

Tactile distance anisotropy on the tongue

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Abstract

A large literature has described illusions of tactile distance perception. Across many body parts, there is an anisotropic bias for tactile distances to be perceived as larger when oriented across body part width than when oriented along body part length. This study investigated whether there is a similar bias on the tongue. A forced-choice judgment task was used in which participants judged which of two tactile distances felt larger either on the tongue or on the hand dorsum, a region for which anisotropy is well established. Anisotropy was measured using the method of constant stimuli. Clear anisotropy was found on both body parts, with distances oriented with body part width overestimated compared to those oriented with body part length. These results provide further evidence that tactile distance anisotropy is widespread across the body.

Keywords

Touch; tongue; tactile distance perception

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The distance between two points touching the skin is not experienced uniformly across the body. This was first reported by Ernst Weber in his pioneering research in the 19th century (Weber, 1834). Weber found that the points of a compass were perceived as farther apart in areas of higher tactile sensitivity, such as the hand, compared to areas of lower tactile sensitivity, such as the forearm. This classic version of what has come to be known as *Weber's Illusion* has since been widely replicated (Anema et al., 2008; Cholewiak, 1999; Fitt, 1917; Goudge, 1918; Miller et al., 2016; Taylor-Clarke et al., 2004). Other studies have extended this idea, showing comparable illusions based on the orientation of stimuli on a single skin surface (e.g., Green, 1982; Longo & Haggard, 2011).

Such anisotropy of tactile distance perception has been most widely studied on the hand (Longo & Golubova, 2017; Longo & Haggard, 2011; Tamè et al., 2021). For example, Longo and Haggard (2011) found that healthy individuals perceive tactile distances oriented across the width of the hand dorsum as around 30% to 40% larger than distances oriented along hand length. Such effects are not specific to the hand dorsum, however, and have been described on several other parts of the body. Anisotropies of tactile perception have also been found on the palm of the hand (Fiori & Longo, 2018; Longo, 2020), the forearm (Knight et al., 2014), the upper arm (Chang & Longo, 2022), the dorsal surface of the feet (Manser-Smith et al., 2021), the thigh (Green, 1982; Tosi & Romano, 2020), the

face (Fiori & Longo, 2018; Longo et al., 2015, 2020), the back (Nicula & Longo, 2021; Plaisier et al., 2020), and the shin (Stone et al., 2018).

The majority of studies have shown a trend for overestimating distances oriented across the mediolateral axis of the body, though the strength of this illusion varies across body parts. There is also evidence, however, that the overestimation of width is not universal across the body. On the belly, for instance, studies of healthy participants have found no apparent anisotropy (Green, 1982; Longo et al., 2019; Marks et al., 1982), although such a bias may appear in clinical conditions such as eating disorders (Keizer et al., 2011, 2012; Spitoni et al., 2015) and obesity (Mölbart et al., 2016; Scarpina et al., 2014). The lower back is the only body region where a tactile anisotropy has been found in the opposite direction, with distances oriented along it perceived as larger than those oriented across (Nicula & Longo, 2021; Plaisier et al., 2020).

The present study investigated tactile distance perception on the tongue. Like the hand, the tongue mucosa has a high density of mechanoreceptors making it extremely

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sensitive to touch and pressure (Bono et al., 2022). Some studies suggest it has tactile acuity equal to, or perhaps greater than the fingertip (Miyamoto et al., 2006). The tongue has a high density of rapidly adapting mechanoreceptive afferents, with very small receptive fields (Trulsson & Essick, 1997). This has led the tongue to be described as an “oral fovea,” analogous to the fingertips (Haggard & de Boer, 2014). While modern humans do not generally use the mouth and tongue for discriminative touch or tool use, many apes do, such as chimpanzees (McGrew, 1992) and orangutans (O'Malley & McGrew, 2000), and the same may have been true of extinct hominin species like Neanderthals (Bruner & Lozano, 2014). This is unsurprising, given that infants first explore the world through “mouthing,” a process by which they bring all new and strange objects to their mouth to investigate orally (Bushnell & Boudreau, 1991).

