracy was 21.9/22.4 = 0.98. This value was confirmed by fitting the data with the LMM in Eq. (4), which takes both the variability between and within participants into account. The model relates the perimeter drawn by the participants as a linear function of the actual displacement produced by the device. The slope coefficient γ estimated by the model was equal to 0.98. That is, the fitting was very close to the identity line.

Next, we focused on the direction errors. As explained before, the surface moved first along the x-cathetus, then along the z-cathetus, and finally along the hypotenuse, with the right angle always occurring first. Therefore, the perception of the right angle was not affected by the geometrical constrains of the figure and provides a fair estimate of the direction errors. Note that participants were not informed about the right angle always occurring first. Fig. 4d shows the angle drawn by each of the 6 observers for each of the 15 trials. The grand mean of the angle was 84.7°. The angle was clearly underestimated in 3 out of 6 participants.

There are two possible explanations for this underestimation of the right angle. The participants might have misestimated the direction per se, irrespective of the motion along the first cathetus. Alternatively, participants might have misperceived the direction of motion of the second cathetus, due to possibly a motion aftereffect. If the second hypothesis were true, then the angle bias would be larger as the length of the (preceding) x-cathetus increases. Therefore, using the LMM illustrated in Eq. (5a) we tested if the direction bias was related to the actual length of the x-cathetus. Although not significant ($p = 0.13$) the model shows a clear trend in a way that with a longer x-cathetus, the perceived angle was biased to be smaller ($\eta = -1.0 \pm 0.4$; Estimate ± SE).

In order to further evaluate the aftereffect hypothesis, we reverted the direction of motion in Experiment 2b. This way, the motion path produced in Experiment 2b was the mirror image along the sagittal axis of the stimulus used in Experiment 2a. If the aftereffect hypothesis were true, the inner angle between the two catheti would be underestimated in a similar way as in Experiment 2a. Instead, if the angle bias was the consequence of a direction anisotropy in world- or skin-framed reference, the angle would be overestimated in Experiment 2b and not underestimated as in Experiment 2a. As shown in Fig. 5a, four out of six participants underestimated the inner angle between the x- and the z-cathetus. The average angle bias was $-5.4 \pm 2°$ (mean ± SE). These results are only consistent with the motion aftereffect hypothesis. The bias was larger (i.e., the angle was more underestimation) for short ISIs (see Fig. 5b); the effect was statistically significant ($\eta_1 = 6.1 \pm 2.8$, $p < 0.05$). Instead, the effect of path length was not statistically significant ($\eta_2 = 0.4 \pm 0.5$). The reproduced path length was accurate in 4 participants and slightly overestimated in 2 of them. The average drawn perimeter was equal to 26.3 ± 2.0 cm (mean ± SE), corresponding to an accuracy of 22.4/26.3 = 0.85.

The results on the angle bias prompted us to conduct a third experiment in which we systematically tested the hypothesis of the direction bias as a consequence of a motion aftereffect.

