Felt hole size

Running Head: FELT HOLE SIZE

Holes feel smaller when the skin bends less at the hole’s edges

Knut Drewing

Institute for Psychology, Justus-Liebig University, Giessen (Germany)

Submitted to Journal of Experimental Psychology: Human Perception & Performance

Author note

Correspondence concerning this article should be addressed to: Knut Drewing, Institute for Psychology, Giessen University, Otto-Behaghel-Str. 10F, 35394 Gießen (Germany), Phone: +49 641 99 26 104, Email: Knut.Drewing@psychol.uni-giessen.de.

The authors wishes to thank Dora Szöke, Steffen Bruckbauer, Alham Qadri and Sara Khateb, who set up part of the experiments, collected data and helped with the figures within the framework of their Bachelor theses. Part of the results of Experiment I and V have been pre-published in a conference paper (Drewing, Bruckbauer, & Szöke, 2015). The research was supported by Deutsche Forschungsgemeinschaft, SFB/TRR 135, A5 assigned to Knut Drewing.
Abstract

When small holes are felt with the tongue they are perceived to be larger as compared to when felt with the index finger. This oral illusion has yet not been consistently explained. We suggest that the effectors, finger and tongue, differ in their skin’s bending at the hole’s edges, because they differ in pliability. And that with less skin bending, which is an effective stimulus for mechanoreceptors, felt hole size gets less accurate and decreases. Results from Experiments I and II confirmed that felt hole size decreases with the pliability of the exploring effector (tongue > index finger > big toe) and that size perception with the highly pliable tongue is more accurate than with the less pliable finger and toe. Experiment III showed that holes of intermediate size are perceived to be larger with the tongue’s tip than with its dorsum, which is in accordance with expectable influences of the effector’s shape on the skin’s bending. Finally, exploration styles that lessen the skin’s bending (encircling of holes with the finger vs. stamping them in Exp. IV, using low vs high tongue forces in Experiment V) decreased perceived hole size. Overall, our results corroborate the bending-neural code hypothesis.

Keywords

oral illusion, tactile perception, size perception, haptic exploration, human skin
Cavities in the teeth, in particular small ones, are often perceived to be larger when felt with the tongue as compared to when felt with the finger (Anstis, 1964; Dellow, Lund, Babcock, & Van Rosendaal, 1970; Waterman, 1917). It is still unclear why this “oral illusion” occurs, and what it reveals about haptic size perception. Explanations of the illusion that pertain to the finger’s low spatial resolution (Anstis & Loizos, 1971) or to the spacious stimulation of the pliable tongue (Bittern & Orchardson, 2000), fail to account for existing observations on the perception of holes. We tested in five experiments whether instead the differential extent of the skin’s bending at the edge of an explored hole explains differences in size perceived with different effectors.

In previous studies, participants explored the size of a circular reference hole with their tongue, while selecting with their index finger a matching hole from a series of comparison stimuli. The finger selected holes that were about 1-2 mm larger than the reference hole, when the reference hole was small. With larger diameters of the reference hole of about 10 to 15 mm the difference between the size perceived with finger and tongue disappeared (e.g., Anstis, 1964; Bittern & Orchardson, 2000; Melvin & Orchardson, 2001). An exception is found in LaPointe, Williams, and Hepler (1973), where the difference increased up to a hole size of 20 mm diameter. But differences in procedure and stimuli between this and other studies can well account for the deviating results (Albashaireh & Orchardson, 1988): LaPointe et al. (1973) used holes drilled in discs of 25.4 mm that were explored within the mouth, whereas typically, the holes were drilled in the center of plastic squares and explored with the protruded tip of the tongue.

Anstis and Loizos (1971) speculated that the typical oral illusion leads back to the low tactual spatial resolution at the finger. They argued that the finger’s resolution is too close to the diameter of the smaller holes used in the experiments (2-3 mm diameter). Therefore, the finger is not able to identify the smaller comparison holes and, hence, prefers to select larger holes that can be clearly identified. In contrast, the tongue has higher spatial resolution and can identify small holes. As a consequence small holes at the tongue are matched by larger holes at the finger. In line with this “spatial-resolution hypothesis”, Anstis and Lozos (1971) showed that
the index finger selects comparison holes that are larger than small reference holes irrespective of whether the reference hole is presented to the eye or to the tongue, and that comparison holes selected by the eye accurately match reference holes at the tongue. This fits with the assumption that the typical oral illusion links to characteristics of the finger. However, meanwhile improved methods of assessing spatial resolution suggest that the finger’s spatial resolution is better than assumed in the spatial-resolution hypothesis. Two-point discrimination thresholds, which were the classical estimates of spatial resolution, are indeed around 2-3 mm for the finger and 1-2 mm for the tip of the tongue (e.g., Louis, Greene, Jacobson, Rasmussen, Kolowich, & Goldstein, 1984; Ringel & Ewanowski, 1965; Sato, Okada, Miyamoto & Fujiyama, 1999). But when assessed by the more accurate method of identifying grating orientation, spatial resolution is estimated to be 0.9 mm for the index finger and 0.6 mm for the tip of the tongue (Van Boven & Johnson, 1994; Johnson & Phillips, 1981). There is no reason to assume that the finger’s spatial resolution of less than 1 mm would not allow to identify holes of more than 2 mm diameter. Finally, the spatial-resolution hypothesis is at odds with the lack of any size illusion when exploring cylindrical protrusions (‘pegs’) instead of holes. The hypothesis predicts that the finger encounters similar problems to identify small pegs and small holes, yielding similar illusions in both cases. But this was not observed. Using 1 mm-deep holes and 1 mm-high pegs, Orchardson and colleagues (Bittern & Orchardson, 2000; Melvin & Orchardson, 2001) observed the typical oral illusion, when both the finger and the tongue explored holes, and when the finger explored holes and the tongue explored pegs. There was no illusion when the finger explored pegs and the tongue explored pegs or holes. That is, whether an illusion occurred or not varied with the shape at the finger, peg or hole. Given the counterevidence of the spatial-resolution hypothesis, Bittern and Orchardson (2000) suggested an alternative explanation. They emphasized that the tongue’s surface has higher pliability than that of the finger. Whereas the tongue is a mobile, muscular organ covered by a mucous membrane, the finger has a bone inside and dermis covered by a dry keratinized
epidermis. Because the tongue’s skin is more pliable, it can be more deeply intruded into small holes than the finger. A deeper intrusion results in the stimulation of a larger surface area at the tongue, as compared to at the finger when exploring a small hole of the same diameter. Bittern and Orchardson (2000) speculated that perceived hole size relates to the size of the stimulated area of skin surface and, hence, a small hole is perceived to be larger by the tongue than by the finger. This “pliability-area hypothesis” is consistent with the observation that the illusion occurs for smaller holes in which the finger’s skin hardly intrudes, and that it vanishes for larger holes, in which the entire finger can be inserted. The hypothesis is also consistent with the finding that the illusion is observed for hole, but not for peg stimuli at the finger (Bittern & Orchardson, 2000; Melvin & Orchardson, 2001): There is no reason to assume that the finger’s relatively low pliability constrains the skin’s covering of a small 1 mm-high peg to the same extent as it constrains the skin to intrude into a small hole. Finally, the hypothesis fits with speculations regarding the oral perception of spheres: The size of small spheres of 4 mm diameter is underestimated when explored by tongue and palate, but perception is accurate if the palate is covered and the tongue alone explores the sphere (Engelen, Prinz, & Bosman, 2002): The tongue might enclose the sphere contacting it at a large area from different sides, whereas the hard palate has only limited contact with the sphere. But an experiment by Bittern and Orchardson (2000) failed to confirm a central assumption of the pliability-area hypothesis: The authors presented a 1 mm-deep and a 5-mm deep reference hole at the tongue. The tongue can be more deeply inserted into the deeper hole, leading to the stimulation of a larger skin area, which should increase the oral illusion. But the illusion was of similar magnitude for both holes, rejecting the assumption that the size of the stimulated skin area determines perceived hole size. Here, we suggest another alternative explanation for the oral illusion. We also assume that pliability differences between tongue and finger play a role, but mediated by the different extent of skin bending at the hole’s edges, not by the size of the stimulated surface area (Drewing, Bruckbauer, & Szöke, 2014). The skin’s pattern of bending (=degree of curvature) at the upper
Felt hole size