Tactile size perception is an important function of the tongue since it is critical to determine when a bolus of food has been chewed sufficiently so that it is safe to eat. Tactile and other sensory signals from the tongue, mouth, and throat, are known to make important contributions to the control and regulation of swallowing (Steele & Miller, 2010). Sensory dysfunction is also commonly linked to clinical disorders of swallowing—*dysphagia* (Alvarez-Berdugo et al., 2016; Labeit et al., 2023; Santoso et al., 2019). Indeed, dysphagia can be experimentally induced by anesthetizing the internal superior laryngeal nerve (Jafari et al., 2003). Dysphagia has been found to result from a wide range of disorders, including stroke (Hamdy et al., 1997), Parkinson's disease (Suttrup & Warnecke, 2016), Alzheimer's disease (Humbert et al., 2010), schizophrenia (Kulkarni et al., 2017), and frontotemporal dementia (Langmore et al., 2007), as well as in otherwise healthy elderly individuals (Serra-Prat et al., 2011). Remarkably, one review suggested that dysphagia may occur in as many as 50% of elderly people and 50% of all neurological patients (Clavé & Shaker, 2015).

Dysphagia is also common in children (Lawlor & Choi, 2020) and is linked to feeding difficulties. Indeed, there are numerous reports of cases in which dysphagic disorders have been initially misdiagnosed as eating disorders such as anorexia (Däbritz et al., 2010; Letranchant et al., 2020; Richterich et al., 2003; Stacher et al., 1990). Aspects of dysphagia may also be related to some forms of eating disorders. For example, avoidant restrictive food intake disorder (ARFID) is a disorder where there are highly restrictive attitudes to food but without a desire for weight loss or thinness. It is considered to have three primary factors: a low interest in food, avoidance of food or drink based on sensory sensitivities, and anxiety around the possible consequences of eating, such as choking or vomiting (Thomas et al., 2017). Relatively little is understood about the causes of ARFID, however, one of the primary mechanisms is suspected to be neurobiological abnormalities in sensory perception.

The critical role of sensory information in swallowing makes it interesting to investigate sensory processing on the tongue. An early study exploring oral size perception found that participants perceived the size of brass rings as larger on the tongue than on the palm of the hand (Waterman, 1917). This phenomenon was studied further by Anstis (1964), who noted that holes are often perceived as enormous when felt by the tongue. He reported that participants overestimated the size of holes that were perceived orally, compared to when they were felt digitally. This illusion only appeared for the smallest holes in the stimuli set (diameters of 1/8 and 1/4 inches). However, for these sizes, the illusion was fairly strong, with the 1/8-inch hole overestimated by ~50%. A later version of this study also found a general trend toward overestimation when stimuli were perceived orally but found the smallest hole (1/6-inch) was underestimated (La Pointe et al., 1973). Alternatively, a recent study argued that the illusion only exists because the nature of previous experiments had put the fingertips at a disadvantage. They suggest that the fingers are unable to probe the smaller holes as successfully as the tongue and thus make underestimations in size (Melvin & Orchardson, 2001). Other factors that influence oral perception include hunger, with one study demonstrating that hungry participants underestimated the size of objects to a lesser degree than sated participants (Crutchfield et al., 2018).

Tactile illusions of object size are thus well established on the tongue, but tactile distance perception has not been investigated. Recent results have shown that anisotropy illusions operate very differently for tactile distance perception and for the perception of continuous object size (Tamè et al., 2022). The present study thus investigated the presence of tactile distance anisotropy on the tongue and compared this to the hand dorsum, a region in which anisotropy is well established.

Method

Participants

Thirty-eight participants (21 female) between 20 and 55 years of age (M : 29.9; SD : 8.8) took part in the study. Two additional participants were tested but were excluded from analyses on account of poor model fit (see below). The majority of participants were right-handed (M : 80.3, range: -100 to 100), as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants gave written informed consent. The study was given approval by the School of Psychological Sciences Research Ethics committee at Birkbeck, University of London.