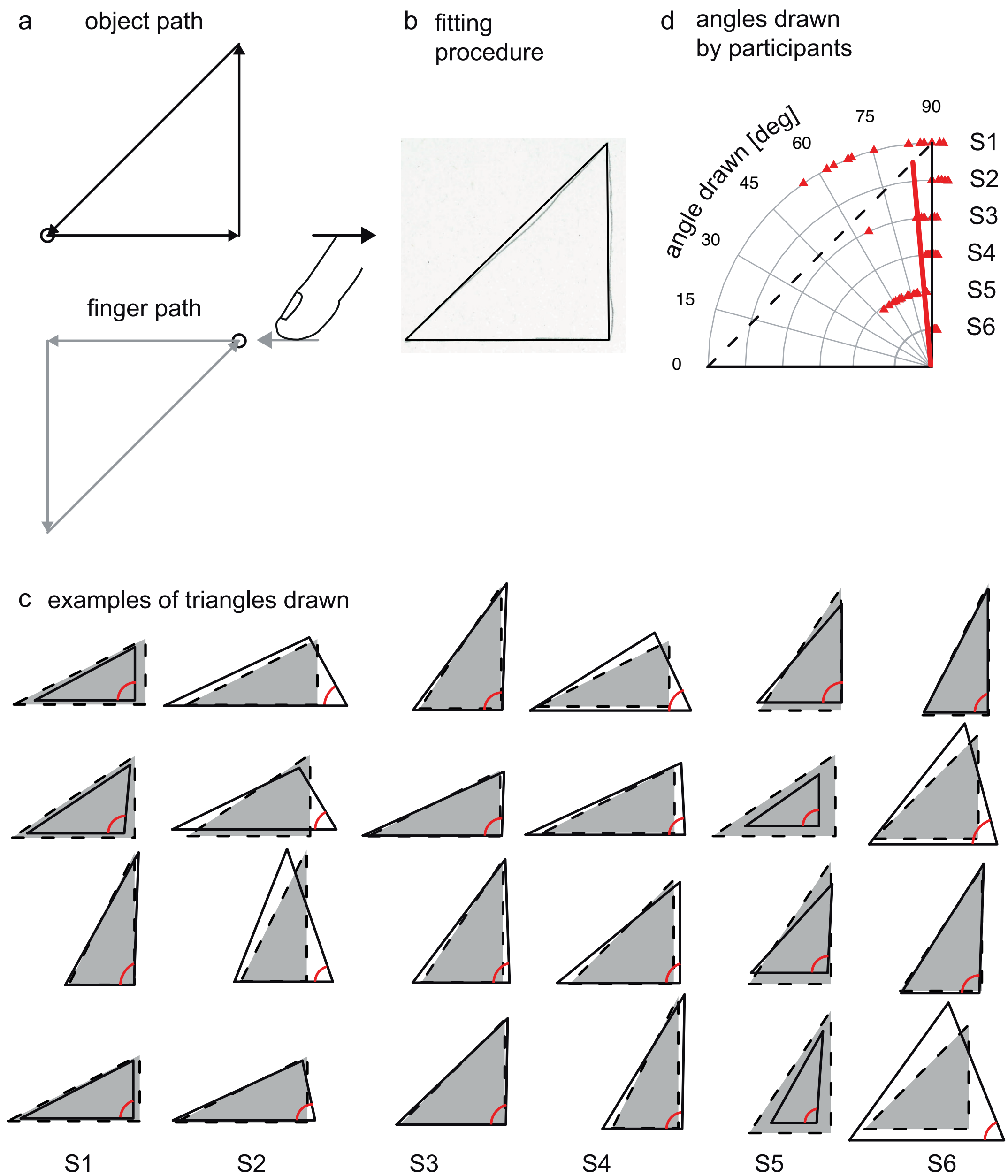

Fig. 4. Experiment 2a (drawing experiment): Procedure and results. (a) During the administration of the stimulus, the participant imagined a movement of the finger (upward path) that would match with the tactile stimulus produced by the device (downward path). After that, they drew the imagined movement on a squared paper sheet. The home position is indicated as a black dot. (b) For the analysis and the plot, we digitized the participants' drawings by connecting the vertices of the drawn triangle by straight lines. (c) The physical path (filled triangles), and the drawings from the participants (blank triangles). Examples for 6 different participants are illustrated in different columns. The R package *spatstat* was used to produce this plot. (d) The polar plot represents the perceived size of the bottom-right angle (i.e. the right angle of the stimulus, in red in the figure). For each trial, the size of the angle drawn by participants is represented as a triangle-shaped data point. To easily see the angles drawn by each of the six participants we plotted each of them on one of the six concentric arcs. The two solid lines are for illustrative purposes and show the 90° angle of the stimulus. The red line represents a fit to the participant's data and shows the average angle drawn by participants.

Experiment 3: the direction bias as a motion aftereffect

In the second experiment, participants were able to sketch the triangular shape of the tactile motion stimuli quite accurately. However, the angle between the two catheti was systematically underestimated, respectively in 3 (Experiment 2a) and 4 (Experiment 2b) out of 6 participants. In this third experiment we now attempted to directly investigate whether this angle bias could be the result of a motion aftereffect.

