Sub-surface deformation of individual fingerprint ridges during tactile interactions

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The human fingertip can detect small tactile features with a spatial acuity roughly the width of a fingerprint ridge. However, how individual ridges deform under contact to support accurate and high-precision tactile feedback is currently unknown. The complex mechanical structure of the glabrous skin, composed of multiple layers and intricate morphology within which mechanoreceptors are embedded, makes this question challenging. Here, we used optical coherence tomography to image and track sub-surface deformations of hundreds of individual fingerprint ridges during contact events at high spatial resolution in vivo. We calculated strain patterns in both the stratum corneum and viable epidermis in response to a variety of tactile stimuli, including static indentation, stick-to-slip events, sliding of a flat surface in different directions, and interaction with small tactile features, such as edges and grooves. We found that ridges could stretch, compress, and undergo considerable shearing orthogonal to the skin surface, but there was limited horizontal shear. Therefore, it appears that the primary components of ridge deformation and, potentially, neural responses are deformations of the ridge flanks and their relative movement, rather than overall bending of the ridges themselves. We conclude that the local distribution of mechanoreceptors across the ridges might be ideally suited to extract the resulting strain gradients and that the fingertip skin may possess a higher mechanical spatial resolution than that of a single ridge.

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Introduction

The human fingertip is a highly effective tactile sensing organ housing thousands of mechanoreceptors (Corniani and Saal, 2020) that convert deformations into neural responses (Handler and Ginty, 2021), which underlie our capacity for fine tactile discrimination and object manipulation (Lieber and Bensmaia, 2022; Johansson and Flanagan, 2009). The ridged structure of the volar skin of the fingertip gives rise to fingerprints, which are thought to determine the spatial resolution at which we can resolve small tactile features. Ridge spacing correlates with perceptual spatial acuity (Peters et al., 2009) and the size of receptive sub-fields of type-1 tactile afferents has been estimated in the sub-millimeter range, roughly matching the width of a single ridge (Jarocka et al., 2021; Sukumar et al., 2022).

However, understanding how the mechanical properties of individual fingerprint ridges support high-precision tactile feedback presents significant challenges: any force applied to a ridge on the skin's surface causes deformations within multiple skin layers with distinct mechanical properties and complex morphology, before being transduced into neural activity by mechanoreceptors situated at the epidermis-dermis border and distributed at regular intervals relative to the ridges (see illustration in Fig. 1A).

While numerous studies have investigated ridge deformations (Cauna, 1954; Gerling and Thomas, 2005, 2008; Willemet et al., 2021; Delhaye et al., 2016) and the mechanical properties of different skin layers (Pereira et al., 1991; Leyva-Mendivil et al., 2015, 2017), most of this work has focused on ex-vivo specimens, surface measurements, or computer simulations. Consequently, the mechanical response of the skin below its immediate surface remains largely unknown, leading to conflicting interpretations in the literature. For instance, when the skin on the fingertip conforms to the shape of an external object, the ridges might be stiff and maintain their shape while bending occurs primarily in the flexible grooves (Swensson et al., 1998; Gerling and Thomas, 2008). Alternatively, the grooves may be stiffer or less prone to movement than the ridges, which might depress to conform to the object's shape (Cauna, 1954). Similarly, during contact with a small tactile feature (Johansson and LaMotte, 1983) or stick-to-slip transitions on a flat surface (Delhaye et al., 2016), the ridge flanks experience stretching and compression at the skin's surface. However, it remains uncertain whether these deformations are mirrored in deeper layers or if the ridges undergo complex bending (see Cauna, 1954; Gerling and Thomas, 2008, for two opposing ideas).

From a mechanical standpoint, these conflicting interpretations raise the question of to what extent ridges stretch or compress along the plane of the skin's surface, how much they shear horizontally, and whether ridges do also shear orthogonal to the skin surface (see examples in Fig. 1B). Additionally, all these deforma-