A weighted average of effect sizes from 15 previous experiments from our laboratory measuring tactile distance anisotropy on the hand (total $N=300$) gave an average effect size of Cohen's $d=1.56$. A power analysis using G*Power 3.1 (Faul et al., 2007) with an alpha of

.05 and a power of .95 indicated that eight participants were required. Our sample size of nearly five times this number gives us substantial power to detect potential effects on the tongue even substantially smaller than found on the hand dorsum.

Materials

Three tactile stimuli were used on the hand. The tactile stimuli used were pairs of wooden cuticle sticks embedded in foam board. The cuticle sticks were tapered to a blunt point (~1 mm width). The different distances between the two sticks were 2, 3, and 4 cm. These tactile stimuli are similar to those used in previous studies (e.g., Calzolari et al., 2017; Fiori & Longo, 2018; Manser-Smith et al., 2021).

The tactile stimuli for the tongue used wooden toothpicks rather than cuticle sticks. Toothpicks were chosen as they were comparable to cuticle sticks but were smaller and designed for safe oral use. Like the hand stimuli, these toothpicks were embedded in foam board with a certain distance between the two points. The different distances were 1, 1.5, and 2 cm. These distances are well above the two-point discrimination threshold on the tongue (Jacobs et al., 2002). For example, Calhoun et al. (1992) reported a mean two-point discrimination threshold of between 2.0 and 2.7 mm across different ages, while Maeyama and Plattig (1989) reported mean thresholds of between 1.6 and 2.7 mm at different locations on the tongue.

The present study also sought to investigate whether tactile distortions might be exaggerated in participants with an increased number of traits related to ARFID, which as discussed above is linked to abnormalities in oral sensory processing. We therefore wished to conduct an exploratory analysis of the relation between tactile anisotropy on the tongue and ARFID traits. A subset of participants was thus asked to complete a section of the Pica, ARFID, and Rumination Disorder Interview ARFID Questionnaire (PARDI-AR-Q; Bryant-Waugh et al., 2019). This is a self-report questionnaire that measures traits of disordered eating found in ARFID, PICA, and Rumination Disorder. For this study, only the ARFID section of the questionnaire was used. There are two versions of this section: one for individuals aged 14 and above, and one for parents/careers to fill in on behalf of their children. The 14+ self-report was chosen as all participants were over 18.

To measure hunger, participants answered four questions relating to their hunger levels at that moment based on the Grand Hunger Scale (Grand, 1968) and similar to another recent study in our lab (Millbank et al., in press). These questions include the following, each based on a 1 to 5 scale: “time since last meal” (0–30, 30–60, 60–120, 120–180, 180+ min); “how would you describe your hunger right now” (totally satisfied, not uncomfortable, hunger is gone for a while; satisfied, slightly full stomach but

could eat a little more; neutral, neither hungry nor full; slightly empty stomach, starting to feel hungry, could wait if needed; very hungry, eager to eat something, stomach growling); “How much of your favorite food subject could you imagine eating at this time” (none at all; not much; indifferent—take it or leave it; considerable amount; as much as I can get); and “time until next meal” (0–30, 30–60, 60–120, 120–180, 180+ min). A hunger composite score was calculated using the mean score of all four individual hunger questions ($M: 3.36, SD: 0.50$).

Procedure

Two body parts were tested: the dorsum of the left hand and the dorsal surface of the tongue. For the hand, the participant sat with their hand resting palm-down on a table. Stimuli were presented approximately in the center of the dorsum, though the exact location was jittered across trials to avoid adaptation or sensitization of the skin. For the tongue, the participant protruded their tongue as much as was comfortable and was asked to keep the tongue as relaxed as possible. Stimuli were presented approximately in the center of the accessible portion of the dorsal body of the tongue.

In every trial, participants were touched twice with two of the tactile stimuli. One touch was oriented across the body part (mediolaterally), and the other touch was along the body part (proximodistally). Each touch lasted approximately one second with a gap of a second between stimuli placements. Participants were then asked to give untimed verbal judgments on whether the distance between the two points felt larger on the first or second stimulus. Participants were blindfolded throughout the stimulation.