edge of a hole is highly informative for perceiving the size of the hole. And it is known that pliability moderates the depth of the skin’s intrusion into structures that are notched into a surface and, thus, the skin’s bending at the structure’s upper edges (cf. Gibson & Craig, 2006; Vega-Bermudez & Johnson, 2004). Further, bending is an effective stimulus for the SA-1 (slowly adapting, type 1) associated receptors in the finger’s skin, which have high spatial resolution and play a crucial role in tactile shape perception: These receptors code how much the innervated skin area bends (Johnson, 2001). A stronger bending comes along with a more intense neural response on an edge, which yields a more accurate representation of that edge. We speculate that the oral illusion is due to the influence of the skin’s bending at the hole’s edge on the neural codes to hole diameter. Weak bending yields inaccurate neural codes leading to an underestimation of hole diameter. The highly pliable tongue intrudes more into a small hole and thus bends more at its edges as compared to the less pliable index finger. Hence, the diameter of small holes is underestimated by the finger. In contrast, for larger holes, in that the finger can be completely inserted, bending of the finger’s skin sharply increases, and size perception with finger and tongue are accurate. The illusion vanishes. Certain aspects of this “bending-neural code hypothesis” fit with observations from a smooth-grooved task (Gibson & Craig, 2006). In this task, participants decided whether a stimulus pressed onto the skin is smooth or a grooved tactile grating. Similar to our assumptions regarding hole perception, bending at the groove’s edges correlated with perceptual accuracy in this task. Both correct responses and skin intrusion/bending increased with groove width, the use of the more pliable finger pad as compared to the less pliable finger base, and high as compared to low finger force (0.5N vs 2 N).

The present study aimed to test predictions from the bending-neural code hypothesis. In five experiments we tested whether the haptic perception of hole size systematically depends on factors that affect the skin’s bending at the hole’s edges. In Experiment I to III we tested the influence of mechanical characteristics of the effectors. Bending should increase with the effector’s pliability, but it should reach a level sufficient for accurate perception when an
effector can be completely inserted into a hole. Experiment I tested size matching between the big toe, the finger, and the tongue. The skin at the big toe is less pliable than that at the finger, where it is less pliable than at the tongue. We predicted that the toe perceives holes to be smaller than finger and tongue, and that the effects disappear when both effectors can be inserted into the hole. Experiment II tested size matching of big toe, index finger, and tongue relative to seen holes, presuming that visual perception of size tends to be accurate. Experiment III tested size matching of the tip and the dorsum of the tongue relative to the index finger. Whereas tip and dorsum are of similar pliability, parts of the dorsum are less well inserted into a hole as compared to the tip of the tongue. We, hence, expected a smaller oral illusion for the dorsum. In the third condition of Experiment III and in Experiment IV to V, we tested the influence of the interaction between effector and stimulus, by instructing different ways to explore the stimuli (stamping vs. encircling in Experiment IV: high vs. low tongue force in Experiment V).

**Experiment I**

Experiment I studied the matching of hole sizes between the big toe, the finger, and the tongue. Participants explored a reference hole with one effector and used another effector to select a comparison hole that subjectively matches in size. Each participant performed this task for either pair of effectors (toe-tongue, toe-finger, finger-tongue). The reference hole was presented either on the effector of higher pliability (tongue for pairs including the tongue; finger for the pair toe-finger) or on the effector with lower pliability. We expected an underestimation of a hole’s size when the toe is used relative to the finger and even more so relative to the tongue. We used 5 reference holes between 2.4 and 19.2 mm diameter.

**Methods**

*Participants.* We tested 18 participants, mostly university students (22-48 years; mean age 26 years; 14 females, 4 males; 16 right-handed, two left-handed), who were naïve to the purpose of the study. Two-point discrimination thresholds were assessed to be 2-3 mm (mean: 2.3) at the dominant hand’s index finger and 5-11 mm (mean: 8.2) at the corresponding big toe (assessed
Felt hole size with a resolution of 1 mm). The index fingers had a width of 13 - 17 mm (mean: 14.6) and the big toes had a width of 22-32 mm (mean: 24.2) as assessed at two thirds of the distal phalanx. 9 participants were paid (8€/h). None of the participants in all experiments reported cutaneous or motor impairments, none had evidence of oral disease or of calluses on hands and feet. Methods and procedures in all experiments reported were approved by the local ethics committee (LEK) of FB 06 at Giessen University and were in accordance with the ethical standard laid down in the Declaration of Helsinki (1964). Participants provided their written informed consent.

Setup and stimuli. In a quiet room participants sat at a table next to the experimenter. During the experiment the participants wear a blind. Haptic reference stimuli were cuboids of 35 mm length, 35 mm width and 6 mm height made from acrylic glass (Fig. 1). A circular hole of 4 mm depth with a planar bottom was centered on the top side. Reference holes had diameters of 2.4, 5.6, 9.6, 14.4, and 19.2 mm. There was a separate set of reference stimuli for each effector (tongue, toe, finger). Further, two practice stimuli with holes of 5 and 15 mm diameter were used to instruct participants. Comparison holes that were explored with finger or toe were set in an acrylic disc of 405 mm diameter and circularly arranged in ascending order of diameter (Fig. 1). There were 43 circular holes of 4 mm depths and 15mm of padding between neighbours and the edge of the disc. Their diameters ranged from 0.8 to 25.6 mm with steps of 0.4 mm below a diameter of 9.6 mm and steps of 0.8 mm for higher diameters. One “comparison disc” was on the table for the use with the finger, another disc was on the ground for the use with the big toe (Fig. 2). A “comparison wheel” was designed for use with the tongue in a sitting position. The wheel was a vertical disc, on the edge of which 43 detachable cuboids of acrylic glass were fixed with magnets. The comparison holes in the cuboids corresponded to the holes in the discs. Between participants, the cuboid stimuli were sanitized by boiling them for 5 minutes and the comparison discs were cleaned using a disinfecting wipe. The experimenter wore fresh medical gloves when handling the stimuli.
Design and procedure. The participant’s task was to feel a reference hole with one effector and to select a comparison hole of subjectively matching size with another effector. The design comprised three within-participant variables, the diameter of the Reference Stimulus (2.4, 5.6, 9.6, 14.4 and 19.2 mm), the Effector Pair (toe-tongue, toe-finger, finger-tongue) and the pliability of the Reference Effector (higher vs. lower in the pair). Pliability is highest for the tongue and lowest for the toe. Thus, for instance, the combination of the conditions ‘toe-tongue’ and ‘higher pliability of reference effector’ meant that the tongue explored the reference hole and the toe the comparison holes. To indicate such combinations of conditions, we use the notation “reference effector->comparison effector” (in the example tongue->toe). Trials of each of the 6 combinations of Effector Pair and Reference Effector were blocked, the order of blocks was counterbalanced across participants according to a Latin square design. In each block, each reference stimulus was presented 3 times in random order resulting in 5 X 6 [combinations of conditions] X 3 [repetitions] = 108 trials. The dependent variable was the average of the diameters of matched comparison holes.

