Fingerprint lines may not directly affect SA-I mechanoreceptor response

Gregory J. Gerling a, Geb W. Thomas b

a Department of Systems and Information Engineering, University of Virginia, Charlottesville, VA, USA

b Department of Mechanical and Industrial Engineering, University of Iowa, Iowa City, IA, USA

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Fingerprint lines may not directly affect SA-I mechanoreceptor response

GREGORY J. GERLING1, & GEB W. THOMAS2

1Department of Systems and Information Engineering, University of Virginia, Charlottesville, VA, USA and
2Department of Mechanical and Industrial Engineering, University of Iowa, Iowa City, IA, USA

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Abstract
Understanding how skin microstructure affects slowly adapting type I (SA-I) mechanoreceptors in encoding edge discontinuities is fundamental to understanding our sense of touch. Skin microstructure, in particular papillary ridges, has been thought to contribute to edge and gap sensation. Cauna’s 1954 model of touch sensibility describes a functional relationship between papillary ridges and edge sensation. His lever arm model proposes that the papillary ridge (exterior fingerprint line) and underlying intermediate ridge operate as a single unit, with the intermediate ridge acting as a lever which magnifies indentation imposed at the papillary ridge. This paper contests the validity of the lever arm model. While correctly representing the anatomy, this mechanism inaccurately characterizes the function of the papillary ridges. Finite element analysis and assessment of the critical anatomy indicate that papillary ridges have little direct effect on how SA-I receptors respond to the indentation of static edges. Our analysis supports a revised (stiff shell–elastic bending support) interpretation where the epidermis is split into two major layers with a stiff, deformable shell over an elastic bending support. Recent physiological, electrophysiological, and psychophysical findings support our conclusion that the function of the intermediate ridge is distinct from the function of the papillary ridge.

Keywords: Tactile, sensation, fingertip, skin microstructure, neural response, finite element model

Introduction and background
Understanding the functionality of skin microstructure may help explain the sensitivity that slowly adapting type I (SA-I) mechanoreceptors exhibit in response to edge and curvature stimuli (Phillips and Johnson 1981a; Johnson 2001). Solid mechanics techniques, in particular, have furthered our insights into the physiological and psychophysical factors that underlie touch sensation. Several researchers have used solid mechanics models to investigate the deformation and the stress and strain distributions in fingerpad skin in response to contact with a tactile stimulus (Phillips and Johnson 1981b; Van Doren 1989; Srinivasan and Dandekar 1996; Serina et al. 1997; Maeno et al. 1998; Pawluk and Howe 1999; Dandekar et al. 2003; Wu et al. 2004). In these investigations, an indenter deforms simulated skin tissue. Distributions of stress and strain in the underlying tissue are calculated, and compared to the in vivo neural response of skin mechanoreceptors, for the same stimulus. Existent models by Phillips and Johnson (1981b), Srinivasan and Dandekar (1996), Dandekar et al. (2003), and Sripati et al. (2006) achieve a high correlation for the SA-I receptor (usually between 0.80 and 0.97) for indenters with multiple, square gratings. This previous research suggests that the mechanics of the skin, particularly the way that stresses and strains are distributed throughout the tissue, enhance edge sensation. So far the focus has been on skin macrostructure.

Exploring the impact of skin microstructure on mechanoreceptor neural response is of particular interest because current macrostructural models can neither fully explain the skin’s role nor adequately differentiate stimuli. Skin macrostructural factors, such as fingerpad surface curvature, gross tissue properties, and homogeneous skin layers, generally determine how stress and strain is distributed through skin tissue. However, skin macrostructural models seem unable to completely account for how
people differentiate gap indenters (Gerling and Thomas 2005) and might help explain gap discrimination at different fingerpad locations (Gibson and Craig 2005). Adding skin microstructures—such as elasticity, thickness, and geometry of multiple skin layers and the interconnection between layers—may improve the robustness of current models and more closely link the arrangement and function of complex skin and receptor physiology to the neural response. In fact, skin microstructure alone may help embed spatial structure within the SA-I neural response (Darian-Smith 1984; Pubols and Benkich 1986; Pubols 1988), although the receptor capsule and neurite, not considered here, likely play a role, as with the Pacinian corpuscle (Loewenstein and Skalak 1966).

The papillary ridge is one skin microstructure often thought to contribute to the way SA-I receptors translate edge indentation into neural signals (Cauna 1954; Jabaley 1981; Thomine 1981; Van Doren 1989; Hoffman et al. 2004). The papillary ridge is the fingerprint line at the exterior of the epidermis (Figure 1). Interestingly, each papillary ridge is positioned directly above its corresponding intermediate ridge (Bolanowski and Pawson 2003). Intermediate ridges consist of irregular, wavy epidermal tissue that extends into and interlocks with the dermis (specifically, dermal papillae) (Bolanowski and Pawson 2003). At the tip of the intermediate ridge, in the epidermis at the border between epidermal and dermal tissues, are the Merkel cells, the physiological transducers of the SA-I receptors (Guinard et al. 1998). Typically, five to ten Merkel cells cluster in a tree-like complex (a Merkel cell–neurite complex or MCNC) encircling the sweat ducts. The Merkel cells help convert mechanical distortion into electrical pulses (Mills and Diamond 1995; Ogawa 1996; Tachibana and Nawa 2002; Halata et al. 2003), although the details of this mechanism remain unresolved. When the skin surface is deformed, the MCNC responds to either stress, strain, displacement, or some invariant measure (Sriniwasan and Dandekar 1996; Ge and Khalsa 2002; Sripati et al. 2006). Because it has long been known that the MCNCs lie at the tips of the intermediate ridge, opposite the papillary ridge, many researchers believe that papillary ridges directly influence how SA-I receptors respond to indentation at the skin surface (Cauna 1954; Jabaley 1981; Thomine 1981; Van Doren 1989; Hoffman et al. 2004).