The motion aftereffect is defined as the illusory motion of a stationary test stimulus in the opposite direction to the previously adapting motion. Unlike in vision, the existence of motion aftereffect was largely debated in touch [21–24]. Recently, robust tactile motion aftereffects have been demonstrated using tactile displays, which generate apparent motion by means of vibrating pins [25–27]. The studies above limited the tactile stimulus to a uni-dimensional, back-and-forth motion. Here, we conducted a 2D, direction discrimination task in order to quantify the contribution of the motion aftereffect to the perceived direction of tactile motion. We used the same apparatus as in Experiments 1 and 2 (see the Method session). The experimental procedure is illustrated in Fig. 6a. Each trial included an adapting stimulus and a test stimulus. In the adapting stimulus (indicated in black in Fig. 6a), the tactile motion was along the x-direction, either leftward or

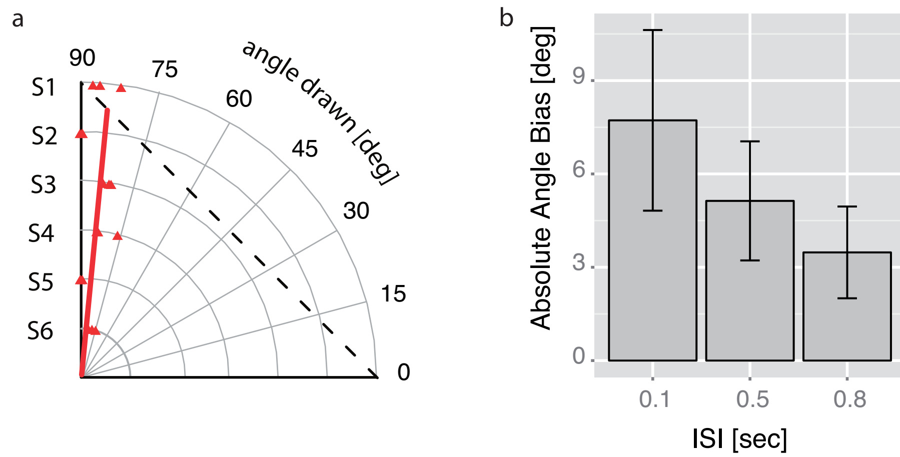

Fig. 5. Experiment 2b (mirrored triangles), results. (a) The polar plot represents the perceived size of the bottom-left angle (i.e. the right angle of the stimulus; data averaged with respect to shapes and trial repetitions). The red line represents a fit to the participant's data and shows the average angle drawn by participants. (b) The absolute angle bias as function of the inter-stimulus-interval (ISI), mean and SE (between-participants variability).

rightward depending on the experimental block. Shortly after the adapting stimulus, a test stimulus (indicated in grey) moved along a proximal-to-distal direction, tilted either leftward (<90°) or rightward (>90°). Participants indicated whether the orientation of the test stimulus was perceived to be tilted leftward or rightward with respect to his/her sagittal plane (i.e., with respect to straight ahead). It is worth noting, this time the participant's task was not about the angle between the adapting and the test stimulus and thus it was not explicitly mentioned. In fact, participants were asked to ignore the adapting stimulus and to perform the discrimination task in body coordinates with respect to straight ahead. From the PSE we could still infer the perceptual effects on the angle between adapting and test stimulus.

In accordance with Experiment 2, Experiment 3 revealed a strong directional bias in the test stimulus, which depended on the direction of motion of the adapting stimulus. In all participants, the PSE was <90° in leftward-adapting blocks, and >90° in rightward adapting blocks. The GLMM confirmed these results: the PSE was 107° (95% CI: 99–114°) when the rightward adapting stimulus preceded the test stimulus and it was 77° (95% CI: 71–81°) when the leftward adapting stimulus preceded the test stimulus (Fig. 6b and c). The results are consistent with a motion aftereffect biasing the tactile motion direction percept. Therefore, the angle bias reported in Experiment 2 might well be accounted for by a tactile motion aftereffect.