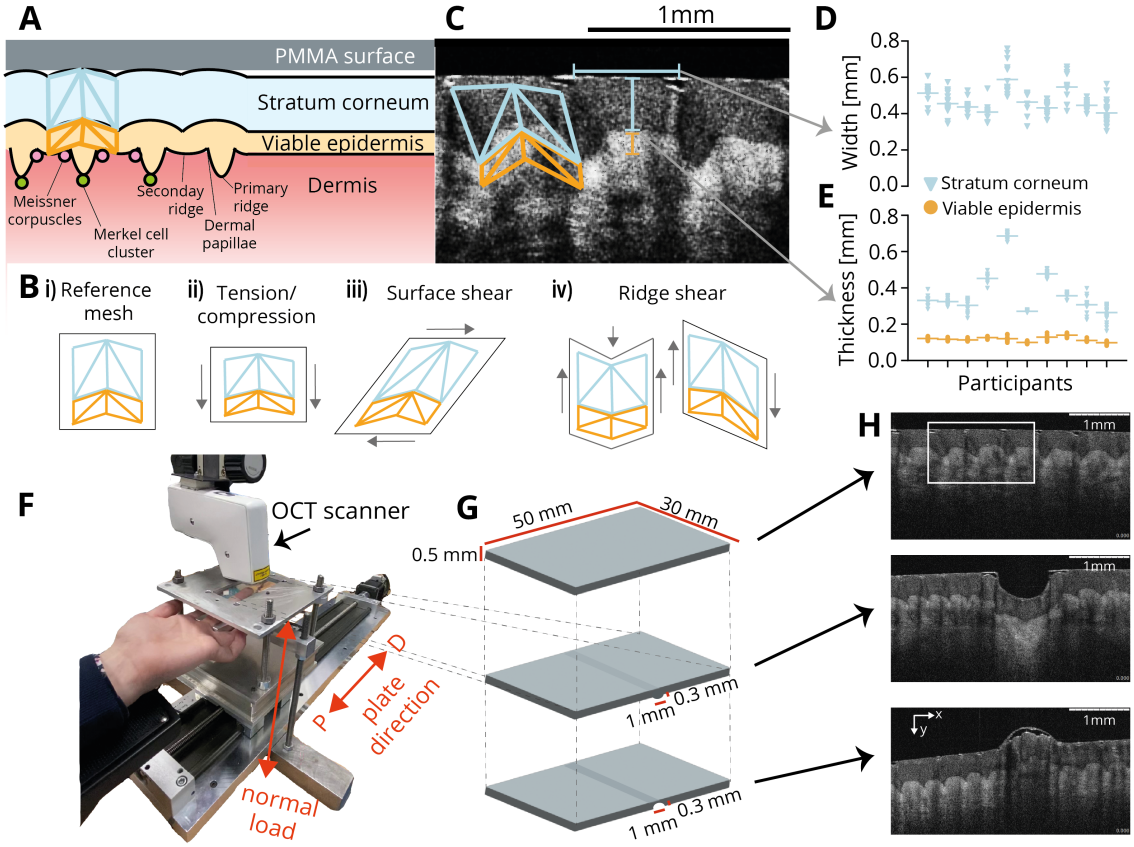

Figure 1. Experimental setup and identification of individual fingerprint ridges. A. Two main mechanically relevant skin layers constitute the epidermis on the human fingertip: the stratum corneum (blue shading) and the viable epidermis (orange). The ridged structure of the fingerprints extends to deeper layers with increasing morphological complexity. Interactions with surfaces (grey shading, flat surface) take place at the outer boundary of the stratum corneum, while mechanoreceptors are located at the border between the epidermis and the dermis (red shading), at distinct landmarks associated with the ridge structure. Identification of specific morphological landmarks, such as the tops and valleys of a ridge, allows the creation of a fine-grained mesh covering the sub-surface structure of a single ridge (blue and orange overlaid meshes). **B.** Potential ridge deformations during tactile interactions, with arrows indicating the directions of relative deformation. i) Reference mesh (undeformed); ii) Tension and compression of the whole ridge along or orthogonal to the surface axis of the skin; iii) surface (horizontal) shear, where the ridge tilts sideways; iv) ridge (vertical) shear, where the ridge tilts along the axis orthogonal to the surface of the skin. These deformations need not apply to the whole ridge but could also manifest locally, e.g., in individual layers or, as in one of the ridge shear examples, differently across both ridge flanks. **C.** Detail view of a single OCT frame clearly showing ridged skin structure and sub-surface layers, with mesh covering a single ridge overlaid. **D.** Ridge widths ($n = 153$) across all participants based on data obtained using the flat surface Each dot corresponds to a unique ridge with the participant mean indicated by the horizontal line. **E.** Thickness of stratum corneum (blue) and viable epidermis (yellow) as calculated from the same data as above. Markers are the same as in D. **F.** The experimental apparatus consisted of a finger holder to which the left middle finger of the participant was secured. A horizontal plate with a smaller inlaid transparent surface could manually be moved to indent the fingertip. A motorized linear stage moved the plate in the distal/proximal direction across the fingertip. An OCT scanner recorded images of the top skin layers through the transparent surface, while forces were recorded using a 3-axis force sensor. **G.** Transparent surface stimuli used in the experiment: a flat surface, a plate embossed with an edge, and a grooved plate. **H.** Individual images recorded by the OCT scanner display the complex morphology of the skin and its changes in response to tactile features.

tions might apply to ridges in bulk or might only manifest locally, such as in individual skin layers or within a single ridge flank. To empirically address this question, we employed Optical Coherence Tomography (OCT) to precisely measure the sub-surface deformation of individual fingerprint ridges in response to a variety of mechanical events. OCT has been used previously to investigate sub-surface skin properties, however, its application has been limited to static characterization of the skin morphology, such as measuring tissues' thickness and roughness (Maiti et al., 2020; Ding et al., 2021; Adabi et al., 2017; Czekalla et al., 2019; Lin et al., 2021). In the present study, we aimed to investigate the ways in which ridges are able to deform during dynamic contact events as well as the role played by different skin layers in order to better understand how the ridged structure of fingertip skin supports tactile sensing.

Results

Measuring skin deformation on a sub-ridge scale

We developed a setup for tactile stimulation of the fingertip, which involved lowering a custom-made transparent thin plate onto the participant's fixed fingertip at a set normal load and smoothly sliding the plate in both distal and proximal directions at a set speed (Fig. 1F, G). Concurrently, we used an OCT scanner to capture images of the skin's surface and sub-surface morphology. The scanner obtained 4 mm wide slices with 4.5 µm lateral and 5 µm axial resolution at a sampling frequency of 10 Hz. The images were taken by scanning through the transparent plate along the proximal-distal axis of the finger. Both the stratum corneum and viable epidermis were clearly distinguishable (Fig. 1C, H).

After acquiring and pre-processing the OCT images,

we used semi-automatic methods to track sub-surface landmarks associated with individual ridges across different video frames (see Methods). The resulting triangular mesh consisted of eight facets per ridge, distributed between the stratum corneum and viable epidermis, as well as the two flanks of the ridge (Fig.1B). Importantly, the mesh was fine-grained enough to identify canonical sub-surface ridge deformation patterns in response to various tactile events. The mesh also extended to and partially covered the dermis-epidermis border, where low-threshold mechanoreceptors are located (Fig. 1A). On average across participants, we measured a ridge width of 0.47 mm (Fig. 1D), along with a thickness of 0.38 mm for the stratum corneum and 0.12 mm for the viable epidermis (Fig. 1E), consistent with previous studies (Moore, 1989; Maiti et al., 2020).

We gathered a large and varied dataset to be able to make robust claims: across four protocols and ten participants, we identified a total of 393 unique ridge slices, which were tracked for 34 s on average and more than a minute in some cases, supported by hundreds of thousands of individually tracked landmarks.

Static normal load

To investigate the response of individual ridges to static normal loads, we applied a flat stimulus to the fingertip, incrementally increasing the load from initial contact in steps of 0.5 N until reaching a maximum of 3.5 N (see examples in Fig. 2A, B). Deformation was measured relative to the unloaded ridge's stereotypical configuration, and the principal tensile and compressive components of the strain experienced by each mesh facet were obtained (see Methods).

Under load, the central part of individual ridges depressed, while the flanks stayed in place (vertical shear), which led to a flattening of the ridge structure and which was consistently observed across participants (see examples in Fig. 2C). Ridges could also display horizontal shear and bend proximally or distally depending on their unloaded configuration and sometimes stretch horizontally along the axis of the skin surface. Both tensile and compressive strains increased monotonically with normal load, with rapid changes and, therefore, larger deformations at initial contact followed by slower and mostly linear changes from 0.5 N onwards (Fig. 2D, E). Across all facets in a given layer, tensile strains reached around 15% in the stratum corneum and 10% in the viable epidermis, while compressive strains were above 20% in the viable epidermis and steadily increased with the load but remained below 10% in the stratum corneum. We noted a small increase in the area of the stratum corneum, which was likely an artifact due to the fit of the mesh to the ridge's curvature, but a notable decrease in the area of the viable epidermis (Fig. 2F). Our results, therefore, indicate that both the stratum corneum and the viable epidermis undergo deformation under static load, mostly manifested as a