Each single trial started with the experimenter handing a reference stimulus over to the participant’s non-dominant hand. The participant, then, explored the reference hole with the designated reference effector and at the same time rotated the designated comparison device at the comparison effector to select a hole that felt the same size (Fig. 2). Comparison discs were used with the dominant hand or the corresponding foot, the comparison wheel for the tongue was rotated using either hand. The reference stimulus was held in the non-dominant hand except for the condition finger->tongue in which it lay on the table. Participants were instructed to stamp the holes, that is to press the effector orthogonally to the stimulus surface into the hole, minimizing lateral movements across the hole’s edges. The participants had to respond within 30 seconds and the experimenter noted the diameter of the indicated comparison hole. Between trials, the experimenter rotated the comparison disc or wheel to a random orientation.
Before the experiment, we assessed the two-point discrimination thresholds and recorded the width of index fingers and big toe. Participants were also shown the two practice stimuli, but they were not allowed to touch them at the same time. Afterwards the participants were blindfolded. Before each block, participants were instructed how to explore the stimuli and the exploration techniques were practiced for two practice trials. Then, the experimental trials started. The experiment lasted approximately 120 minutes.

**Data analyses.** First, we calculated the individual average diameter of the matched holes for each condition. We, then, calculated, the difference between these averages and the diameter of the reference hole by subtracting the value associated with the effector of higher pliability (matched or reference diameter) from the value associated with the effector of lower pliability (matched or reference diameter). The individual difference values were submitted to ANOVAs; p-values were corrected according to Greenhouse and Geisser (1959), if required. Significant effects in the ANOVA were further analysed using pair-wise Bonferroni-corrected post hoc t-tests (overall-α-level 5%). In addition, we tested the difference value for each reference hole against zero by using a single-sided t-test.

**Results**

The overall average diameters of the matched holes are depicted in Fig. 3a; the average differences between matched and reference hole diameters can be found in Fig. 3b (reference effector of lower pliability) and Fig. 3c (reference effector of higher pliability). Difference values were, first, analyzed using two separate ANOVAs for each pliability of Reference Effector with the within-participant variables being Effector Pair and Reference Stimulus.

--------------- insert Figure 3 about here -------------------------------

When the reference effector was of higher pliability (Fig. 3c), difference values were, as expected, larger for the pair tongue->toe than for finger->toe and they were smallest for tongue->finger (main effect Effector Pair, $F_{2, 34}=24.47, p<.001, \eta^2=0.59$; all pairwise single-sided post-
The ANOVA revealed no other significant effects (Reference Stimulus, $F_{4,68}=2.26$, $p=.103$, $\epsilon^2=0.12$; Reference Stimulus X Effector Pair, $F_{8,136}=1.41$, $p=.233$, $\epsilon^2=0.08$).

When the reference effector was of lower pliability (Fig. 3b), difference values were larger for the pair toe->tongue, as compared to the pairs toe->finger and finger->tongue (Effector Pair, $F_{2,34}=11.99$, $p<.001$, $\epsilon^2=0.41$, significant differences only in post-hoc tests that include toe->tongue). There were also a main effect of Reference Stimulus, $F_{4,68}=14.33$, $p<.001$, $\epsilon^2=0.46$, and an interaction Reference Stimulus X Effector Pair, $F_{8,136}=4.77$, $p=.003$, $\epsilon^2=0.21$. We further analyzed these two effects by additional separate analyses per Effector Pair (3 ANOVAs with variable Reference Stimulus): In the finger->tongue condition the difference value hardly varied with the diameter of the reference hole, $F_{4,68}=1.11$, $p=.338$, $\epsilon^2=0.06$. But in the toe->finger and the toe->tongue conditions the difference value was smaller for the smallest reference stimulus (toe->finger) or the two smallest reference stimuli (toe->tongue) as compared to the larger reference stimuli (main effect for toe->finger: $F_{4,68}=11.74$, $p<.001$, $\epsilon^2=0.41$, for toe->tongue: $F_{4,68}=15.98$, $p<.001$, $\epsilon^2=0.49$, in pair-wise post-hoc tests the smallest or the two smallest stimuli, respectively, have with a single exception significantly smaller values than all larger stimuli).

In another ANOVA we compared the data from the three largest reference stimuli between the conditions with the reference effector of higher vs. of lower reliability (variables Reference effector, Effector Pair, Reference Stimulus [9.6, 14.4 and 19.2 mm only]). For the 3 largest reference stimuli the difference value depended only on the effector pair: It was largest for the pair toe-tongue (4.3 mm), followed by toe-finger (2.8 mm), and, finally, finger-tongue (1.2 mm; main effect Effector Pair, $F_{2,34}=20.36$, $p<.001$, $\epsilon^2=0.55$, all pairwise single-sided post hoc tests significant). Other effects in this ANOVA were not significant ($ps>.10$, $\epsilon^2s<0.11$).

Single-sided $t$-tests against 0 showed that difference values were significantly positive in each of the 30 combinations of conditions except for the two largest reference holes in the finger->tongue condition, the largest reference hole in the tongue->finger condition and, the smallest reference hole in the toe->tongue and toe->finger conditions. That is, the diameter of the hole
associated with the effector of higher pliability was in nearly all cases larger than the subjectively equal diameter of the hole associated with the effector of lower pliability.

Discussion
We studied the matching of hole sizes between the big toe, the finger, and the tongue. As predicted, in almost all conditions participants matched a hole at a more pliable effector by a larger hole at the less pliable effector and vice versa. Reference holes felt by the tongue were matched to larger holes at the index finger and to even larger holes at the toe; reference holes at the index finger were matched by larger holes at the toe. These effects were almost mirrored, when the less pliable effector explored the reference hole. Whether the more or less pliable effector obtained the reference hole hardly influenced the magnitudes of these effects—with the single exception when small reference holes were presented to the toe (see below). We conclude that holes feel smaller with the toe than with the finger than with the tongue. This fits our prediction that felt hole size decreases with decreasing pliability of an effector. Because lower pliability decreases the skin’s bending at a hole’s edges, the findings corroborate our bending-neural code hypothesis, which states that felt hole size decreases with the skin’s bending.