There were five pairs of stimuli for the hand (across/along): 2/3, 2/4, 3/3, 3/2, 4/2. The tongue also had five pairs (across/along): 1/1.5, 1/2, 1.5/1.5, 1.5/1, 2/1. The order of across/along stimuli within a trial was randomized. There were 200 trials in total, with 2 blocks of 50 trials for the hand and 2 blocks of 50 trials for the tongue. The inter-trial interval was not precisely controlled but was approximately 3 to 4 s while the experimenter organized stimuli for the upcoming trial. The order of blocks was organized in an ABBA design, with the first condition, counterbalanced across participants. Participants were allowed a short, self-timed break between blocks.

Twenty participants then completed the ARFID-specific section of the PARDI-AR-Q. Eighteen participants completed the hunger questionnaire.

Analysis

Analysis procedures were similar to previous studies from our lab (Calzolari et al., 2017; Chang & Longo, 2022; Longo et al., 2015). Responses were analyzed as the proportion of trials where they judged the across stimuli as

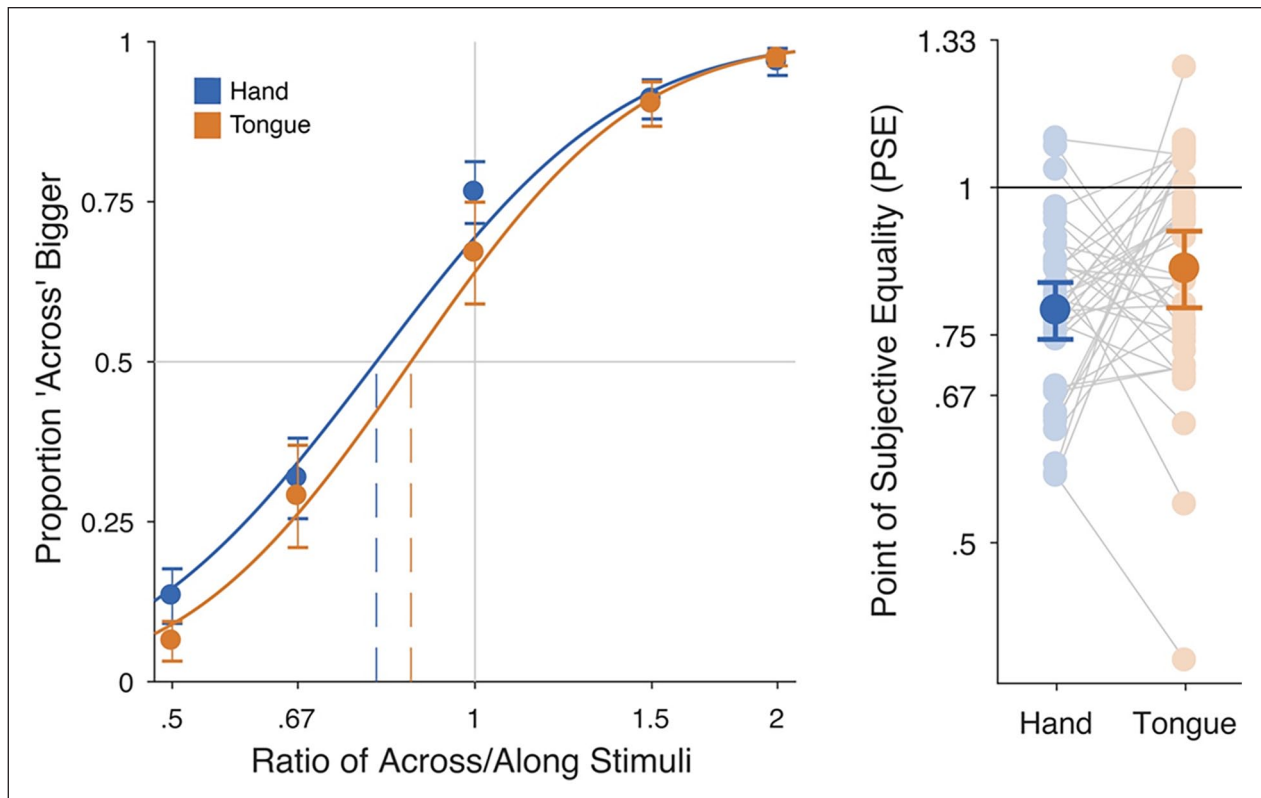


Figure 1. Left panel: Proportion of trials in which the “across” stimulus was judged as larger than the “along” stimulus as a function of the ratio between stimuli (across/along). Curves are cumulative Gaussian functions. Error bars indicate one standard error. Vertical lines indicate the point of subjective equality (PSE), the ratio between the across and along stimuli that participants perceive as equal. Clear anisotropy was apparent both on the hand and on the tongue, with distances across body part width perceived as larger than equivalent distances along body part length. Right panel: PSE values on each surface. Dark circles are grand means and pale circles are individual participant data. Error bars are 95% confidence intervals.

larger. The proportion of trials in which the across stimulus was judged as larger was analyzed as a function of the ratio of the across/along stimuli and was plotted logarithmically to create a symmetrical distribution around a ratio of 1:1 indicating the point of actual equality. Values greater than 1 indicate a bias to perceive tactile distances along body part length to be larger than distances across body part width. Conversely, values less than 1 indicate a bias to perceive tactile distances along body part length as smaller than those across body part width. Our analysis then focused on the point of