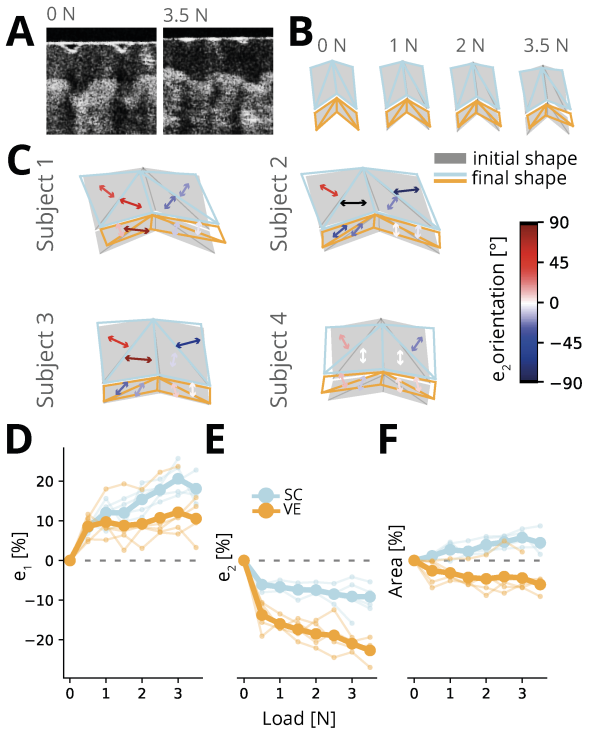

Figure 2. Ridge deformation under normal load. A. Example frames showing a single ridge unloaded (0 N; left) and maximally loaded (3.5 N; right). **B.** Examples of ridge deformation under static normal load for different load conditions. Shown is the unloaded ridge outline (grey shaded regions) with the deformed ridge mesh superimposed (blue and orange), under 1 N, 2 N, and 3.5 N loading. **C.** Examples of ridge deformation under static normal load for different participants. Shown is the unloaded ridge outline (grey shaded regions) with the ridge mesh under 3.5 N loading superimposed. Arrows indicate the principal compressive axis for each facet, with colors indicating different orientations relative to vertical. In the lower panels, the magnitude of principal tensile (e_1, **D.**) and compressive (e_2, **E.**) strains as well as area change (e_a, **F.**) as a function of normal load. Thin lines denote individual participants, and thick lines show the average. Data from five participants with seven individual ridges tracked each.

flattening of the ridge structure, but that compression is higher in the viable epidermis.

Lateral sliding and stick-to-slip

After characterizing the deformation resulting from a static normal load, we investigated sliding interactions between the fingertip and the flat surface. The flat surface was first lowered onto the fingertip until stable contact was established (with a normal load below 0.5 N), then displaced at a constant speed of 0.8 mm/s by 7.6 mm in the distal or proximal direction for a total of 8 movements. In accordance with previous findings, we observed two distinct phases of relative movement between the skin and the plate: stick, where the ridges adhered to the plate and were dragged along with it, and slip, where the ridges stopped moving, and the plate slipped over them. The clear distinction between the stick and slip phases allowed us to classify each phase based on the average horizontal velocity over all tracked features (see Fig. 3A for an example from a single participant).

Previous studies have shown that stick-to-slip events elicit strain waves on the surface of the fingertip skin (Delhaye et al., 2021; Willemet et al., 2022; du Bois de

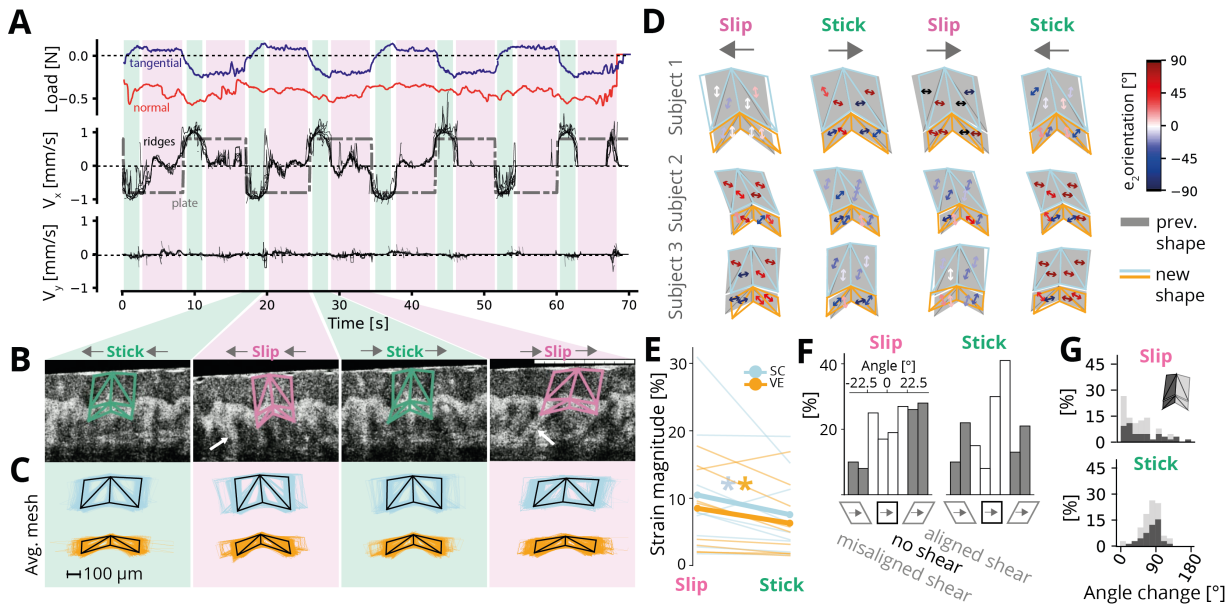

Figure 3. Ridge deformations during sliding. A. Measurements during repeated movements of the flat plate along the distal-proximal axis for a single participant. Top: Tangential (purple) and normal (red) load as a function of time. The normal load was set at 0.5 N at the start of the trial by adjusting indentation and then not further controlled. Tangential load alternates between positive and negative values depending on the movement direction of the plate. Middle: Horizontal velocity of the plate (dash-dotted grey line) and average velocity of each tracked fingerprint ridge (thin black lines) during all eight transitions of the flat plate. Two phases are evident: when the ridge is moving along with the plate (stick, indicated by green shading) and when the ridge is stationary, but the plate is moving (slip: indicated by pink shading). Bottom: Vertical velocity of all tracked ridges along the normal axis, which is close to zero. **B.** Example frames showing a single-tracked ridge for the stick and slip phases of the two movement directions. White arrows point to presumed collagen fiber bundles anchoring the skin to the bone. **C.** Average ridge meshes (black lines) during each of the four phases calculated over all tracked ridges and all time points assigned to each phase for the same participant as in A, B. Colored lines indicate individual sample meshes ($n = 3773$; blue: stratum corneum, yellow: viable epidermis). **D.** Examples showing ridge deformation across the four phases for three participants. Shown are the ridge outline for the previous phase (grey shaded regions) with the ridge mesh for the current mesh superimposed. Arrows indicate the principal compressive axis for each facet, with colors indicating different orientations relative to vertical. **E.** Average magnitude of maximal shear strains as a proxy for overall deformation in the stick-to-slip transition compared to the movement reversal. Thin lines denote individual participants (averaged over facets and movement directions), and thick lines show the grand average. Asterisks denote statistically significant differences (paired Wilcoxon tests). Strains are about a third higher during stick-to-slip transitions than during movement reversals. **F.** Histograms of average principal strain angles for all mesh facets and participants in stick-to-slip transitions (left) and movement reversals (right). White bars denote angles that are within 22.5° of the coordinate axes (horizontal or vertical) and therefore denote tension or compression without considerable shear. Grey bars denote angles within 22.5° of the diagonal and therefore denote horizontal shear. Positive angles denote shear acting in the same direction as the plate movement, while negative angles denote shear in the direction opposite to the plate movement. **G.**Change in principal strain angles when transitioning to slip (top) or stick (bottom) phases, separated by ridge flank (light and dark grey). Movement reversals cause a 90-degree shift in the strain angle, while stick-to-slip transitions cause little change, with no differences between ridge flanks evident.