Cauna’s 1954 theory of touch sensibility associates the functionality of papillary ridges with both RA (rapidly adapting) and SA-I mechanoreceptors (Cauna 1954). Only the link between the papillary ridges and SA-I receptors is relevant for the current analysis. Cauna’s model, otherwise known as the lever arm mechanism (Figure 2), postulates that the papillary ridge and underlying intermediate ridge operate as a single unit, with the intermediate ridge acting as a lever that magnifies indentation imposed at the papillary ridge. The image of the rubber band model indicates that the intermediate ridge tilts outward in response to indentation applied at the papillary ridge. Force and/or displacement applied at the papillary ridge controls the direction and movement of the intermediate ridge tip deeper in the skin. Consequently, the lever arm model indicates that small displacements applied at the papillary ridge magnify intermediate ridge tip displacement at the location of the MCNCs. The image of the lever arm mechanism is easy to interpret and is therefore frequently referenced in medical textbooks and various research domains (Jabaley 1981; Phillips and Johnson 1981b; Thomine 1981; Van Doren 1989; Hoffman et al. 2004; Bensmaia et al. 2006). This analysis does not dispute Cauna’s basic anatomical representation. Instead, it challenges the functional relationship between the papillary ridges and the SA-I response to static edge indentation, such as a grating pressed against the fingertip. The analysis does not consider a dynamic stimulus, as in texture perception, such as roughness when sandpaper is moved across the skin (Yoshioka et al. 2001).

To examine the functional representation of Cauna’s model, we initially considered if (i) an individual SA-I receptor at one papillary–intermediate ridge structure can report the location of a stimulus positioned relative to its centerline and (ii) the stresses, strains, and/or displacements to
which a population of SA-I receptors respond
depend upon papillary ridges. We quickly focused
on point (ii). While Cauna’s model seems to argue
that point (i) is important, no existing data (neither
neurophysiological nor psychophysical) support a
capability to discriminate the placement of a thin
(\( \sim 0.1 \) mm diameter) probe to either side of the same
papillary ridge. To the contrary, researchers believe
that the collective information from a population of
receptors is utilized, not merely information from a
single unit, to differentiate the structures of various
indenters (Johansson and Vallbo 1976).

Point (ii) then is analyzed with respect to three
criteria necessary to support a lever arm mechanism:
(1) there must be a solid lever, (2) movement at one
end of the lever must cause movement at the other,
and (3) there must be a fulcrum. Cauna’s model
assumes that the components of the skin act like a
solid lever with a fulcrum with criteria (1) and (2) by
statements that “the intermediate ridge acts as a
magnifying lever for the transmission of touch stimuli
to the receptors underneath” and “the intermediate
ridge follows the movements of the papillary ridge”,
and by Figure 2 itself. He also notes that “the
intermediate ridge ‘floats’ freely in a loose connective
[dermal] tissue”, and Figure 2 represents no dermis,
but rather only the papillary, intermediate, and
limiting ridges, which are all part of the epidermis.
The model then explicitly supports criterion (3) in
that the limiting ridges, adjacent to the intermediate
ridges, are indicated to be fixed and can therefore
serve as pivot points. Cauna demonstrates fixed
limiting ridges in Figure 2 and states “the limiting
ridges are fixed to the corium [i.e., the dermis]”.

Figure 2. Rubber model from Cauna (1954). New labels refer to the papillary, intermediate, and limiting ridges. These
circles correspond to the anatomy in Figure 1. The original labels refer to the intermediate ridge (I), Meissner’s corpuscle
(Co), and the limiting ridge (L). While not explicitly labeled, the Merkel cells would be found near the arrow labeled (I).
Scale: image of the finger is 0.1 mm in diameter.

Figure 3 represents the solid lever (shaft) that
connects the papillary and intermediate ridges
(criterion 1), the movement at the papillary ridge
that is tied to movement at the intermediate ridge
(criterion 2), and the limiting ridges that are fixed and
serve as a fixed base for a pivot (criterion 3).

This work uses finite element analysis (FEA) and
detailed assessment of the anatomical literature to
analyze the three criteria. Specifically, we consider
the feasibility of the biomechanical motion of the
intermediate ridge to tilt outward in response to
movement of the papillary ridge. In Cauna’s model,
this outward tilt is necessary for, and intertwined
with, sensation—via displacement of the intermedi-
ate ridge tips. This would link the papillary ridges
to the SA-I response. The mechanism may
fundamentally change upon detailed analysis, however, specifically when an elastic dermis is introduced.

Methods

We mapped the three criteria needed to support a lever arm mechanism to three finite element analyses (i.e., Criterion 1 $\rightarrow$ FEA 1, 2, Criterion 2 $\rightarrow$ FEA 2, and Criterion 3 $\rightarrow$ FEA 3). Specifically, FEAs 1 and 2 examine whether gaps between adjacent papillary ridges and the introduction of dermal tissue would allow (Criteria 1) a set of papillary and intermediate ridges to form a solid shaft. Then in FEA 2 by modifying material properties, we determine which dermal properties would promote (Criteria 2) displacement of the intermediate ridge tip as a result of stimulation at the papillary ridge. Finally, FEA 3 considers if affixing the limiting ridges to underlying tissue with collagen fibers would allow (Criterion 3) a fulcrum. Each FEA seeks to identify conditions necessary to promote the outward motion of the intermediate ridge. Per Cauna’s description, the outward tilt relates to tip displacement, and tip displacement may be correlated to the neural response.