The bending-neural code hypothesis further predicts that perceived hole size differs between effectors, when the holes are small, but less so when the holes are large enough to insert the effectors. Consistently, in previous studies a tongue-finger difference was observed for smaller holes, but not for holes of about 10-15 mm diameter (e.g., Anstis, 1964; Albashaireh & Orchardson, 1988). Results on the tongue-finger difference in the present analyses are mixed: Effects of reference hole diameter failed to reach significance, but consistent with the hypothesis the tongue-finger difference significantly differed from 0 only for the smaller, not for the larger reference holes (14.4 mm and 19.2 mm). In contrast, the analyses of the toe-finger and the toe-tongue differences did not show any significant decrease with increasing hole diameter. This lack of effect is also consistent with the hypothesis, because participants were not able to insert
their big toe (width 22-32 mm) even into the largest hole (19.2 mm). Hence, the bending of the toe’s skin was limited even for the largest hole, and even the largest hole was underestimated. A salient exception from the general pattern of results was observed when small reference holes (2.4 and 5.4 mm) were presented to the toe. Then, the finger or tongue selected matching holes that differed less from the reference hole as compared to when the toe explored larger reference holes or when the toe selected the comparison hole. This specific finding might be due to the limited spatial resolution of the toe. Participants had a two-point discrimination threshold for the toe between 5-11 mm. Thus, when being presented with a very small hole at the toe, participants likely perceived an unstructured stimulus rather than a hole. Their decision on a matching hole might have been biased towards selecting one of the larger holes that they had typically matched with other reference holes. In contrast, when the toe was selecting a hole that matched a small reference hole at finger or tongue, the toe aimed at holes that were larger than the reference holes, and the limited spatial resolution at the toe was less relevant. That is, we believe this specific finding reflects only a strategy to deal with the inability to identify the small reference holes with the toe, which is of less interest in the present theoretical context.

Overall, the results are consistent with the bending-neural code hypothesis. They confirm that holes feel smaller with the toe than with the index finger than with the tongue. The hypothesis also predicts that size perception is more accurate for the tongue as compared to the finger as compared to the toe. This implies that the finger and more so the toe underestimate hole size, at least of holes in that the effectors cannot be inserted. Experiment II tests these predictions.

**Experiment II**

Participants assessed the perceived size of reference holes (the same as in Exp. I) presented to tongue, index finger and big toe by selecting a matching hole from a series of visual comparison stimuli. While it is clear that in diminished visual scenes perceived size can be biased, it has also been shown that under more natural viewing conditions visually perceived size is remarkably constant (Haber & Levin, 2001; Holway & Boring, 1941). Hence, we presume that visual
matches are an appropriate means to approximate in how far haptic estimates are accurate or underestimate actual hole size. Underestimation means that participants visually select a larger hole to match the subjective size of a touched hole. We expected that the toe underestimates hole size more than the finger, which underestimates hole size more than the tongue.

**Methods**

*Participants.* A total of 24 naïve healthy participants, students of Giessen university were tested (mean age: 23 years, range: 18-30 years; 13 females, 11 males; all right-handed). The experiment was conducted in German or in Arab language (8 participants). Participants volunteered, or received course credit. Two-point discrimination thresholds (resolution 0.5mm) were assessed to be 1.5 - 3.0 mm both at the tongue (mean: 2.1 mm) and at the right index finger (mean: 1.9 mm), and to be 4- 12 mm at the right big toe (mean: 7.6 mm). On average, index fingers were 13.5 mm wide (range: 11.0 to 19.9 mm) and big toes 24.0 mm (18.8 to 29.3 mm).

*Stimuli, setup* (Fig. 4). We used the same reference and practice stimuli as in Experiment I. A comparison disc from Experiment I was placed with its holes in the participant’s viewer plane at 50 cm viewing distance. Their head position was stabilized by a chin rest. The disc was hidden behind a blind except for a viewing window through that participants saw a single comparison hole at any time. The disc could be rotated so that the participants were able to successively view each comparison hole. Depending on the reference effector different specific blinds were used to hide the reference stimuli from view. In the tongue condition participants wear a visor cap between eyes and mouth, in the finger condition the right hand was placed below a cardboard box and in the toe condition the participants placed their right foot on their left lower leg hidden from view behind a cardboard blind. Care was taken that participants received the reference stimuli from the experimenter without ever seeing them.

---------------- insert Figure 4 about here ------------------------

*Design, procedure and data analyses.* The participant’s task was to feel a reference hole with one effector and to visually select a matching comparison hole. The comparison discs was
rotated using one of the hands depending on the condition. Within participants we varied the Reference Stimulus (2.4, 5.6, 9.6, 14.4 and 19.2 mm), and the Reference Effector (index finger of dominant hand, tip-of-tongue, big toe on the dominant hand’s side). Trials for each Reference Effector were blocked, and in each block the 5 reference stimuli were presented in random order for 3 times (=5 X 3 [combinations of conditions] X 3 [repetitions], 45 trials overall; 60 minutes duration). In all other aspects, procedures and analyses were similar to Experiment I.

**Results**

The average diameters of the matched holes and average differences to the reference holes (reference minus matched) are depicted in Fig. 5. Difference values were analyzed using an ANOVA with two within-participant variables, Reference Effector and Reference Stimulus.

On average, the difference value, i.e. the underestimation of felt relative to seen hole diameter, was, as expected, largest when exploring with the toe (2.63 mm), followed by the finger (0.87 mm) and then the tongue (0.11 mm; main effect Reference Effector, $F_{2, 46}=20.85$, $p<.001$, $\epsilon^2=0.48$; all pair-wise single-sided post hoc tests significant). There were also a main effect of Reference Stimulus, $F_{4, 92}=11.51$, $p<.001$, $\epsilon^2=0.33$, and an interaction Reference Stimulus X Reference Effector, $F_{8, 184}=10.90$, $p<.001$, $\epsilon^2=0.32$. We further analyzed these two effects by additional separate analyses per Reference Effector (3 ANOVAs with variable Reference Stimulus). In the tongue and the finger conditions the difference value hardly varied with the diameter of the reference hole (main effect for tongue: $F_{4,92}=2.98$, $p=.062$, $\epsilon^2=0.12$; for finger: $F_{4,92}=2.34$, $p=.093$, $\epsilon^2=0.09$). But in the toe condition the underestimation of felt relative to seen diameter was less pronounced for the smallest and the second smallest as compared to each larger reference stimulus (main effect: $F_{4,92}=19.61$, $p<.001$, $\epsilon^2=0.46$, in post-hoc tests the two smallest stimuli have with a single exception significantly smaller values than all larger stimuli).
Finally, single-sided $t$-tests against 0 showed that difference values were significantly positive in all finger conditions except for the largest reference hole of 19.2 mm, in all toe conditions except for the smallest reference hole of 2.4 mm, but in none of the tongue conditions.

**Discussion**

Reference holes felt by the tongue were matched to seen holes of similar size, whereas holes felt with the index finger and even more so with the big toe were matched to smaller holes. This confirms the conclusion from Experiment I that holes feel smaller with the toe than with the finger than with the tongue. Given that under natural viewing conditions visually perceived size is constant and tends to be accurate, the findings also confirm the predictions that size perception is more accurate with the tongue than with the finger and toe, and that the finger and more so the toe underestimate hole size. We had predicted a higher accuracy for more pliable effectors, because their skin bends more at the hole’s edges, yielding a more intense neural response. Our hypothesis also predicts more accurate size perception for large holes in that an effector can be inserted: In line with this prediction, the finger significantly underestimated the diameter of smaller holes, but not of the largest hole of 19.2 mm. Thus, the results further corroborate the bending-neural code hypothesis.