Dunilac et al., 2022), but their effects on the sub-surface structure are unclear. Additionally, reversing the plate's movement direction changes the tangential force applied to the skin and induces shear deformations within the tissue, but it is unclear whether these are absorbed in surface skin layers or in deeper tissues. To quantify the deformation that occurred between the transitions from stick to slip and between different movement directions of the plate, respectively, we calculated a stereotypical mesh covering a single papillary ridge by averaging the meshes of all tracked ridges ($n = 140$ in total) across image frames within the same phase for each participant (Fig. 3B, C, see Methods). We then calculated the principal tensile and compressive strain components experienced by each mesh facet on the transition from one phase to the next.

Examining the ridge deformation changes between movement phases revealed large variability across participants, both in the magnitude and the orientation of the deformations (see individual examples in Fig. 3D and all participants in Fig. S1). This variability is likely explained by the fact that, during stick-to-slip transitions, some parts of the fingertip experience tension, while others experience compression (Delhaye et al., 2016), and therefore measurements depend on the precise location. Additionally, the mechanical properties of each individual fingertip influence its own mechanical response and, crucially, at what time during the plate transit the stick-to-slip transition will happen (see Methods), leading to varied mechanical environments. Nonetheless, several consistent findings emerged from the data.

First, we found that, across participants, strain magnitudes (quantified as maximal shear strain, see Methods) were consistently larger by about a third during the stick-to-slip transitions compared to the plate reversal transition (Fig. 3E) for both the stratum corneum and viable epidermis ($p < 0.01$ for both based on paired Wilcoxon signed-rank tests across all facets, movement directions, and participants). This was also true for individual participants, with strain largest during stick-to-slip transitions for eight out of nine participants. Thus, ridge deformations are most pronounced during stick-to-slip transitions rather than in response to different movement directions of the surface.

Second, while the orientation of the principal strain axes

varied between participants, they were relatively consistent within participants in individual phases: the average angular standard deviation was 26 degrees when considering all facets of the ridge within a given phase and, subsequently, averaging over phases and participants. Consequently, strains tended to act in a consistent direction along the entire extent of the ridge (see also examples in Fig. 3D). Notably, the principal strain directions exhibited a greater alignment with the cardinal axes (0 and $\pm$ 90 degrees) rather than diagonal axes ($\pm$ 45 degrees) for the majority of participants across most phases (averaging 60% overall, see Fig. 3F). This alignment implies a predominance of tension and compression in the ridge rather than horizontal shear. When shear did manifest, it was more pronounced during stick-to-slip transitions compared to direction changes, and generally aligned with the direction of plate movement, although this alignment was not always observed. We did not find any significant differences in the distribution of principal angles between the stratum corneum and the viable epidermis for either stick-to-slip transitions or movement reversals ($p > 0.37$ for both based on two-sample Kolmogornov-Smirnov tests across all facets, directions, and participants).

The low amount of shear was surprising, as during stick phases the skin was typically dragged along with the surface for several millimeters (mean: 3.4 mm, range: 0.9-6.3 mm). Assuming no motion of the bone, and a distance of 5-10 mm between the lightly loaded skin surface and the bone (Birznieks et al., 2001) yields large expected shear strains of 45% on average (range: 9-126%), clearly much in excess of what we observed. Thus, most of this shearing must be sustained by deeper tissues. In agreement with this idea, we noticed that collagen fiber bundles visible in the recorded frames often displayed much higher tilt than was visible in the stratum corneum or viable epidermis (see highlighted examples in Fig. 3B).

Finally, when switching movement direction, which caused the skin to stick to the surface again, we observed a 90-degree rotation of the principal axis of deformation (see Fig. 3G, bottom panel). In contrast, there was relatively little change in the angle when transitioning to slip (Fig. 3G, top panel). Thus, changing direction caused a reversal in the tension and compression axes but relatively little deformation in itself; this deformation then occurred during the transition to slip. The observed changes in orientation occurred consistently for both ridge flanks and therefore applied uniformly to the whole ridge.

In summary, our findings indicate that the primary deformations occurring during contact with a flat plate predominantly involve tension and compression of individual ridges along the skin's surface. Horizontal shear is only occasionally present and does not consistently align with the direction of movement. When shear is observed, it is more prominent during stick-to-slip transitions rather than during reversals of the plate movement.

Ridge interactions with small tactile features

Finally, we investigated ridge deformation during contact with small tactile features that were close in size to that of a single ridge itself (1 mm in width and 0.3 mm in height/depth). For this experiment, we used the plates with the edge and groove, respectively, keeping all other stimulation parameters the same. We identified five consecutive phases for each tracked ridge based on its position relative to the edge or groove: 1) sliding under the flat part of the surface, 2) approach of the feature, 3) located centrally under the feature, 4) withdrawal from the feature, and 5) sliding under the flat part of the surface (see illustrations in top rows of Fig. 4A, D). We again quantified the deformation of the average ridge during all these phases (see Methods), with the strains calculated relative to the initial mesh before contact with the feature was made (phase 1).

Ridge deformations were remarkably similar across participants but differed clearly across movement phases (see ridge deformations for a single participant in Fig. 4A, D bottom rows and all participants in Figs. S2 and S3). There was minimal evidence supporting the notion of a rigid ridge maintaining its shape, and instead, the central part of the ridge deformed considerably. Horizontal shear was relatively modest, with generally little bending of the ridge observed. Instead, our findings highlighted that the primary mechanism through which the ridge conformed to the shape of a feature involved vertical shearing of the whole ridge or the two ridge flanks against each other, as the skin moved vertically to conform to the feature. Consequently, during the transit of the edge, the full ridge initially sheared orthogonally to the skin's surface with both the strain orientations of both flanks aligned (Fig. 4B, left panel). When the edge was directly above the ridge, both flanks sheared against each other, leading to opposite strain orientations across the two flanks (Fig. 4B, middle panel) before the ridge returned to its original configuration during the withdrawal of the edge Fig. 4B, right panel). This pattern was mirrored, but with strain orientations reversed, during the transit of the groove (Fig. 4E).