In general, the FEAs utilized two-dimensional, linear elastic models, based on a previous model of fingertip skin (Maeno et al. 1998) (Figures 4 and 5). The Appendix contains a detailed description of and validation for each model, one with papillary ridges, one without. For each FEA, a 3.0 mm wide probe indents the mesh surface to a depth of 1.0 mm, typical of past efforts (Phillips and Johnson 1981b; Srinivasan and Dandekar 1996; Dandekar et al. 2003). Two indentation-sampling strategies are used: the first with multiple adjacent indentations and a single sampling location (the traditional “reciprocal interpretation” method) and the second with a single indentation and multiple sampling locations (Mountcastle and Powell 1959). For more information see Sections A.2 and A.3 of the Appendix.

**FEA 1: Papillary ridge gap vs no gap**

FEA 1 tests whether the presence or absence of gaps between adjacent papillary ridges (using models with and without the exterior ridges) affects the displacement of the intermediate ridge tips. Tip displacement would presumably be promoted, to a larger extent, by a solid lever (of the papillary–intermediate ridges) than by an elastic lever. In addition to correlating tip displacement to the neural response, various stress and strain measures (strain energy density, maximum compressive strain, maximum compressive stress, and von Mises stress) are considered where values are calculated at the intermediate ridge tip. The two models (with and without papillary ridges) are indented with the 3.0 mm indenter under both indentation-sampling methods.

**FEA 2: Modification of dermal stiffness to produce outward tilt of the intermediate ridges**

To determine if any dermal stiffness would cause the papillary and intermediate ridges to act as a solid lever, the Young’s modulus values were systematically varied over two orders of magnitude. First, an analysis of the dermal stiffness at 8000 Pa (reduced from a modulus of 80,000 Pa) was compared for the ridges and no ridges models. Then using only the model with papillary ridges, the dermal stiffness was further decreased to a Young’s modulus of 800 Pa. For comparison, 5000 Pa is the lowest value reported in the literature (Daly 1982). The stiffness of the epidermis (both papillary and intermediate ridges) remained at 136,000 Pa. The design for FEA 2 was based on the findings from FEA 1 that (a) elastic bending of the intermediate ridges conflicts with the anticipated solid shaft and (b) intermediate ridge tip displacement correlates weakly to the neural recordings. For the 8000 Pa case both models were used, to determine if the papillary ridge had anything to do with producing movement of a solid shaft.

**FEA 3: Solidly fixing the limiting ridges with collagen fibers**

FEA 3 examined, via two separate analyses, if greater outward tilt of the intermediate ridge could be produced by affixing the limiting ridges to underlying tissue (Figure 1) to promote a fulcrum. In the first analysis, the fibers’ stiffness was set equal to the epidermal stiffness (136,000 Pa) while the rest of the dermis was unchanged (80,000 Pa). In the second analysis, the fibers’ stiffness was set to the original...
dermal stiffness (80,000 Pa) while the rest of the dermis was set to 800 Pa. Only the model with papillary ridges was used. By changing the material properties of the mesh, limiting ridges were connected to subcutaneous tissue by stiff elements representing collagen fibers (Figure 5). While collagen fibers in reality stretch tight in tension and provide little support in compression (Daly 1982), the structures were modeled as overly conservative supports, to be similar to Cauna’s representation.

Results

Figure 6 compares the predicted response to the neural response for models with and without papillary ridges. In Figures 7 and 8, four dependent variables from FEAs 1 and 2 (strain energy density, maximum compressive stress, maximum compressive strain, and intermediate ridge tip displacement) are correlated to the neural response, specifically for the model with the papillary ridge gap. Figure 7 gives results for the moving indenter—one sampling point method and Figure 8 gives results for the stationary indenter—multiple sampling points method, where these methods and figure generation are described in detail in Sections A.2, A.3, and A.5 of the Appendix. The predicted values are compared to neural recordings for similar stimuli (Phillips and Johnson 1981b). While no graphical data is displayed for the second model, that without the gap between papillary ridges, correlation data for both models is given in Table I. Table I correlates the modeled predictions to the neural recordings.

FEA 1: Papillary ridge gap vs no gap

The presence of exterior papillary ridges negligibly affects the neural response, regardless of dependent measure. Figure 6 indicates graphically the similarity of fit for both models to the neural data, under the moving indenter—fixed sampling points case. In

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**Figure 5.** Close view of elliptical mesh where grey represents the epidermis and white the dermis. To create the mesh with no papillary ridges, the gap (furrow) between the exterior ridges (marked by 0.15 mm) was filled to create a continuous surface (identified by inset). The lighter shade of grey represents the simulated collagen strands. Note the four small circles link with Figures 9 and 10.

**Figure 6.** Comparison of measured strain energy density for models with and without papillary ridges to the neural data, as the indenter is moved horizontally via the “reciprocal interpretation” method.
Figure 7. Data using the traditional “reciprocal interpretation” method, with a moving indenter and single sampling point; model with papillary ridges. Stress and/or strain measure on left ordinate varies between sub-figures.

Figure 8. Data using the stationary indenter with multiple sampling points; model with papillary ridges.
Table I. Correlation values for modeled predictions to previously recorded neural data from Phillips and Johnson (1981b) under various skin properties and indenter-sampling conditions.