Similar to Exp. I small reference holes at the toe (2.4 and 5.4 mm) were matched with relatively small seen holes. As elaborated above, this, however, likely only reflects a strategy to deal with the toe’s problems to identify small holes, and is of less interest here. Overall, the present results are highly consistent with the results from Experiment I and fit with our hypothesis that mechanical factors that affect bending at the hole’s edges, systematically influence felt hole diameter. So far, we had compared hole perception of different effectors that differ both in pliability and size. Experiment III tested for predictable effects of the size relation between the effector and the hole, while keeping pliability constant, and it tested for effects of the interaction between effector and stimulus in active exploration.
Experiment III

Participants explored reference holes with the tongue and selected a comparison hole of matching size with their index finger. Exploration with the tongue varied in three conditions: In the “tip-of-tongue” and “dorsum-of-tongue” conditions participants were instructed to stamp the tip of the tongue or the mid of the dorsum of the tongue, respectively, into the hole that was held in their left hand. Stamping means that they had to press the tongue orthogonally to the stimulus surface into the hole. In the “stroking”-condition participants explored the reference holes by a lateral movement from the mid of their tongue’s dorsum to the tip of the tongue. Whereas tip and dorsum are of similar pliability, parts of the dorsum can be less well inserted into a hole as compared to the tip of the tongue, which constrains the bending of the skin. We, hence, expected that the tongue’s dorsum perceives holes to be smaller than the tip, meaning that felt hole size is more similar to the size felt at the finger. Further, we supposed that holes explored with stroking are also perceived smaller, because the lateral movement interferes with the intrusion of the tongue’s skin into the hole, also yielding to less bending.

Methods

Participants. 24 healthy naïve participants, 13 students and 11 working persons, were tested (mean age: 31 years, range: 18-54 years; 15 females; 23 right-handers, 1 left hander). Two participated for course credit, the others obtained a candy after the experiment. Two-point discrimination thresholds (resolution 0.5 mm) were between 1.5 - 3 mm both at the dominant hand’s index finger (mean: 1.9 mm) and at the tip of the tongue (mean: 2.2 mm), and between 2-4.5 mm at the dorsum of the tongue (mean: 3.0 mm). The index fingers had an average width of 13.5 mm. We had to remove data from two participants from data analysis due to extremely outlying matches in some conditions (values deviated > 3.5 standard deviations from mean).

Setup, stimuli. Setup and stimuli were the same as in Experiment I, tongue-> finger condition.

Design, procedure and data analyses. Within participants we varied the Reference Stimulus (2.4, 5.6, 9.6, 14.4 and 19.2 mm), and the Tongue Exploration: In the “tip-of-tongue” and
“dorsum-of-tongue” conditions participants were instructed to stamp the reference hole with the tip of their tongue or the mid of their tongue’s dorsum, respectively. In the “stroking”-condition participants explored the reference holes by a lateral movement from the mid of their tongue’s dorsum to the tip of the tongue, as if licking the all-aluminium cover of a chocolate cream cup. Comparison holes were stamped with the dominant hand’s index finger. The experimenter monitored the participants and gave verbal feedback if they deviated from the instructed exploration. Trials for each Tongue Exploration condition were blocked. In each block each reference stimulus was presented in random order for 3 times, (=5 X 3 [combinations of conditions] X 3 [repetitions], 45 trials overall; 60 minutes duration). In all other aspects, procedures and analyses were similar to Experiment I.

Results

Fig. 6 shows the average matches diameters of matched holes and differences to the reference holes (matched minus reference). Difference values were analyzed using an ANOVA with two within-participant variables, Tongue Exploration and Reference Stimulus.

The average difference value, i.e. the underestimation of the hole diameter felt with the finger relative to that felt with the tongue varied with the diameter of the Reference Stimulus, $F_{4,84}=6.30$, $p=.006$, $\varepsilon^2=.23$, but did so differently depending on the way how the tongue explored, Tongue Exploration X Reference Stimulus: $F_{8,168}=2.45$, $p=0.040$, $\varepsilon^2=.10$. The main effect of Tongue Exploration was not significant, $F_{2,42}=0.91$, $p=0.38$, $\varepsilon^2=.04$. Additional separate analyses per Tongue Exploration (3 ANOVAs with variable Reference Stimulus) revealed a significant influence of Reference Stimulus in the tip-of-tongue and dorsum-of-tongue-conditions, but not in the stroking condition (main effects: $F_{4,84}=4.46$, $p=.001$, $\varepsilon^2=0.29$; $F_{4,84}=4.87$, $p=.016$, $\varepsilon^2=0.19$; and $F_{4,84}=2.01$, $p=.133$, $\varepsilon^2=0.09$, respectively). Difference values in the tip-of-tongue condition were significantly smaller for the largest as compared to each smaller reference hole (according to pairwise post hoc tests). Numerically, difference values in
Felt hole size

the dorsum-of-tongue condition show a pattern of decrease from the smallest (2.4 mm diameter) to the middle hole (9.6 mm), again a larger value at the second largest hole (14.4 mm), and then decrease for the largest hole (19.2 mm). Pairwise post-hoc tests partly confirm this pattern: They were significant for the smallest as compared to the next two larger holes and for the second-largest as compared to the largest hole.

Single-sided $t$-tests against 0 showed that difference values were significantly positive in all combinations of Tongue Exploration X Reference Stimulus conditions except for the largest reference hole of 19.2 mm diameter under each type of tongue exploration and except for the middle reference hole of 9.6 mm diameter in the dorsum-of-tongue condition.

**Discussion**

We had expected that the holes would feel smaller when explored with the dorsum of the tongue as compared to the tongue’s tip, because the dorsum’s skin can be less well inserted into holes. Our findings are consistent with this prediction: In the tip-of-tongue condition reference holes between 2.4 and 14.4 mm diameter were matched by constantly larger holes at the finger, and this effect was only smaller for the hole of 19.2 mm. In contrast, in the dorsum-of-tongue condition the tongue-finger difference was less pronounced or vanished for the holes of 5.6, 9.4, and 19.2 mm diameter as compared to other holes. This suggests, in line with our prediction, that the 5.6 mm and 9.4 mm diameter holes were perceived to be smaller with the dorsum than with the tip of the tongue and provides evidence that, besides pliability, the size of the effector modifies perceived hole size on their own. But why were the expected effects only observed for holes of 5.6 mm and 9.4 mm diameter? A closer look at the tongue’s shape can explain this: Both the tip of the tongue and, when the tongue is rounded in the coronal plane, also the dorsum of the tongue can well enter the larger holes of 14.4 mm and 19.6 mm (for size & shape of the rounded dorsum cf. Slud, Stone, Smith, & Goldstein, 2002). And both tip and dorsum have similar access to the smallest hole of 2.4 mm. However, the small size and shape of the tip-of the tongue allows to enter holes of intermediate diameter (5.4 & 9.6 mm) better than it is
Felt hole size possible by the larger sized, flatter dorsum of the rounded tongue. So, overall the differences between tip- and dorsum-of-tongue conditions are well explained by differences in the access of these tongue parts to the holes. Constrained access of the dorsum to holes of intermediate size predicts decreased skin bending, and thus an underestimation of hole size—similar as for the finger. Thus, results are consistent with the bending-neural code hypothesis.