Strains increased and reached their maximum with respect to the initial configuration when the ridge was located directly under the feature and then decreased again as the ridge reverted to its original shape. For the edge, both strain components differed between the viable epidermis compared to the stratum corneum when the ridge was located directly below the feature ($p < 0.01$ in Bonferroni corrected paired Wilcoxon tests across all facets and participants), resulting in an expansion of the area of the viable epidermis, as it was stretched around the edge feature, while the mostly incompressible stratum corneum retained its area (Fig. 4C). Conversely, while interacting with the groove, a ridge experienced high compressive strains,

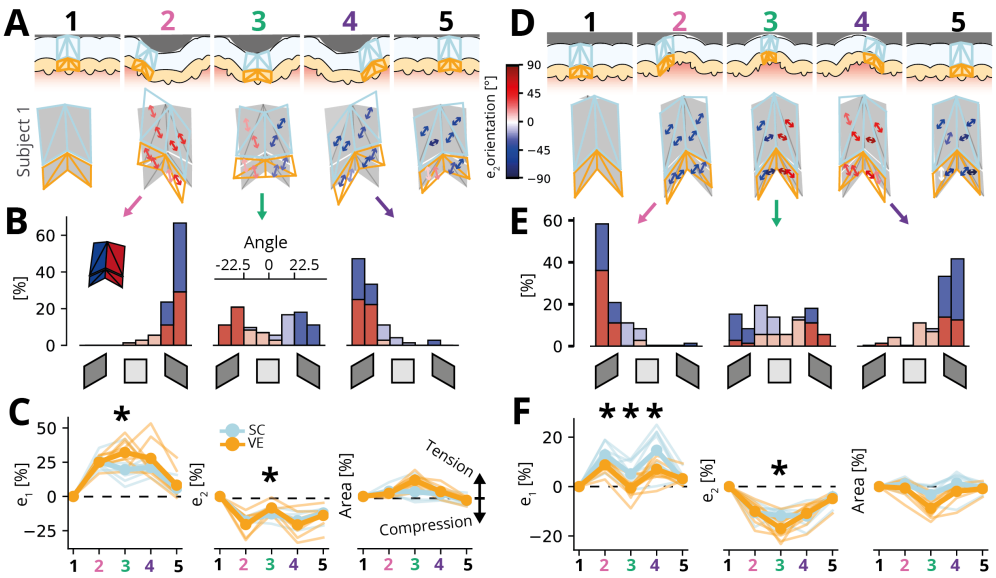

Figure 4. Ridge deformations and skin strains during transit of small tactile features. A. Top row: Illustration of identified movement phases with the edge feature in different locations relative to the tracked fingerprint ridge. Bottom row: Average ridge deformation and associated principal compressive strain orientation for a single participant. Note that all strains are calculated with respect to the mesh shown in the left-most column, which represents the ridge during full slip before the interaction with the tactile feature. **B.** Histograms of principal strain orientations across all ridge facets and participants for the approach (2), central (3), and withdrawal (4) phases. Red bars denote distal ridge flanks and blue bars denote proximal ones. Darker shading denotes orientations close to diagonal indicating shear, while lighter shadings denote angles aligned vertically or horizontally and therefore denote no shear. **C.** Average magnitude of principal tensile (e_1, left panel) and compressive (e_2, middle panel) strains as well as area change (right panel) relative to the stereotypical ridge under full sliding (phase 1). Thin lines denote individual participants ($n = 9$), and thick lines show the average. Ridges are most deformed when directly under the edge feature when strains are higher in the viable epidermis than the stratum corneum. While the stratum corneum is incompressible, the area of the viable epidermis expands when directly under the ridge. **D-F.** Same as in A-C, but for a small groove transitioning over the ridge. Note that the findings broadly reflect those obtained with the edge feature, but with the direction of compressive and tensile strains reversed.

which again were larger in the viable epidermis compared to the stratum corneum, and as a result, the area covered by the viable epidermis contracted, while the stratum corneum retained its area (Fig. 4F).

Discussion

This study measured the sub-surface deformation of individual papillary ridges in the fingertip skin during tactile interactions in vivo. The dataset included hundreds of individual ridges, whose deformations were tracked using high-resolution meshes during static normal load, lateral stick, and slip using a flat surface, as well as during contact with small tactile features. We found that individual ridges tended to flatten even at relatively low forces. Lateral sliding elicited strong tension and compression, often aligned with the surface orientation of the skin, which was especially strong during stick-to-slip transitions. Contact with edges and grooves yielded strong vertical shear, with ridge flanks moving relative to each other. We observed horizontal shear during static contact and sometimes when sliding the flat surface, however, it was limited in magnitude and was present only for some participants.

Canonical ridge deformations during tactile interactions

One of the main objectives of our study was to investigate the primary deformation patterns exhibited by individual ridges during tactile interactions. Previous studies combining mechanical measurements at the ridge surface and histology (Cauna, 1954) or analyzing the spatial keratin expression patterns within single ridges (Swensson et al., 1998) have suggested the presence of alternating softer and stiffer regions within the ridges. These findings implied a mechanically constrained set of canonical deformations, yet the specific nature of these deformations has been a subject of debate, lacking direct empirical evidence.

In this study, we have provided conclusive evidence that ridge peaks are not rigid and, instead, individual ridges undergo significant flattening during contact. This finding challenges previous speculation that the grooves between the ridges act as 'hinges' (Swensson et al., 1998). Instead, our results demonstrate that the fingerprint predominantly conforms to an external object through vertical shearing. Thus, the primary mechanism through which the ridge conforms to the object involves the relative movement and shearing of the ridge flanks, rather than relying on the grooves as articulated joints.

In contrast to the prominent vertical shearing observed, our study revealed minimal and inconsistent horizontal shear. We propose that the flattening of the ridges during contact may prevent further bending of the ridges, thus limiting the occurrence of horizontal shear. The absence of horizontal shear during the stick phase of lateral sliding on the flat surface was particularly unexpected. During these periods, the skin re-adhered to the plate and was subsequently dragged along, of-

ten over a distance of several millimeters. Our findings strongly indicate that the majority of the surface movement of the skin was absorbed by deeper tissue rather than the surface layers of the skin. Previous studies investigating tactile afferent responses to tangential skin movements have reported strong activation of SA-2 receptors, thought to measure skin stretch mainly in deeper tissues (Saal et al., 2023). Thus, the mechanical response of the fingertip during tactile interactions involves a complex interplay between the surface layers and deeper tissues, which warrants further investigation (see Duprez et al., 2023, for some recent work).

Implications for neural coding of touch

Ridge deformations are ultimately transduced into neural activity by mechanoreceptors, and our findings provide new insights into this process.

First, the magnitude of sub-surface deformation measured in our study correlated with neural response strengths observed in other studies. In trials with the flat surface, we measured larger deformations during stick-to-slip transitions than during reversals of the plate's movement direction. Analogously, a previous study recorded neural responses during sliding stimulation of the fingertip and reported that rapidly adapting type I afferents (RA-I) showed little to no response during the onset and offset of the tangential load but strongly encoded the stick-to-slip transition (Delhaye et al., 2021), suggesting that mechanoreceptors directly encode the local amount of deformation. Our findings also extend these prior results by demonstrating that the large surface strains measured during the transition from stick to slip are mirrored in tissues below the surface and specifically at the depth at which type-1 mechanoreceptors are located. Altogether these results provide a physiological explanation for the widely observed human capacity of fine-tuned grasping with quick adjustments of the grip force to friction changes (Johansson and Westling, 1984; Cadoret and Smith, 1996; Schiltz et al., 2021).