<table>
<thead>
<tr>
<th>Condition</th>
<th>800 Pa dermis</th>
<th>8000 Pa dermis</th>
<th>80,000 Pa dermis</th>
<th>80,000 Pa dermis</th>
<th>Data from Dandekar et al. (2003)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moving indenter—fixed sampling point</td>
<td>With papillary ridges</td>
<td>Without papillary ridges</td>
<td>Homogeneous model</td>
<td>Layered model</td>
<td></td>
</tr>
<tr>
<td>SED</td>
<td>0.86</td>
<td>0.88</td>
<td>0.96</td>
<td>0.97</td>
<td>0.87</td>
</tr>
<tr>
<td>MC strain</td>
<td>0.79</td>
<td>0.81</td>
<td>0.96</td>
<td>0.95</td>
<td>0.81</td>
</tr>
<tr>
<td>VM stress</td>
<td>0.79</td>
<td>0.81</td>
<td>0.96</td>
<td>0.97</td>
<td>–</td>
</tr>
<tr>
<td>MC stress</td>
<td>0.56</td>
<td>0.66</td>
<td>0.84</td>
<td>0.83</td>
<td>–</td>
</tr>
<tr>
<td>Tip displacement</td>
<td>0.34</td>
<td>0.32</td>
<td>0.34</td>
<td>0.34</td>
<td>–</td>
</tr>
</tbody>
</table>

Stationary indenter—multiple sampling points

<table>
<thead>
<tr>
<th>Condition</th>
<th>800 Pa dermis</th>
<th>8000 Pa dermis</th>
<th>80,000 Pa dermis</th>
<th>LR 1 (136K 80K)</th>
<th>LR 2 (80K 800)</th>
<th>800 Pa dermis</th>
<th>8000 Pa dermis</th>
<th>80,000 Pa dermis</th>
</tr>
</thead>
<tbody>
<tr>
<td>SED</td>
<td>0.55</td>
<td>0.40</td>
<td>0.73</td>
<td>0.78</td>
<td>0.82</td>
<td>0.61</td>
<td>0.47</td>
<td>0.74</td>
</tr>
<tr>
<td>MC strain</td>
<td>0.49</td>
<td>0.40</td>
<td>0.65</td>
<td>0.69</td>
<td>0.72</td>
<td>0.58</td>
<td>0.47</td>
<td>0.65</td>
</tr>
<tr>
<td>VM stress</td>
<td>0.49</td>
<td>0.40</td>
<td>0.65</td>
<td>0.69</td>
<td>0.72</td>
<td>0.58</td>
<td>0.48</td>
<td>0.65</td>
</tr>
<tr>
<td>MC stress</td>
<td>0.45</td>
<td>0.39</td>
<td>0.49</td>
<td>0.53</td>
<td>0.45</td>
<td>0.50</td>
<td>0.42</td>
<td>0.54</td>
</tr>
<tr>
<td>Tip displacement</td>
<td>0.40</td>
<td>0.39</td>
<td>0.40</td>
<td>0.40</td>
<td>0.93</td>
<td>0.40</td>
<td>0.40</td>
<td>0.41</td>
</tr>
</tbody>
</table>

Figure 9. Deformed mesh in models (a) with and (b) without papillary ridges illustrating the lack of outward tilt suggested by Cauna’s model. Only portion of mesh near edge of indenter is shown. Here the dermis has a stiffness of 80,000 Pa. Distribution of von Mises stress is overlaid. Note that ridge tips concentrate von Mises stress (dark color), under the indention. Units in Pa. Note small circles link to Figure 10.

Tip displacement correlates most weakly with the neural response.

In this case, the existence of the papillary ridges does not cause the intermediate ridges to tilt outward as a solid shaft as anticipated from the lever arm model (see deformed mesh and contour plot in Figure 9(a) for the section of the model beneath the indenter contact). Rather, the intermediate ridges elastically bend inward as further observed in Figure 10, which gives the displacement of one papillary–intermediate ridge shaft, near the edge of the indenter’s contact. The “straightness” of the three-segment line with four nodes (see node locations in Figures 5 and 9(a)), extending from...
the exterior of one papillary ridge through its intermediate ridge tip, is nearly equal for both models.

**FEA 2: Modification of dermal stiffness to produce outward tilt of the intermediate ridges**

Experimenting with two stiffness changes to the dermis in FEA 2, only an unrealistic decrease promotes the outward tilt of the intermediate ridge. First, with a Young’s modulus of 8000 Pa, the intermediate ridges tilt outward, but not as a rigid lever (Figures 10 and 11(a)). The generation of greater outward tilt with the 8000 Pa case, in comparison to the 80,000 Pa case, is not due to the existence of papillary ridges as both with and without ridges cases with an 8000 Pa dermis give similar node displacement patterns in Figure 10. Rather, elastic bending is observed as the tip of the ridge in Figure 10 bends inward. Any change from the 80,000 Pa case is not due to the existence of papillary ridges as both with and without ridges cases with an 8000 Pa dermis give similar node displacement patterns in Figure 10. Further, the predictions do not correlate to the neural data as well as in the 80,000 Pa case.

Then, with a Young’s modulus of 800 Pa for the dermis, the intermediate ridges do clearly tilt outward, even the intermediate ridge tips (Figure 11(b)). However, while outward tilt of the intermediate ridge is observed (Figure 10), the surface deflection (descriptions of data and plots in Section A.6 of the Appendix) and neural correlation fits are weak, for all measures. Analysis of the surface deflection data in the 800 Pa dermis case shows that the exterior skin surface rises above its initial vertical position...
(i.e., Figure 12, “Soft Dermis (800 Pa)” curve crosses below zero on the y-axis). This behavior contradicts experimental observations of skin deflection (Figure 12, “Experimental Data”) (Srinivasan 1989). Also, the stress, strain, and tip displacement correlation with the neural data decreases for the 800 Pa dermis case.