4. Discussion

In three experiments we asked our participants to estimate or reproduce the simulated path of a moving tactile stimulus. These tasks required participants to integrate the perceived velocity over time—a process analogous to path integration in locomotion [11]. Participants were surprisingly good at these tasks: In Experiment 1a, the accuracy of the responses was comparable with the control task, but also the precision did not differ significantly. According to Experiment 1b, the participants took the velocity of motion into account in order to perform their estimate, rather than simply using a time-based heuristic. This suggests that the participants formed a spatial representation of the stimulus, that is, they correctly integrated the spatial attributes – angles, direction and path length, to perform the task. This spatial representation of the motion stimulus is also referred as *the survey map* of the motion path in the navigation literature [28].

Although the estimate of the path length was accurate, the perceived direction was biased, that is, the right angle was systematically underestimated (Experiments 2a and 2b). In [29], the

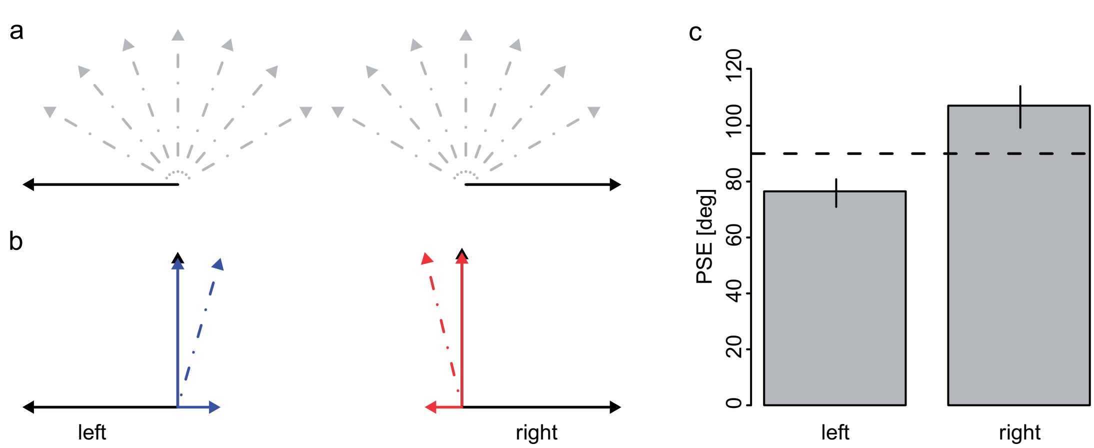

Fig. 6. Experiment 3 (motion aftereffects): Stimulus, results and vector model. (a) The adapting (black) and test (grey) stimuli in the two experimental conditions. (b) We modelled the perceived displacement in tactile navigation as a vector addition. The physical displacements of the adapting and test stimuli are represented as the orthogonal black vectors. We represented the perceived displacement (the dash-dotted vectors) as a linear combination of the physical displacement of the test stimulus and the motion aftereffects. The solid coloured vectors represent these two motion components. (b) PSE and 95% CI ($n = 6$). The dashed line represents the ideal, unbiased response.

authors also reported a directional bias in the perceived motion direction. That is, their participants perceived two stimuli as parallel when the second motion direction was slightly clockwise with respect to the first – though the effect was not statistically significant. From the results of Experiment 3, we inferred that the angle bias described in our experiments was the consequence of the percept being affected by a tactile motion aftereffect.