Second, our finding that contact with small tactile features elicits shearing of both ridge flanks against each other suggests that the mechanical resolution of the fingerprint skin is on the order of half the width of an individual papillary ridge. In principle, such fine-grained and local differences in strain might be detectable by mechanoreceptors. Indeed, Meissner corpuscles innervate each flank of a fingerprint's ridge, and prior work has shown that separate fibers can innervate the two flanks of the same ridge (Nolano et al., 2003). Previous psychophysical work also appears to support this idea because it has estimated the spatial resolution of static touch at around 200 µm, thus approximately half the width of a single ridge of the fingerprint (Hollins and Risner, 2000; Bensmaia and Hollins, 2003). However, it should be pointed out that such estimates are notoriously difficult to obtain reliably as they depend on both the precise stimulus and the mode of contact and that this limit has traditionally been associated with the responses of Merkel cells rather than Meissner corpuscles. Previous neural recordings measured the spatial acuity of the receptive sub-fields of RA1 and SA1 afferents, which were estimated to lie in the submillimeter range, roughly matching the width of a single ridge (Jarocka et al., 2021; Sukumar et al., 2022). Our results also suggest that complementary features (edges and grooves, respectively) generate symmetrical deformation. Recording responses from the same tactile afferent to such complementary features might help to disentangle what aspects of shearing the afferent is sensitive to. Therefore further electrophysiological and psychophysical work is needed to determine whether the sub-ridge mechanical resolution of the fingerprint skin does indeed translate into corresponding neural and perceptual acuity.

Limitations and future work

While our study was based on a large dataset, which contained a variety of tactile interactions, there are a number of limitations. First, while we could confidently track landmarks associated with the stratum corneum, we could not reliably identify the primary ridges of the epidermis, though they were visible in some of the frames. We hypothesize that the additional depth combined with their slender morphology might have degraded the signal. Primary ridges are of importance because Merkel cell clusters are located at their tip, and they are therefore likely important for mechanotransduction. Indeed, primary ridges feature in the so-called 'lever hypothesis' of tactile transduction (Cauna, 1954), which has been called into question (Gerling and Thomas, 2005, 2008), though direct empirical evidence is currently lacking. Ideally, future studies would improve imaging resolution and clarity to visualize morphological structures in more detail and at greater depth. We employed a state-of-the-art, clinical OCT scanner, routinely used in dermatological clinical assessments. Data from a recently developed experimental scanner demonstrated the possibility of resolving smaller structures in the tissues, even as small as Meissner corpuscles, by applying a technique called speckle-modulating OCT (Liba et al., 2017). Coupling such advanced imaging techniques with our experimental set-up and analysis pipeline would further advance the understanding of sub-surface skin properties and deformation mechanisms and allow more direct investigation of neural mechanisms. Such advanced imaging could also be combined with electrophysiological recordings from afferent fibers using microneurography (see Delhaye et al., 2021, for an example).

Second, while the edges and grooves of our feature plates were only marginally larger than a single papillary ridge and mimic those employed in other studies (Jarocka et al., 2021), even smaller stimuli would be capable of delivering much more localized forces (Johansson and LaMotte, 1983). In the present study, we

were limited by the resolution of the 3D printing technique employed to manufacture the transparent plates. Additionally, sharp corners elicit optical artifacts in the obtained images, which can occlude landmarks.
Third, we obtained two-dimensional slices oriented orthogonal to the orientation of the fingerprints, but the skin is a three-dimensional structure. Some of our tactile interactions might have caused skin deformations out-of-plane that were thus not measurable. Future studies could consider creating three-dimensional reconstructions of the fingerprint structure to study such effects.
Finally, in our study, we focused on young, healthy participants. However, several studies have shown that morphological and mechanical skin properties can greatly vary with physiological and physical factors such as age (Jobanputra et al., 2020; Püllen et al., 2021; Skedung et al., 2018), sex (Luebberding et al., 2014; Diridollou et al., 2000), level of skin moisturization (Tomlinson et al., 2011), as well as room temperature and humidity (Klaassen et al., 2016). All these factors might therefore also influence how individual ridges deform.

Material and Methods

Participants

Ten healthy participants (3 males, average age 20.5 years) participated in the experiment after providing informed consent. Due to low imaging quality for data from one participant, which precluded consistent tracking, all sliding experiments included data from nine participants; the static protocol was run on a subset of five participants. The experiment was performed on the subjects' left middle finger. Before any trial, the finger was thoroughly cleaned with water and dried carefully, and a thin layer of petroleum jelly was applied to moisturize the skin; this helped prevent repeated stick-slip events while sliding the surface. Environmental conditions during the test were controlled with 20° C room temperature and 50% relative humidity. The study protocol received ethical approval from The University of Sheffield Research Ethics Committee (ethics number 039144). All experiments took place in the Skin Barrier Research Facility, operated by Sheffield Dermatology Research at the Royal Hallamshire Hospital in Sheffield, UK.

Experimental set-up

The experimental set-up for the present study was adapted from the design of an earlier study (Lee et al., 2019). Transparent plates were secured by a support rig fixed on a linear stage that could move in both distal and proximal directions with respect to the participant's fingertip, allowing the plate to slide against the finger. The fingertip was glued onto a finger holder to maintain its position during the acquisitions. The support rig was mounted on a force plate (HE6X6-10, Advanced Mechanical Technology, Inc.) to measure the load along the axes parallel and perpendicular to the direction of the movement and along the axis normal to the plate surface. The plates were made from polymethyl methacrylate (PMMA) and were 30x40x0.5 mm in size (produced by Shape Technology S.r.l., Casale Monferrato, Italy). One plate was flat, while the two others had an embossed oriented half-circular edge (1 mm base diameter and 0.4 mm height) or an engraved oriented groove (1 mm based diameter and 0.3 mm depth) traversing the middle of the surface (see Figure 1F).
Prior to each trial, the plate specimens were cleaned with deionized water and dried thoroughly with paper towels. In the static loading experiment, the plate was initially positioned in contact with the participant's fingertip without exerting any pressure (0 N). Afterward, the load was manually incrementally increased in 0.5N steps, reaching a maximum of 3.5N. At each step, 20 frames were recorded. In the sliding experiments, before commencing the imaging acquisition in each trial, the plate was manually lowered onto the participant's fingertip until a normal load of 0.2N was reached. During each trial, the plate was moved 7.6mm in each direction (proximal to distal and vice versa) four times at a constant speed of 0.8mm/s.

Image acquisition and pre-processing

For image acquisition, we utilized the Vivosight® OCT system (Michelson Diagnostics, Kent), which is clinically approved and features a Fourier domain with a 20 kHz swept-source laser at 1300 nm center wavelength. The image capture rate was 10 frames per second, and the dimension of each image was 895 × 483 pixels with 256 gray levels with a 4.5µm lateral and 5µm axial resolution.
Following the acquisition, we preprocessed the images using the cv2 library in Python. Firstly, we normalized the brightness and increased the contrast by applying histogram equalization. Then, to further enhance the contrast and adjust the image saturation, we performed a gamma transformation ($\gamma = 5$). Lastly, we removed noise while preserving sharp edges by applying a bilateral filter (diameter of pixel neighborhood: 5, sigmaColor: 110, sigmaSpace: 190).