**FEA 3: Solidly fixing the limiting ridges with collagen fibers**

One of two limiting ridges analyses indicates that a fulcrum may be produced, but only given unrealistic material properties. In the first analysis for FEA 3 (136,000 Pa Collagen Fibers and 80,000 Pa Dermis), no outward tilt of the intermediate ridges is observed (Figure 10). However, in the second analysis for FEA 3 (80,000 Pa Collagen Fibers and 800 Pa Dermis), the fulcrum and outward tilt (similar to Figure 11(a)) was produced, that is, the 8000 Pa dermis case. However, as can be observed in Figure 10, while the ridge appears initially to tilt outward, it experiences elastic bending as the tip deflects inward. This is not a solid shaft and gives similar behavior to the 8000 Pa case in which the existence of a papillary ridge did not affect its motion. Still, in this second analysis,
while the correlation to the neural data was more accurate (Table I, SED of 0.91 compared to 0.73, 0.74, 0.78), the surface deflection data was less accurate (‘‘Fixed L.R. (80,000 Pa, 800 Pa)’’) especially further from the line load.

Discussion
In sum, the finite element analysis indicates that the papillary ridges have little direct effect on how the SA-I receptors might respond to the indentation of static edges. The results of FEAs 1–3 are discussed in the context of skin anatomy and the three criteria needed to support a lever arm mechanism. Recall the mapping FEA 1, 2 → Criterion 1, FEA 2 → Criterion 2, and FEA 3 → Criterion 3.

Criterion 1: Is there a solid lever?
Findings from FEAs 1 and 2 and the anatomical literature indicate that papillary and intermediate ridges do not form a solid lever. First in FEA 1, the removal of the papillary ridges from the model does not affect the correlation of stress and strain measures to the neural data, nor tip displacement. Neither does the removal of the papillary ridges affect the outward tilt of the intermediate ridge, which is not found with either model, and which explains the weak correlation of tip displacement. Instead, FEA 1 demonstrates that the intermediate ridges are elastic in both models; and they bend inward when dermal tissue is introduced (Figures 9 and 10). When in FEA 2 a solid lever appears plausible with an 800 Pa dermal stiffness, both the correlation to the neural data (Table I) and fit to the surface deflection (Figure 12) are significantly weakened. The plausibility of a solid lever appears only at a cost of an unrealistically plant dermis (impact of dermis on movement of intermediate ridge discussed further in Section 4.2).

Second and further, the anatomical literature contradicts even the idea of a single material property to characterize the papillary and intermediate ridge as one solid structure. The epidermal tissue is commonly broken into two parts: the exterior stratum corneum (that maps to papillary ridge) and four interior layers (that map to intermediate ridge). These two parts of the epidermis have distinct material properties. The stratum corneum is stiffer than the four internal epidermal layers because it is composed of dead, dry cells (Park and Baddiel 1972; Holbrook and Odland 1974; Quilliam 1978; Takahashi et al. 1980; Jabaley 1981). The stiffness of the four interior layers—a living mass of cells, encapsulated by the stratum corneum—probably lies somewhere in between that of the dermis and stratum corneum, although the stiffness of the interior epidermal layers has not, as yet, been measured. Therefore, modeled as two distinct portions, an even greater degree of elastic bending is expected.

Criterion 2: Does movement at one end of the lever cause movement at the other?
Findings from Section 4.1 indicate that the papillary and intermediate ridges do not form a solid lever, rather the intermediate ridges are elastic and their movement is not dependent on the presence of the papillary ridges. However, even with that solid lever were possible, Criterion 2 shows that any outward tilt would be impeded by (1) solid dermal tissue and (2) a firm connection of the epidermis with the dermis. First, FEA 2 considers what dermal stiffness would be required to create outward tilt at one end (intermediate ridge tips) as a result of movement at the other (papillary ridges). Only by radically modifying the dermal stiffness (to 800 Pa) and maintaining the papillary and intermediate ridges as a single material do we observe the required outward tilt. Not only does this lead to inaccurate surface deflection and lack of correlation to neural response, but the modulus of 800 Pa is also not consistent with that of the dermis. The 800 Pa value is two to three orders of magnitude less than elastomeric materials such as soft rubber or elastin. Such a material would be unstable given the magnitude of compression, and is more similar to thin cell gel samples that range from 100 to 1000 Pa (Mahaffy et al. 2000). These materials also are not in keeping with a dermal tissue that is more resistant to shear and stronger (Harkness 1971; Kawabe et al. 1985) than epidermal tissue. Images from various sources clearly show structurally solid, fingerlike dermal projections, which mirror and interlock with the epidermis (Montagna and Parakkal 1974; Kawabe et al. 1985). The values of 80,000 Pa and 8000 Pa are, by contrast, in agreement with reported measurements (Daly 1982; Maeno et al. 1998) and models (Maeno et al. 1998; Dandekar et al. 2003).

Second, the strong bond between epidermis and dermis creates an extremely firm, uniform attachment that does not allow the dermis to separate from the epidermis as the intermediate ridge moves. Three factors illustrate the strength of the attachment: (1) adhesion at the basement membrane, (2) wave-like interdigitation of the epidermis to the dermis, and (3) sweat ducts that tie the epidermis to the dermis at the intermediate ridges (Tregear 1966; Quilliam 1975, 1978; Misumi and Akiyoshi 1984; Yamada et al. 1996) (Figure 1). This bond likely helps prevent blisters, caused by separation of the epidermis from the dermis.
Criterion 3: Is there a fulcrum?

Findings from FEA 3 indicate that a fulcrum can be produced, but only if the function of the collagen fibers are misrepresented and their compressive properties are set unrealistically. Cauna proposed that limiting ridges act as pivot points. He notes that the relatively massive limiting ridge has basal projections that interlock with underlying connective tissue. Misumi and Akiyoshi also note the strong epidermal–dermal adhesion at the limiting ridge (Misumi and Akiyoshi 1984).