Another expectation was that holes explored by a tongue stroke feel smaller than holes explored by a stamping movement (tip- and dorsum-of-tongue conditions). The present experiment, however, failed to show the expected effect. We had supposed that lateral movement would interfere with the skin’s intrusion into the hole, yielding a weaker bending of the skin and a decrease in perceived hole size relative to stamping. Instead effects in the stroking condition were highly similar to the effects when stamping the holes with the tip of the tongue. Probably, it was a problem that stroking movements were instructed to end at the tip of the tongue. Rather than estimating hole size while moving the tongue, the participants’ assessment might have been dominated by the final information from the tip of the tongue when the tongue stopped to move. This can explain the high similarity of the results in these two conditions and suggests that the stroking condition was inappropriate to investigate the influence of movement. In Experiment IV and V we tried to use more appropriate manipulations to investigate influences of the interaction between effector and stimulus on perceived hole size.

**Experiment IV**

Participants varied the technique by that the holes were explored. They were instructed to either stamp the holes or to “encircle” the holes, meaning that they followed the contours of the hole by a lateral circular movement. Again, reference holes were presented at the tongue, and matched by a comparison hole selected with the finger. We varied both the exploration technique of the finger (stamping vs. encircling) and of the tongue (stamping vs. encircling). We expected that holes would feel larger with stamping as compared to encircling techniques. Encircling techniques interfere with the skin’s intrusion and the effector’s insertion into a hole,
Felt hole size

whereas stamping techniques should foster the skin intrusion and the skin’s conformance to the hole’s edges, and thus the skin’s bending. It is consistent with this view that participants tend to use stamping techniques for smaller holes in that the skin does not easily intrude and the effector cannot be inserted, whereas they tend to use encircling for holes with diameters of 10 mm or larger (Albashaireh & Orchardson, 1988). Given holes are perceived smaller with the finger as compared to the tongue, the tongue-finger difference in felt hole size should be largest when the finger encircles the holes and the tongue stamps, smaller when both finger and tongue either stamp or encircle, and smallest when the finger stamps and the tongue encircles the holes.

Methods

Participants. 28 healthy and naïve participants, students from Giessen University, were tested (mean age: 25 years, range: 18-42 years; 20 females; all right-handers). Most participated for course credit, 4 were paid (8€/ hour). Two-point discrimination thresholds (resolution: 1 mm) at the right index finger were assessed to be 2-3 mm (mean: 2.5 mm). The index fingers were 12.3-17.9 mm wide (mean: 14.4 mm).

Setup, stimuli. Setup and stimuli were the same as in Experiment I, tongue-> finger condition.

Design, procedure and data analysis. We varied the Reference Stimulus (2.4, 5.6, 9.6, 14.4 and 19.2 mm), the exploration technique of the tongue (stamping vs. encircling) and the exploration technique of the index finger (stamping vs. encircling) within participants. Encircling means that participants were instructed to follow the upper edges of the hole by a lateral circular movement of the finger or tongue without stopping. Stamping means that participants had to press the effector orthogonally to the stimulus surface into the hole and minimize lateral movements across the hole’s edges. In cases, where the hole was larger than the finger participants were allowed to slightly rotate the finger towards the edges of the hole without losing contact in the middle. The experimenter monitored the participants and gave verbal feedback if they deviated from the instructed exploration. Trials of each combination of exploration techniques for tongue and finger were blocked. In each block, the 5 reference stimuli were presented in random order
Felt hole size

3 times (=4 [combinations of exploration techniques] X 5 [reference stimuli] X 3 [repetitions]; 60 trials overall; 80 minutes duration). In all other aspects procedures and data analyses were similar to Experiment I. Participants subsequently participated in Experiment V.

Results

Fig. 7 shows the average diameters of the matched holes and average differences to the reference holes (matched minus reference). Difference values were analyzed using an ANOVA with the three variables Tongue Technique, Finger Technique and Reference Stimulus.

Overall, the difference value, i.e. the underestimation of hole diameter by the finger relative to the tongue was, as expected, slightly larger when the finger encircled the holes instead of stamping them (1.46 vs 1.22 mm; main effect Finger Technique: $F_{1,27}=3.22$, one-sided $p=0.042$, $\eta^2=0.10$). The Tongue Technique did not significantly affect the results (encircling: 1.35 mm; stamping: 1.32 mm, $F_{1,27}=0.027$, $p=0.87$, $\eta^2=.01$). Further, there was a main effect of Reference Stimulus, $F_{4,108}=5.618$, $p=.007$, $\eta^2=.17$. Pair-wise post-hoc tests indicated that the difference value for the largest hole was significantly smaller than for two of the smaller holes (2.4 and 14.4 mm diameter). None of the interactions in the ANOVA reached significance (Finger Technique X Tongue Technique, $F_{1,27}=0.860$, $p=0.362$, $\eta^2=.03$; Reference Stimulus X Tongue Technique, $F_{4,108}=0.448$, $p=.719$, $\eta^2=.02$; Reference Stimulus X Finger Technique, $F_{4,108}=1.790$, $p=.154$, $\eta^2=.06$; 3-way interaction, $F_{4,108}=1.675$, $p=.184$, $\eta^2=.06$).

Single-sided $t$-tests against 0 showed that the difference value (collapsed over conditions of Tongue technique) was significantly positive for each reference hole in each condition of Finger Technique except for the largest hole in the stamping condition.

Discussion

We found that the underestimation of hole size by the finger relative to the tongue was larger when the finger encircled the holes as compared to when it stamps the holes. The tongue’s technique had no reliable effect. Thus, as predicted, the finger perceived holes to be smaller with
encircling as compared to stamping. In contrast to our prediction this did not hold for the tongue. Similar to the previous experiments, tongue-finger differences in perceived size were less pronounced for the largest as compared to the smaller holes. We had expected that stamping techniques should foster the skin’s intrusion into the hole and its conformance to the hole’s edges, and thus increase the skin’s bending and perceived hole size (bending-neural code hypothesis). The effects of finger technique corroborate this hypothesis and show that the interaction between effector and stimulus plays a role for felt hole size.

However, the effects of the finger’s technique were small, and the tongue’s technique had no effect. Possibly, participants had difficulties to use in each single trial an encircling movement that is clearly different from a stamping movement (and vice versa), and hence the effects were small. But this cannot explain the lack of effect of tongue technique. The high accuracy of hole perception with the tongue (Exp. II) may provide an explanation: According to our hypothesis, hole size is underestimated when the holes’ edges are not well represented in the neural response, and it is accurate with a sufficiently intense response. Possibly, for the tongue a sufficient response is yet obtained during encircling movements and accuracy not further increased by stamping.