To the best of our knowledge, the current study is the first example of path integration in the tactile domain. In our daily life, we move our hands across the surface of an object to haptically explore it. Tactile path integration might provide us with a representation of the global shape of the object. A possible subsequent question is how tactile path integration combines with kinaesthetic information from the movement of the hand for shape recognition. Several studies evaluated *haptic* shape perception from raised-lines that participants traced with their fingertip [28,30–33]. When comparing this literature with our study, it is necessary to take into account three crucial differences. First, when tracing a raised line with the finger kinaesthetic cues are present and so it is impossible to determine the performance of tactile path integration is isolation. Secondly using raised lines in the tactile domain there is not only motion information but also local tactile shape information (i.e., the curvature of the raised line on the finger pat). Thirdly, the shapes typically used in the raised line literature largely vary in path length and shape complexity. Lederman et al. [28] studied the perceived length and Euclidean distance of irregular, curved paths. The response of the participants was likely based on heuristics, such as movement length and duration. The authors attributed the poor performance to the large demand of spatial memory. Notably the path length in their study was considerably longer than those used in our paradigm (up to 100 cm in Lederman's study). In [30], the author applied a triangle completion task in haptics: participants traced the first two sides of a triangle and were then asked to return to the starting position on the shortest path. No angle bias was observed for this task. This might be due to the presence of kinaesthetic cues or the relatively longer ISIs between the outward and inward path in [30] (ISI are not reported in the article, though the procedure is not compatible with sub-seconds ISIs). Conversely, Lakatos and Marks [31] reported that haptic sensed angles are underestimated compared to visual ones. Wijntjes and Kappers [32] further studied the haptic discrimination of raised-line angles. They found that discrimination performance was highly dependent on the exploration/motor strategy. The identification of irregular line drawing increases significantly when the participant could sketch on a paper the perceived figure [33], which might explain the overall good performance in the drawing task reported in the current study (Experiment 2). I all these studies, tactile and kinaesthetic cues were always consistent. It might be of interest in future experiments to characterize the relationship between the two cues by decoupling the tactile and kinaesthetic information.

A second question that might arise from our findings concerns the neural mechanism underlying tactile path integration. For an ideal observer, perceiving the path of motion would require the integration of velocity (i.e., direction and speed) over time. Several models have been proposed for the integration of direction and speed in whole-body navigation in mammals [11,34]. The head direction cells in the hippocampus and in the entorhinal cortex decode the direction of motion of the animal. The attractor-map model is a possible neural mechanism for the integration of the direction of motion. A two-dimensional attractor map, having the shape of a torus, would integrate both the direction and speed of motion and would decode the position of the animal in space [35]. Place cells in the hippocampus and grid cells in the medial entorhinal cortex are possible neural substrates for path integration. Are there equivalent cells in touch? In [36] the authors identified a population of somatosensory neurons accounting for the perceived direction of the stimulus on the skin and they might be analogous to the head direction cells in the hippocampus. However, to the best of our knowledge an analogy to place or grid cells that would perform path integration has not been found in the tactile system so far. Since many of the traditionally thought unimodal neural circuits recently turn out to be multimodal, one hypothesis might be that the neural mechanism for whole-body navigation in the ambulatory space might perform also tactile path integration in the manipulatory space. In addition to the hippocampus and the entorhinal cortex, the medial and the posterior part of the parietal cortex, which are involved in somatosensory processing, spatial orientation, and navigation [37–39], might be good candidates as neuroanatomical substrate.

This study found evidence for tactile motion integration in the small-scale space of the hand. This raises the question of whether tactile integration would provide reliable information in a larger scale space. That is, if tactile integration would play a role in navigation involving in the ambulatory space as well. In the absence of visual information, different animals (particularly nocturnal animals) rely primarily on touch for space exploration. Examples from our daily life, as when searching for something at night (and emphasized in the blind), suggest that similar capabilities exist in humans. As shown by this study, the tactile system integrates the velocity information over time in order to produce a representation of the external space. Thereby we found similar direction bias as has been reported for locomotion. The mechanism causing the direction bias might be different in ambulatory and manipulatory space: A leaky integrator is commonly thought to produce the bias in the ambulatory space [12,35], whereas a motion aftereffect would provide a reasonable explanation for the current findings in the manipulatory space. It is a question for further research to see whether navigation by touch and locomotion might be processed by the same neural structures dedicated to navigation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bbr.2014.08.025.

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