As indicated in FEA 3, when the limiting ridges are connected to deeper tissue via bundles of collagen fibers (Cauna 1954) (Figure 1, label c), a sufficient pivot is observable, however, this fulcrum is present only at the cost of an unrealistic dermal stiffness (800 Pa) and epidermal–dermal bond (both are further discussed in Section 4.2). In reality, the collagen fibers are probably, as they are conservatively modeled here, more effective supports than actual bundles of collagen fibers. Real collagen fibers only effectively provide tension when they act like loose shoestrings until tensile forces tighten the string. In compression their strength is negligible (Lanir 1981).

Overall summary

None of the three criteria support the notion of a lever arm mechanism. To the contrary, our results demonstrate (a) an elastic and bending intermediate ridge, (b) movement of the intermediate ridge tips not tied to movement of the papillary ridges, and (c) no fulcrum. Importantly and perhaps as a consequence of the above, the displacement of the intermediate ridge tips correlates very weakly to the neural response. Even when other stress and strain measures are examined, their correlation to the neural response is not improved by the addition of papillary ridges. While the lever arm model well represents the major anatomical structures, it inaccurately represents the role of papillary ridges with respect to edge sensation and SA-I receptors.

Revised functional representation

Based on the above analysis, this work suggests a revised functional representation of epidermal skin microstructure, that of a stiff but pliable shell (papillary ridges) above an elastic bending support (intermediate ridges) (Figure 13). Intermediate ridges and papillary ridges are separate layers (i.e., no single, solid shaft), the elastic bending of the intermediate ridges is emphasized, and both ridges are shown in the context of known properties of the dermis material. The main characteristics are:

1. A stiff but pliable shell (papillary ridge layer) above an elastic bending support (intermediate ridge layer) with material properties for the stratum corneum associated with the papillary ridges; different material properties for the four interior layers associated with the intermediate and limiting ridges.

Figure 13. Revised functional representation of skin’s response to surface indentation. Stiff shell, elastic bending support (dark background) vs stiff, lever arm motion (black outline). The curved arrow indicates that the two ridges near an indenter’s edge swing away from each other. In contrast, four dark ridges, denoted by A–D, bend rather than tilt outward. Their motion is not related to the angle of indentation at the papillary ridge. Springs show anisotropic stretch.
2. A tight interconnect of stratum corneum to four interior layers and of four interior layers to
dermis.
3. The movement of the intermediate ridge is not directly tied to the papillary ridge.
4. Elastic, inward bending of the intermediate ridges.
5. The concentration of stress and/or strain at tips of intermediate ridges near the MCNCs.
6. Anisotropic skin stretch above the limiting ridges in a direction perpendicular to fingerprint lines.

The revised representation includes many of the same anatomical features emphasized by Cauna. However, rather than a series of solid penetrating levers, outward tilt of the intermediate ridges, and fixed limiting ridges, the revised representation is based on elastic bending of the intermediate ridges in the stiff but pliable shell of the outer epidermis. This interpretation effectively simplifies how forces are transmitted from the skin’s surface to the locations of the MCNCs.

While the papillary ridge microstructures appear to not impact SA-I response to static indentation, two other aspects of skin microstructure may. Both (points 5 and 6) are currently speculative. For point 5, initial analysis demonstrates that stress and/or strain concentrates at the intermediate ridge tips near the locations of the SA-I receptors (Maeno et al. 1998; Gerling 2005) and may be important for SA-I neural encoding of unique spatial patterns for specific stimuli. Our other preliminary analyses have gone further, to say that sampling near the epidermal–dermal border is functionally more relevant than undulating papillary ridges (Gerling 2006). For reference, concentrations of von Mises stress are observable in Figures 9(a) and (b) as the darker areas at the tips of the intermediate ridges.

Point 6 relates to areas of low stress concentration found between the papillary–intermediate ridge sections and just above the limiting ridge (mark “A”, Figure 9(a)). As no anisotropic material properties were assigned to the epidermis, this result could indicate that the epidermis stretches at this particular location, due to geometry alone. While further study is necessary with a more complex model, point 6 could help explain the connection between skin compliance, anisotropic skin stretch, and the results found in grating orientation experiments. It is well established that grating orientation relative to fingerprint line direction does affect SA-I response (Craig 1999; Wheat and Goodwin 2000; Gibson and Craig 2005).

Finally, even if the intermediate and papillary ridges do function independently in this context, the papillary ridges and epidermis certainly do play a role in sensation. The papillary ridges most likely help prevent an object from slipping from one’s grasp (Maeno et al. 1998; Yamada et al. 2002) and are involved in texture perception (Yoshioka et al. 2001).

Conclusion
Understanding the functionality of skin microstructure may be essential to understanding our sense of touch. Cauna developed the lever arm mechanism to explain how papillary ridges impact touch sensation. However, because it suggests that the papillary ridges directly affect SA-I mechanoreceptor response, the lever arm model is anatomically but not functionally precise. Our FEAs and assessment of the critical anatomy do not support the physiological function described by the lever arm model. Three criteria of a lever arm mechanism: (1) there must be a solid lever, (2) movement at one end of the lever must cause movement at the other, and (3) there must be a fulcrum, are not satisfied. The revised interpretation is that of a stiff shell with an elastic bending support whereby the outer layer of the epidermis acts like a stiff but pliable shell located above an elastic underlayer of softer tissue with bendable intermediate ridges. This interpretation separates the direct function of the intermediate ridge from the papillary ridge. The intermediate ridges alone, or stress or strain sampling position relative to these structures, may improve the correlation with the neural data, but the papillary ridges appear to play no role in the encoding of static edges. Continued research on the role of skin microstructure in sensory encoding may help clarify the design of soft tissue sensors and substrates for robot interfaces and neural prostheses for touch.

References


Appendix

The Appendix lists the general methods used. It details the two finite element models, the two indentation-sampling procedures, the main dependent variables, the plotting of data, and finally, the validation of each model using previous methodologies.