**Experiment V**

Experiment V further investigated how the interaction between stimulus and effector influences perceived hole size. Participants varied the force that they applied with their tongue to the holes. Participants were instructed to either “gently insert their tongue into the hole until they reach the bottom” (low force) or to “press the tongue into the hole as forcefully as possible without pain” (high force), emphasizing a full insertion of the tongue in both conditions. Peak forces were controlled to be below 0.75 N in the low-force condition and to be above 2.2 N in the high-force condition, which corresponds to the range of forces that has been observed to produce substantial increases in the mechanical interaction of the finger’s skin with gratings (Gibson & Craig, 2006). Low forces should decrease hole size perceived by the tongue as compared to high
forces and, thus the difference between the reference hole at the tongue and the matched comparison hole at the finger. This prediction derives from the assumption that low force weakens the tongue’s bending at the hole’s upper edges.

**Methods**

**Participants.** Participants in Experiment V were the same as in Experiment IV.

**Stimuli, setup** (Fig. 8). We used the same stimuli and almost the same setup as in Experiment I, tongue->finger condition. Additionally, an electronic scale (Kern, EMB 1200-1) was placed on the table in front of the participants. Reference stimuli were placed on the scale. The scale was used to assess the force that participants applied to the stimuli with their tongue.

--- insert Figure 8 about here ---

**Design, procedure, data analyses.** We varied the diameter of the Reference Stimulus (2.4, 5.6, 9.6, 14.4 and 19.2 mm) and the tongue’s exploration force (low vs. high) within participants. Peak forces were constrained by the experimenter so that they would not exceed 0.75 N in the low-force condition and would not be below 2.2 N in the high-force condition. Trials of each force condition were blocked. In each block, the 5 reference stimuli were presented 3 times in random order (=2 X 5 [combinations of conditions] X 3 [repetitions], 30 trials overall; 40 minutes duration). In each trial, the experimenter put the reference stimulus on the electronic scale and guided the participant so that s/he was able to explore the reference hole with the tongue. The participant had to bend forward to explore the stimulus from top (Fig. 8). The experimenter monitored the applied force with the scale and gave verbal feedback if it deviated from the target force. In all other aspects, procedures and analyses were similar to Experiment I.

**Results**

Participants applied peak forces in the range of 4.0 to 7.4 N in trials of the high-force condition and in the range of 0.2 to 0.5 N in the low-force condition (medians of participants minimum and maximum peak forces). Thus, the manipulation of tongue force was successful.
Fig. 9 shows the average diameters of the matched holes and average differences to the reference holes (matched minus reference). Difference values were analyzed using an ANOVA with two within-participant variables Tongue Force and Reference Stimulus.

As predicted, the difference value was larger when the tongue explored with high as compared to low forces (1.25 vs 0.78 mm; main effect Tongue Force: $F_{1,27}=18.444$, $p<.001$, $\varepsilon^2=.41$; single-sided), suggesting that the tongue estimated the holes to be larger with high force. Further, there was a main effect of Reference Stimulus, $F_{4,108}=15.583$, $p<.001$, $\varepsilon^2=.37$. In post-hoc tests the difference value for the largest hole was significantly smaller and the value for the smallest hole tended to be or was significantly larger as compared to all other holes. There was no significant interaction Tongue Force X Reference Stimulus, $F_{4,108}=0.944$, $p=.422$, $\varepsilon^2=.03$.

Single-sided $t$-tests against 0 showed that the difference value was significantly positive for each Reference Stimulus in each condition of Tongue Force except for the largest hole in the high-force condition and the two largest holes in the low-force condition.

**Discussion**

The finger-tongue difference in perceived hole size was larger if the tongue explored with high as compared to low forces. We conclude that the tongue perceives holes to be larger when it is forcefully pressed into the hole. This finding confirms our predictions and corroborates the bending-neural code hypothesis: The hypothesis assumes that the low forces decrease perceived size through a weaker bending of the tongue’s surface at the hole’s upper edge. Further, as in previous studies (e.g., Anstis, 1964; Bittern & Orchardson, 2000), we observed that the difference between the sizes perceived by finger and tongue were larger for small holes and reduced for large holes. We will come back to these effects in the General Discussion.

**General Discussion and Conclusion**

We investigated how the haptic perception of hole size depends on characteristics of the effector and the interaction between effector and stimulus. In five experiments we tested predictions
Felt hole size

from the bending-neural code hypothesis that states that perceived hole size gets less accurate and decreases, when the skin bends less at the hole’s edges. As predicted, Experiments I and II showed that perceived hole size decreases with the pliability of the exploring effector (tongue > finger > toe). Results from Experiment II further confirmed that hole perception with the most pliable effector, the tongue tends to be quite accurate, whereas the finger and more so the toe underestimate hole size. In Experiment III we observed that size and shape characteristics of the stimulated part of the tongue (tip vs. dorsum) modify felt hole size in accordance with our predictions. Finally, experiments IV and V demonstrated that the way how the holes are explored influences felt hole size: With the finger holes felt larger when using a stamping as compared to an encircling technique, and with the tongue high forces yielded larger perceived hole sizes than low forces. Overall, results from all five experiments confirm predictions from the bending-neural code hypothesis. We conclude that the skin’s bending at the hole’s edge is a crucial factor for haptically perceived hole size, and can also well explain the oral illusion.

The skin’s bending is further influenced by the diameter of the hole. There is a sharp transition in bending and, presumably, felt hole size between the cases when the effector can be fully inserted into the hole and when it has only limited access. It is obvious, that the skin can much better conform to the contour of an edge, when it contacts the edge at a freely chosen angle, which is possible during full effector insertion, as compared to when the skin can contact the edge only at a low angle, which occurs when the effector’s position is constrained by the hole’s surround. We expected that hole perception is accurate when the effector can be completely inserted into the hole. Our results are in line with this expectation: Our participants had fingers of about 14 mm width (11-20 mm), which allowed most participants to fully insert their finger only in the largest holes. Consistently, the finger-tongue difference in felt size disappeared in each experiment for the largest or the two largest holes (14.4 - 19.2 mm). Further, the participants’ toes had a width of about 24 mm (19-29 mm) being larger than the largest hole presented and, when using their toe, participants underestimated hole’s of each diameter in
Felt hole size

Experiment I and II. The specific differences observed in hole perception with the tip vs the dorsum of the tongue have been explained in a corresponding manner in the discussion section of Experiment III. Taken together, we demonstrated sharp transitions in felt size as a function of hole diameter, which fit well to the expected sharp changes in the skin’s bending when the effector can be inserted into a hole.

From results on tactile gratings (Gibson & Craig, 2006) one may additionally expect more subtle differences in the skin’s bending within the range of smaller holes, in that the effector cannot be inserted. The skin should bend slightly less at the smaller holes within this range. According to our hypothesis, these differences should also subtly affect hole size perception. We detected corresponding differences in Experiment 5, where the oral illusion was significantly larger for the smallest as compared to the other holes, but not reliably in the other experiments.

Also previous studies on the oral illusion are mixed: Some previous studies described the difference between matched and reference size as a linear function of the reference size (Anstis, 1964; Anstis & Loizos, 1971; Bittern & Orchardson, 2000), whereas data from other studies do not show a corresponding systematic decrease within the range of smaller holes (Albashaireh & Orchardson, 1988; Melvin & Orchardson, 2001). However, the expected perceptual differences are subtle and their detection might require particularly sensitive methods.