subjective equality (PSE) which occurred when across and along distances were judged as equal in size. Specifically, we used one-sample *t*-tests to compare the mean PSE on each body part to a ratio of 1, since that is the value that would be expected on the null hypothesis that there is no anisotropy. Statistical tests on PSE values were conducted on the logarithms. These were then converted back to ratios for reporting mean values. Cumulative Gaussian functions were fit for every participant’s responses, using the Palamedes toolbox (Prins & Kingdom, 2009) in MATLAB (Mathworks, Natick, MA, USA).

The exclusion criteria were that participants would be excluded if *R*-squared was below .5 for either body part. This exclusion criteria matches that used in similar studies (Chang & Longo, 2022; Longo, 2017; Longo et al., 2015, 2020; Manser-Smith et al., 2021). Two participants fell below this range and were removed from the study and not included in any analyses.

Raw data and the analysis script are available on the Open Science Framework at <https://osf.io/ea25d/>.

Results

The results are shown in Figure 1. *R*² values showed that psychometric functions had a good fit to the data, accounting for an average of 95.7% of the variance on the hand and 95.3% on the tongue. To investigate anisotropy on each skin surface, we first conducted one-sample *t*-tests comparing mean PSEs to 1. There was clear anisotropy on the hand (*M*: 0.786), $t(37) = -8.82$, $p < .0001$, $d = 1.431$, with distances oriented across hand width judged as larger than those oriented along hand length, consistent with previous studies. There was a similar anisotropy on the tongue

(M : 0.852), $t(37)=-4.34$, $p < .0001$, $d=0.704$, with distances again judged as larger across tongue width than along tongue length. There was no significant difference in the magnitude of anisotropy on the two surfaces tested by comparing PSEs using a paired t -test, $t(37)=1.72$, $p=.093$, $d_z=0.279$. There was no significant correlation between the magnitude of anisotropy on the two surfaces, $r(38)=-.051$.

The slope of the psychometric functions was similar on the hand (M : 6.52, SD : 2.39) and the tongue (M : 7.21, SD : 2.66), $t(37)=-1.29$, $p < .205$, $d_z=0.209$.

There was no correlation between the PSE on the tongue and scores relating to ARFID traits, $r(18)=.092$, $p=.70$, nor with general hunger, $r(16)=-.242$, $p=.334$, or age, $r(36)=-.070$, $p=.677$.