A.1. Finite element models

The finite element models (with and without papillary ridges) are two-dimensional and portray an elliptically shaped, cross section of the fingertip (Figures 4 and 5). The model used here includes interior layers, geometry, and material properties similar to Maeno et al.’s fingertip plane section (Maeno et al. 1998), and also includes limiting ridges and collagen fibers (Figure 5). The three skin layers represent the: epidermis, dermis, and subcutaneous fat. The thickness values used for our simulated epidermis (undulations from 0.475 to 0.95 mm) are similar to the literature (where mean is 0.48 mm and maximum of 0.92 mm) (Frühstorfer et al. 2000); as is the dermal thickness (1.27 mm) similar to the literature (mean is 1.16 mm, with a minimum of 1.13 mm and maximum of 1.19 mm) (Southwood 1955). The intermediate ridge structure describes the epidermal–dermal junction with a sinusoid, with the lateral increment of 0.5 mm between adjacent intermediate ridge tips consistent with the 0.4–0.5 mm reported (Yamada et al. 1996). The normal material properties include a Young’s modulus of $1.36 \times 10^5$ Pa for the epidermis, $8.0 \times 10^4$ Pa for the dermis, $3.4 \times 10^4$ Pa for the subcutaneous fat with a Poisson’s ratio of 0.48 for each layer (Maeno et al. 1998). Similar properties are used elsewhere (Dandekar et al. 2003). The only difference between the two models is that the model with papillary ridges represents the furrow found naturally between adjacent ridges while the model without papillary ridges fills this furrow with simulated epidermis (Figure 5). While linear elastic material models are often used with small displacement loads (as used here), more sophisticated hyper- or viscoelastic models that take into account the inhomogeneous, nonlinear, and anisotropic nature of skin (Agache et al. 1980) may be appropriate for large displacement loads (Ge and Khalsa 2002).

MSC/PATRAN 2004 software was used to generate the mesh. The mesh utilizes four-node, bilinear quadrilateral, hybrid with constant pressure elements (ABAQUS type CPE4H). Generalized plane strain elements have been used for fingertip tissue modeling since the work of Phillips and Johnson (1981b). The entire mesh contains about 16,000 nodes and elements. Fixed boundary conditions constrain the nail and bone in the x- and y-directions. The finite element software ABAQUS Standard, version 6.4 was used to analyze the mesh’s response to applied indentation.

A.2. Indentation method 1 (traditional; moving indenter—one sampling point)

The indentation procedure and extraction of basic stress measurements follows the concept of “reciprocal interpretation” introduced by Mountcastle and Powell (1959) and used subsequently by most other researchers. Basically, an indenter is pressed into the skin tissue (or simulated skin) in a series of separate indentations, spaced laterally by 0.2 mm. For the series of indentations, the placement indenter’s center starts at 2.7 mm to the left of the sampling point at the intermediate ridge tip at the $x$-axis center of the model. In a series of 28 total steps, it proceeds to 2.7 mm to the right of that $x$-axis center. A 3.0 mm wide indenter is utilized. A fillet radius of 0.1 mm was used to round the indenter’s corners and better approximate a machined, metal indenter. The stimulus was displaced to a depth of 1.0 mm (Phillips and Johnson 1981b; Srinivasan and Dandekar 1996; Dandekar et al. 2003) using a
contact interaction. A contact surface was defined between the fingerpad and indenter with a friction coefficient of 0.3 (Gitis and Sivamani 2004). The metal indenter was implemented with an analytical rigid surface.

A stress or strain quantity (Section A.4) was measured in selected elements based on their position in the undeformed surface in a manner similar to previous studies (Srinivasan and Dandekar 1996; Maeno et al. 1998; Dandekar et al. 2003; Wu et al. 2004). The stress or strain samples are averaged for six small elements at a depth of 0.95 mm on the epidermal side of the tip of the intermediate ridge, centered at the x-axis. The x- and y-displacement of the tip of the intermediate ridge was also measured. In total, 28 data points correspond to 28 lateral positions of the indenter.

### A.3. Indentation method 2 (stationary indenter—multiple sampling points)

In addition to scanning the indenter across a single sampling location, we also indented a stationary and centered 3.0 mm stimulus, and simultaneously sampled from multiple points in the model. Stress and strain samples from elements, and x- and y-displacement of nodes, were measured at adjacent intermediate ridge tips in lateral increments of 0.5 mm, which yields a density only slightly less than the 0.8 mm spacing reported for SA-Is in the literature (Johansson and Vallbo 1979). Therefore, 13 total data points emerge.

### A.4. Main dependent variables

Tip displacement and relevant stress and strain derivations follow. The tip displacement is calculated according the x- and y-displacement of nodes at the tip(s) of the intermediate ridge(s). Tip displacement is calculated as

\[ u_{\text{total}} = \sqrt{u_1^2 + u_2^2} \]  

(A.1)

where \( u_1 \) and \( u_2 \) are the displacement of nodes in the x- and y-directions, respectively. The relevant stress and strain quantities utilized were maximum compressive stress, maximum compressive strain, von Mises stress, and strain energy density. Four variables were used because while others have shown that SA-I and RA afferents in the skin encode stress-related quantities better than strain-related quantities (Khalsa et al. 1996, 1997; Ge and Khalsa 2002; Del Prete et al. 2003; Robichaud et al. 2003), the issue remains unresolved (Sripiati et al. 2006). These quantities, in particular, have shown the best correlation with the neural response. Maximum compressive stress is calculated as \( \sigma_c \), where \( \sigma_{xx} \) and \( \sigma_{yy} \) represent normal stresses and \( \tau_{xy} \) is shear stress:

\[ \sigma_c = \sigma_1 = \left( \frac{\sigma_{xx} + \sigma_{yy}}{2} \right) + \tau_{\text{max}} \]  