Tracking of individual ridge deformation

In each frame of the experiment, the top and bottom of each ridge within the field of view were semi-automatically tracked at three levels: the surface, the border between the stratum corneum and viable epidermis, and the junction between the dermis and epidermis. For each set of frames obtained during a single trial, a portion of the frames, ranging between 25-50% of the total, were manually annotated using the Python polygonal annotation library Labelme (Wada et al., 2021). The annotated frames were then used to train a DeepLabCut model to automatically estimate the position of each tracked point in the remaining frames (Nath et al., 2019). The accuracy of the models, on av-

erage, was 2.96 pixels on the training set and 14.64 pixels on the test set. We then manually reviewed the automatic annotations to correct any inaccuracies that might have arisen from automatic tracking. To measure the deformation of individual sub-surface ridges, the tracked points were used to create a triangular mesh for each ridge in the field of view. The mesh consisted of 8 facets per ridge, divided between the stratum corneum and viable epidermis and between the proximal and distal flanks of each ridge.

Movement phase classification

To study the skin movement during the transits of the plate, we analyzed the displacement of the tracked points from frame to frame. We calculated the horizontal and vertical components of the skin velocity, v_x and v_y, respectively, by measuring the displacement along the x-axis and y-axis. To determine the velocity components for each ridge, we averaged the velocities of the nine tracked points belonging to that ridge, resulting in v_x^{ridge} and v_y^{ridge}.
For the flat plate trials, four phases were identified by analyzing the horizontal component of the velocity v_x^{ridge}:

1. Sticking proximally ($v_x^{plate} < 0$, $v_x^{ridge} < 0$): the plate is moving in distal to proximal direction, and the skin is sticking to the plate.

2. Slipping proximally ($v_x^{plate} < 0$, $v_x^{ridge} = 0$): the plate is moving in distal to proximal direction, and it is slipping over the stationary skin.

3. Sticking distally ($v_x^{plate} > 0$, $v_x^{ridge} > 0$): the plate is moving in proximal to distal direction, and the skin is sticking to the plate.

4. Slipping distally ($v_x^{plate} > 0$, $v_x^{ridge} = 0$): the plate is moving in proximal to distal direction, and it is slipping over the stationary skin.

To identify the transition between sticking and slipping phases, we took the positive and negative extrema of the first derivative of v_x^{ridge} as markers. Each trial consisted of four plate transits in each direction, resulting in a total of 16 successive phases. We selected the central n_{phase} frames for each phase to ensure an equal number of frames for each occurrence of a single phase during the subsequent mesh averaging. We chose n_{phase} as the minimum duration of each phase among its four repetitions. The time spent in either phase varied markedly across participants (range: 11.4-82.7%, mean: 44.7%). These differences are partly attributable to differences in skin mechanics across participants (e.g., moisture level) but also depend on the precise location of the imaging site on the fingertip, as previous research has shown that stable contact is lost progressively over time across the whole fingertip during the transition from stick to slip (Delhaye et al., 2014).

For trials using the feature plates, all frames where $v_x^{ridge} \neq 0$ were discarded to retain only data where the skin was fully slipping under the plate. Then, by examining the vertical component of the skin speed v_y^{ridge}, four phases were classified for every ridge mesh separately:

1. full slipping ($v_y^{ridge} = 0$): before and after approaching the feature

2. approaching the feature ($v_y^{ridge} > 0$ for the groove plate and $v_y^{ridge} < 0$ for the edge plate)

3. moving away from the feature ($v_y^{ridge} < 0$ for the groove plate and $v_y^{ridge} > 0$ for the edge plate)

4. under the plate feature (frames in between the two previous phases, $v_y^{ridge} = 0$)

In each trial, there were a total of 40 successive phases, as each of the 5 phases identified occurred in each of the 8 transits of the plate. Again, the central n_{phase} frames were selected for each phase in order to consider the subsequent mesh averaging an equal number of frames in each occurrence of a single phase.

Strain computation

The mesh coordinates of each ridge in each frame were centered around the origin by subtracting from the coordinates of any tracked point in a ridge, the average of the coordinates across all the points in that ridge. Then, to obtain a single stereotypical ridge shape for every phase, the mesh coordinates of each ridge were averaged across all the ridges in a frame and all the frames in the same phase. Displacement field gradients were calculated for each triangle in the mesh,

- between two consecutive phases for the flat plate trials

- between the initial slipping phase and every other phase for the feature plates.

Green-Lagrange strains were estimated from the displacement gradient by the equations:

$$\varepsilon_{xx} = \frac{\partial u}{\partial x} + 0.5\left[\left(\frac{\partial u}{\partial x}\right)^2 + \left(\frac{\partial v}{\partial x}\right)^2\right] \quad \textbf{(1)}$$

$$\varepsilon_{yy} = \frac{\partial v}{\partial y} + 0.5\left[\left(\frac{\partial u}{\partial y}\right)^2 + \left(\frac{\partial v}{\partial y}\right)^2\right] \quad \textbf{(2)}$$

$$\varepsilon_{xy} = 0.5\left(\frac{\partial u}{\partial y} + \frac{\partial v}{\partial x}\right) + 0.5\left(\frac{\partial u}{\partial x}\frac{\partial u}{\partial y} + \frac{\partial v}{\partial x}\frac{\partial v}{\partial y}\right) \quad \textbf{(3)}$$

where ε_{xx} and ε_{yy} are the horizontal and vertical strain, ε_{xy} is the shear strain, and u and v are the displacements along x and y axes, respectively.
The principal component of the strain, e_1 and e_2, were obtained by eigenvalue decomposition of the strain matrix ε, as reported in (Delhaye et al., 2016). The principal strain decomposition consists of a rotation of the

reference coordinates so that the shear strain is canceled and the axial strains take their maximal and minimal value. Thus, the principal components e_1 and e_2 represent the maximum tensile and compressive deformation along perpendicular axes.

From the principal strain components, we computed the variation in the area of every triangle composing the mesh as:

$$e_a = \frac{e_1 + e_2}{2} \quad \textbf{(4)}$$

As as measure of overall deformation during sliding of the flat surface, we calculate the maximum shear strain as:

$$e_s = \frac{e_1 - e_2}{2} \quad \textbf{(5)}$$

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Supplementary Information

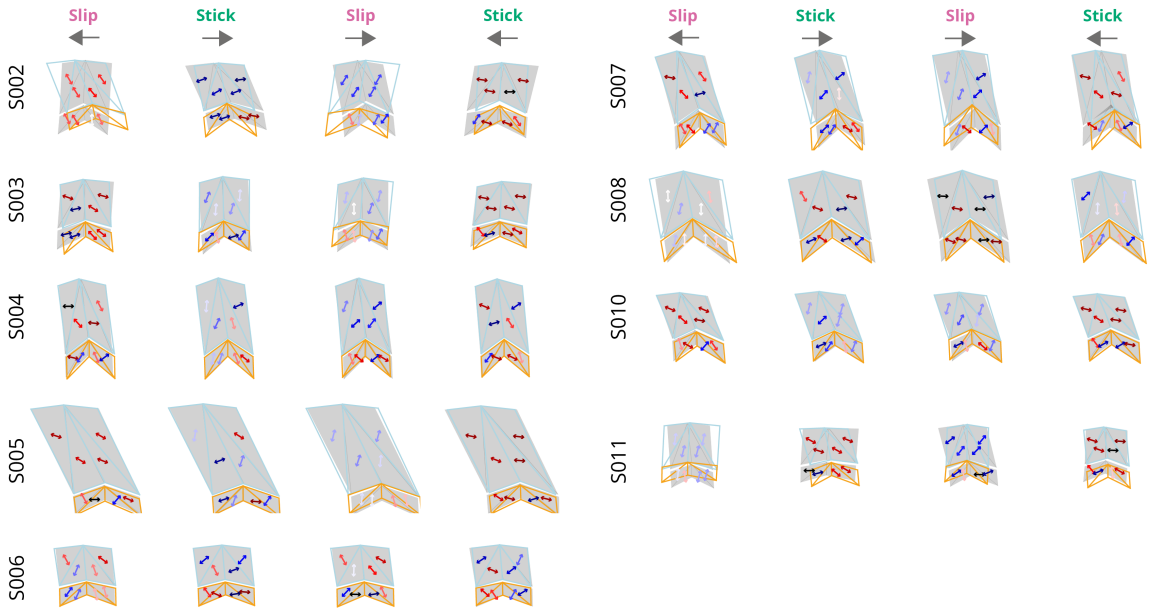

Figure S1. Ridge deformations for all participants during sliding of the flat plate. Ridge deformation across the four phases for all participants. Shown are the ridge outline for the previous phase (grey shaded regions) with the ridge mesh for the current phase superimposed. Arrows indicate the principal compressive axis for each facet, with colors indicating different orientations relative to vertical. Same style as Fig. 3D.

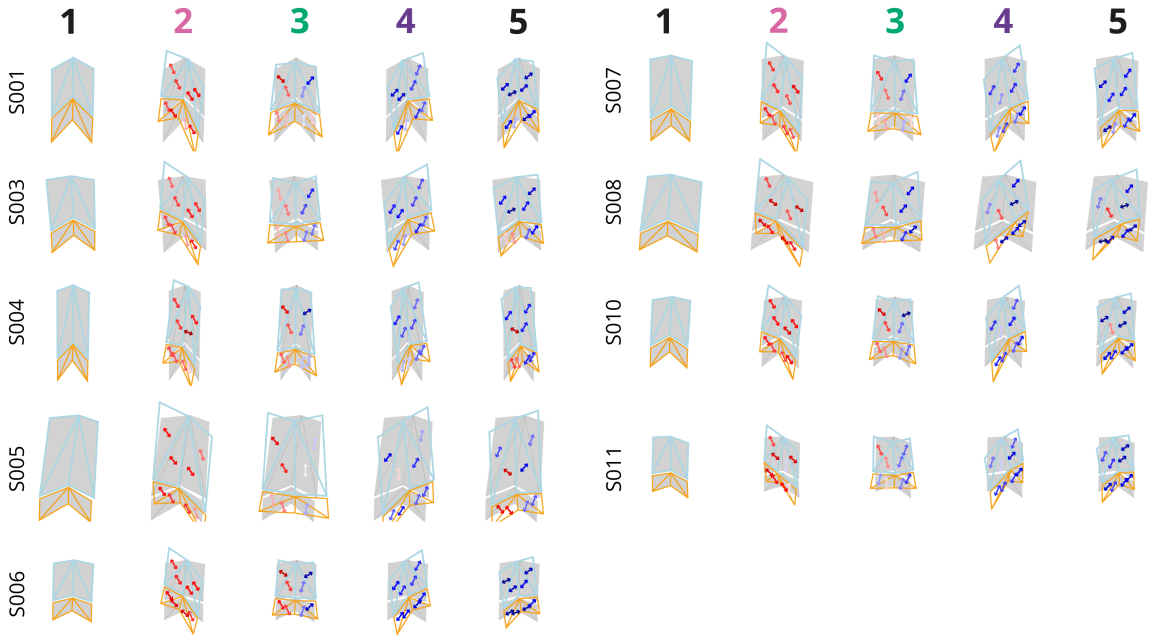

Figure S2. Ridge deformations for all participants during transit of the edge feature. Ridge deformation and associated principal compressive strain orientation for all participants. Note that all strains are calculated with respect to the mesh shown in the left-most column (phase 1), which represents the ridge during full slip before the interaction with the edge feature. Same style as Fig. 4A.

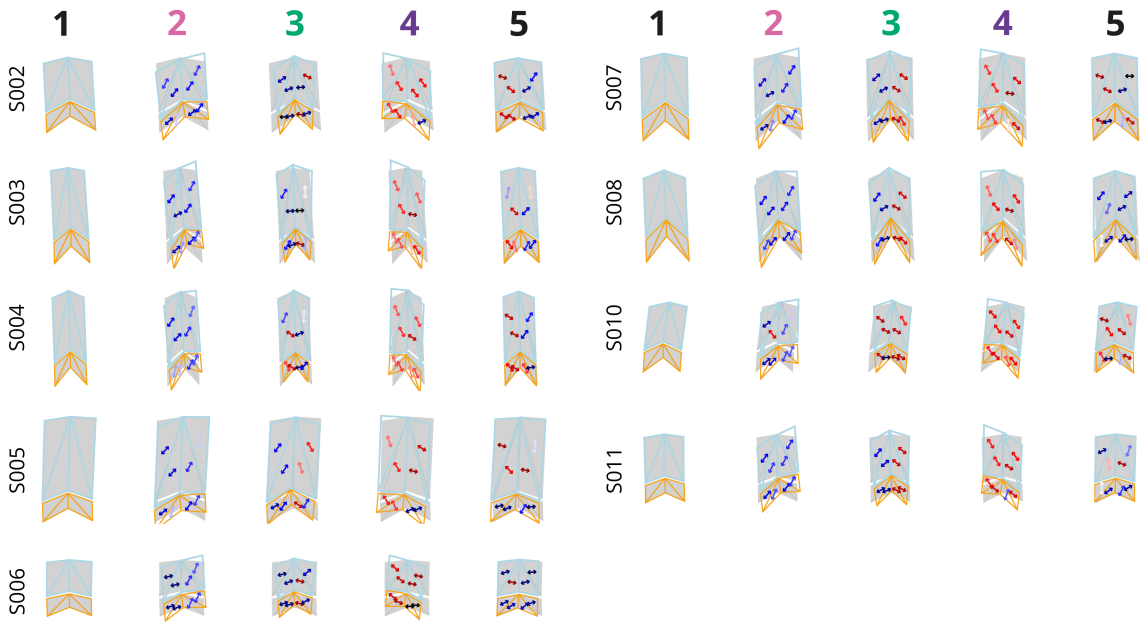

Figure S3. Ridge deformations for all participants during transit of the groove feature. Ridge deformation and associated principal compressive strain orientation for all participants. Note that all strains are calculated with respect to the mesh shown in the left-most column (phase 1), which represents the ridge during full slip before the interaction with the edge feature. Same style as Fig. 4D.