Still, altogether the present findings fit well with our hypothesis that the haptically perceived size of a hole is a function of the extent of the skin’s bending at the hole’s upper edge. A weaker bending comes along with a less intense neural response on an edge (Johnson, 2001), which can be assumed to yield a less accurate representation of that edge. The present results also corroborate our view that hole size is underestimated when bending and the neural response are weak, but accurate with a more intense bending and receptor response. The assumption that a sufficiently intense neural response yields an accurate perception rather than an overestimation of hole size, is, in particular, supported by the findings that hole size perceived with the tip of
the tongue tends to be accurate (Exp. II) and is not easily modified by the type of exploration (Exp. IV). Also the absence of the oral illusion with large holes fits this assumption.

How might the intensity of the neural response link to perceived hole size? A recent study on intraoral size perception supports the assumption that there is a link: Objects in the mouth are perceived to be smaller after adaptation to intense sensory stimulation (e.g. eating, chewing bubble gum), which decreases the neural response, as compared to after sensory deprivation (Topolinski & Türk Perreira, 2012). Further, the neural explanation of findings from a smooth-grooved task (cf. introduction; Craig, Rhodes, Gibson, & Bensmaia 2008; Gibson & Craig, 2006) provides an interesting starting point for detailed considerations: Performance in discriminating grooved gratings from smooth stimuli correlates with the extent of skin bending, which has been explained as follows: It is known that when a spatially structured stimulus contacts the skin, the pattern of skin deformation is preserved with relatively high resolution (about 0.5 mm in finger pad) by the spatial pattern of SA-1 responses in the contact area. Edges in the stimulus, such as the edge of a groove in a grating, yield a locally maximal SA-1 response which marks the edge (Phillips & Johnson, 1981a). Such enhancement of edges in SA-1 responses correlates with the degree of skin bending at an edge (Johansson, Landström, & Lundström, 1982; Johansson & Vallbo, 1983; LaMotte & Srinivasan 1987a, b) and the enhancement is more pronounced if a groove is wide and the skin intrudes well (e.g. Phillips & Johnson, 1981a, b). In contrast, the area of the grooves themselves yields a locally minimally SA-1 response. Performance in the smooth-grooved task is now explained by the detection of grooves via the absolute difference between SA-1 responses to the groove itself and to the groove’s edges (Craig et al., 2008). Both this response difference and detection performance increase with skin intrusion, and, thus with skin bending. The explanation is corroborated by matching predictions from a continuum mechanical model on how tactile stimuli bend the skin’s tissue and convert into responses from peripheral afferents (Sripati, Bensmaia & Johnson, 2006; cf. Phillips & Johnson, 1981b).
When extending these considerations from the detection of grating stimuli to the haptic perception of hole size, one would expect that also for circular holes SA-1 responses are enhanced at the edges and decreased at the hole’s area, the more so the more the skin can bend at the hole’s edge. A neural code for hole diameter might, then, be based on SA-1 response maxima that mark the hole’s edges or on the pattern of decreased SA-1 responses that mark the area of the hole itself. With stronger bending the increase of impulse rates of SA-1 afferents at edges has been observed to be very pronounced as compared to the surrounding afferents, whereas with weaker bending a groove’s edges are less well marked in the SA-1 response pattern (Phillips & Johnson, 1981a, b). One may, hence, speculate that with stronger bending edge enhancement alone provides a highly reliable basis for the perception of notched shapes such as grooves or holes, whereas with weak bending also the decreased response in the notched area needs to be taken into account. In this case holes, in that the effector cannot be inserted might be perceived as being smaller than indicated by their edges, because edge enhancement is low. In contrast, holes in that the effector can be inserted are perceived accurately, because their edges are well marked. Obviously, this approach does not only explain differences in the perception of large and small holes, but any perceptual difference that is associated with differences in the skin’s bending at the hole’s edges. However, this neural explanation needs to be further tested.

One final important aspect in our and previous findings that is not well represented in the neural model is an astonishing constancy of haptic size perception. In the present Experiment III and IV participants had no difficulties to compare holes that were explored by encircling or stroking with holes explored by stamping, albeit these two movements yield highly different spatio-temporal patterns of stimulations from the same hole. Bittern and Orchardson (2000) observed that the tongue well perceives that a 1 mm-deep hole has a similar diameter as a 5 mm-deep hole, albeit, when the tongue is fully inserted, the stimulated skin area and the distance of the holes opposite upper edges on the tongue’s surface differ by a considerable extent (for a hole
diameter of 3 mm the areas are 17 vs. 54 mm² and the distances 5 vs. 13 mm). Such observations demonstrate a surprising ability of oral-tactile perception to deduce size and shape of external objects from diverse patterns of local stimulation while taking into account the tongue’s three-dimensional deformation and movement.

In conclusion, in five experiments we provide evidence that the degree of bending of the skin at the edge of a hole determines whether and how much the size of the hole is underestimated by touch. Different degrees of bending can explain, for example, why small holes are perceived to be smaller at the finger than at the tongue, i.e. the oral illusion which so far has not been explained in a satisfying manner. Also in other cases of haptic size and shape perception, in particular, of notched structures, the degree of bending should be considered as a modifying factor. We suggested a neural response model explaining how a weak bending might impoverish the perceptual representation of edges and thus of hole size. According to the model biases in size perception represent natural mechanical limits in the tactile sensor organs rather than systematic deviations from veridicality in haptic perception. In line with this view is the astonishing perceptual ability to deduce the size of external objects from diverse spatio-temporal patterns of local stimulation at the tactile sensor organs, which itself provides an important focus for future work.
References


Figures and Figure Captions

**Figure 1.** Reference and comparison stimuli.
Figure 2. Experiment I; from left to right: tongue->finger condition (with left-handed participant), finger->tongue condition, finger->toe condition.
Figure 3. Experiment I; average diameter of matched holes (a) and difference between matched and reference hole (value associated with lower pliability minus value associated with higher pliability) with standard errors separately for the reference effectors of lower (b) and higher (c) pliability; the arrows in the legends point away from the reference effector.
Figure 4. Setup in Experiment II; reference holes were explored with either the tongue, the finger or the toe and matched with seen holes. Different opaque blinds were used to hide the reference holes and all but a single comparison hole from view. When participants explored the reference hole with their right index finger, they rotated the comparison disc with their left hand as depicted. In the other conditions the left hand was used to present the reference hole to the exploring effector (tongue, toe) and the disc was rotated with the right hand.
Figure 5. Experiment II; average diameter of matched holes (a) and difference between matched and reference hole (reference minus matched) with standard errors (b) as a function of the reference effector and the diameter of the reference hole.
Figure 6. Experiment III; average diameter of matched holes (a) and difference between matched and reference hole (matched minus reference) with standard errors (b) as a function of the tongue exploration and the diameter of the reference hole.
Figure 7. Experiment IV; average diameter of matched holes as a function of the tongue’s and the finger’s exploration technique and the diameter of the reference holes (a) and difference between matched and reference hole (matched minus reference) with standard errors (b) as a function of the finger’s technique and the diameter of the reference holes.
Figure 8. Setup in Experiment V; side view (a) and top view (b).
Figure 9. Experiment V; average diameter of matched holes (a) and difference between matched and reference hole (matched minus reference) with standard errors (b) as a function of the tongue’s force and the diameter of the reference holes.