(A.2)

\[ \tau_{\text{max}} = \sqrt{\left( \frac{\sigma_{xx} - \sigma_{yy}}{2} \right)^2 + \tau_{xy}^2} \]  

(A.3)

Maximum compressive strain is \( \varepsilon_c \) where \( E = \text{modulus of elasticity} \):

\[ \varepsilon_c = \varepsilon_1 = \frac{3}{2E} \left( \frac{\sigma_1 - \sigma_2}{2} \right) = \frac{3}{2E} \tau_{\text{max}} \]  

(A.4)

\[ \sigma_2 = \left( \frac{\sigma_{xx} + \sigma_{yy}}{2} \right) - \tau_{\text{max}}. \]  

(A.5)

Von Mises stress (\( \sigma_{yy} \)) was calculated as

\[ \sigma_{yy} = \frac{1}{2} \sqrt{\left( \sigma_{xx} - \sigma_{yy} \right)^2 + \left( \sigma_{yy} - \sigma_{zz} \right)^2 + \left( \sigma_{zz} - \sigma_{xx} \right)^2 + 6\left( \tau_{xy}^2 + \tau_{xz}^2 + \tau_{yz}^2 \right)} \]  

(A.6)

where \( \sigma_{xx}, \sigma_{yy}, \sigma_{zz} \) represent normal stresses and \( \tau_{xy}, \tau_{xz}, \tau_{yz} \) represent shear stresses, with their z-components set to zero. Finally, in general strain energy density (\( U_0 \)) is comprised of volumetric (\( U_{vo} \)) and distortional (\( U_{od} \)) components:

\[ U_0 = U_{vo} + U_{od} \]  

(A.7)

(Ugural and Fenster 2003). However, the volumetric term (hydrostatic pressure, \( U_{vo} \)) is omitted because when Poisson’s ratio (\( \nu \)) is set between 0.48 and 0.5 (Srinivasan and Dandekar 1996; Maeno et al. 1998), as it is here, the material is nearly incompressible and \( U_{vo} \) is indeterminate. The remainder then is the distortional stress tensor (\( U_{od} \)), which represents the energy produced by distortion (i.e., a change in the unit volume’s shape) without a change in volume:

\[ U_0 = U_{od} = \frac{3}{4G} \tau_{\text{oct}}^2 \]  

(A.8)

where \( \tau_{\text{oct}} \) is the octahedral shear stress and is \( G \) the shear modulus of elasticity:

\[ \tau_{\text{oct}} = \frac{1}{3} \sqrt{\left( \sigma_{xx} - \sigma_{yy} \right)^2 + \left( \sigma_{yy} - \sigma_{zz} \right)^2 + \left( \sigma_{zz} - \sigma_{xx} \right)^2 + 6\left( \tau_{xy}^2 + \tau_{xz}^2 + \tau_{yz}^2 \right)} \]  

(A.9)

\[ G = \frac{E}{1 + \nu}. \]  

(A.10)
For nearly incompressible materials, strain energy density and von Mises stress are closely related:

\[ U_o = \frac{\sigma_{yp}^2}{G}. \]  

(A.11)

A.5. Plotting calculated stress, strain, and tip displacement data against electrophysiological data

The data from the dependent variables, regardless of indentation-sampling method, were first normalized. If the data set \( X_j \) represents strain energy density, for example, then over the range of \( j \) samples the data are normalized by \( Y_j \):

\[ Y_j = \frac{X_j - \min(X_j)}{\max(X_j) - \min(X_j)}. \]  

(A.12)

Then, the stress, strain, and tip displacement data were compared to experimental results from Phillips and Johnson, using their assumption of linearity (Phillips and Johnson 1981b; Srinivasan and Dandekar 1996; Sripati et al. 2006). The linear equation \( d_i = (a \ast e_i) + b \) was used to correlate the two data sets, where \( d_i \) is the electrophysiological data (impulses per second) when an indenter is positioned at location offset \( i \) (or with indentation procedure 2, where sampling points are at adjacent locations \( i \)) and \( e_i \) is the calculated stress, strain, or tip displacement data under the same condition. Constants \( a \) and \( b \) were found by maximizing goodness of fit, where \( e_i = d_i - \bar{e}_i \):

\[ R^2 = \frac{\sum d_i^2 - \sum e_i^2}{\sum d_i^2}. \]  

(A.13)

A.6. Validation of Maeno et al.’s finite element model

Typically, models validate their accuracy via a fit of both (1) biomechanical skin surface deflection and (2) static neural response rate (impulses per second). Tests were completed for both base models. In sum, both models achieve slightly better accuracy than others in the literature. First to compare surface deflection, a 50 \( \mu \)m wide, line load indenter was displaced 1.0 mm (Srinivasan and Dandekar 1996; Dandekar et al. 2003; Wu et al. 2004). Because the surface deflection result from both models was equal, the result was characterized with a single line “Normal Dermis” (Figure 12). The data “Viscoelastic Model” and “Experimental Data” are plotted for comparison. The “Experimental Data” was collected by Srinivasan in a series of in vivo tests with human and monkey fingers where the finger surface was displaced by a line load indenter and the surface deflection recorded via a camera (Srinivasan 1989). The “Viscoelastic Model” prediction was made with a finite element model (Wu et al. 2004).

Second, a high correlation was found for comparison to the neural response (Figures 7 and 8 and Table I). For the moving indenter method, the correlation was greater than that found by Dandekar for both strain energy density (0.87 compared to 80,000 Pa Dermis = 0.96; No Papillary Ridges, 80,000 Pa Dermis = 0.97) and maximum compressive strain (0.81 compared to 80,000 Pa Dermis = 0.96; No Papillary Ridges, 80,000 Pa Dermis = 0.95).