Discussion

Clear anisotropies of tactile distance perception were found on both the hand dorsum and tongue. In both cases, tactile distances oriented across body part width were judged as larger than those oriented along body part length. There was no significant difference in the magnitude of anisotropy on the two body parts. This study adds to the substantial list of studies that have found an anisotropy on the hand dorsum. More importantly, it adds the tongue to the growing list of body parts where a tactile anisotropy is found, which as discussed in the Introduction includes many regions on the limbs, as well as locations on the face, such as the forehead (Fiori & Longo, 2018; Longo et al., 2015, 2020), the cheeks (Longo et al., 2020), and the tongue (this study). Like the majority of previous studies, the illusion on the tongue in this study had a width-based bias. This means that the distances oriented across tongue width are perceived as wider than equivalent distances along tongue length. This pattern has been found on all body parts studied, with just two exceptions, the belly for which there is no apparent anisotropy in healthy individuals (Green, 1982; Longo et al., 2019; Marks et al., 1982) and the lower back, the only part region for which an anisotropy in the opposite direction has been found (Nicula & Longo, 2021; Plaisier et al., 2020).

Tactile signals from the head are carried to the brain predominantly via the trigeminal nerve, which is divided into three main branches, each of which is represented by a distinct set of neurons in the somatosensory cortex (Dreyer et al., 1975). Previous findings of tactile distance anisotropy on the forehead (Fiori & Longo, 2018; Longo et al., 2015) and cheeks (Longo et al., 2020) have shown similar illusions on skin regions innervated by the ophthalmic and maxillary branches of the trigeminal nerve. The tongue, in contrast, is innervated by the mandibular branch of the trigeminal nerve. The present finding of tactile distance anisotropy on the tongue, thus, indicates that qualitatively similar tactile distance illusions are apparent on all

three branches of the trigeminal nerve. The broadly similar tactile illusions found on regions innervated by each branch of the trigeminal nerve suggest that the illusions are not a result of idiosyncrasies of the peripheral innervation of specific body parts, but likely result from features of the central representations of touch in the cortex.

One relevant aspect of the present study is that on the tongue, tactile distances running across the width of the tongue involved the presentation of stimuli on either side of the midline. Several studies have reported categorical perception effects such that tactile distances are perceived as larger when the two points are on opposite sides of joints (de Vignemont et al., 2009; Knight et al., 2014, 2020). It is possible that the body midline could function as a category boundary and produce analogous categorical perception effects. In a recent study (Longo et al., 2020), we investigated this issue on the forehead, comparing the magnitude of anisotropy at the center of the forehead (i.e., with “across” stimuli crossing the face midline) with conditions in which stimuli were presented entirely on the right or left side of the forehead. A similar magnitude of anisotropy was found at all locations, suggesting that categorical perception from the face midline was not a major factor in producing anisotropic illusions. The apparent absence of categorical perception effects from the midline may be due to the phenomenon of “midline fusion” (Manzoni et al., 1989). Indeed, while distal regions such as the fingers may be represented in a predominantly contralateral fashion in the somatosensory cortex, there is evidence that regions near the midline have more robust ipsilateral representations in the somatosensory cortex (Conti et al., 1986; Dreyer et al., 1975; Iwamura, 2000; Jones & Powell, 1969b) and more rich callosal connections connecting the left and right somatosensory cortices (Jones & Powell, 1969a; Killackey et al., 1983; Shanks et al., 1985). Studies in humans about bilateral somatosensory tongue representations have reached divergent conclusions. While neuroimaging studies using magnetoencephalography have found strikingly early bilateral responses following tongue stimulation (Sakamoto et al., 2008; Tamura et al., 2008), studies using ECoG electrodes to directly stimulate the cortex have found that somatosensory cortex stimulation elicits sensations predominantly on the contralateral side of the tongue (Picard & Olivier, 1983; Roux et al., 2018; Tanriverdi et al., 2009).

Perceptual distortions on the face have not been limited to tactile distance perception (Longo, 2022). Studies using explicit judgments of face size have tended to similarly find overestimation of face width, using measures such as the image marking procedure (Meermann, 1983), the moving caliper procedure (Dolan et al., 1987; Halmi et al., 1977), the adjustable light beam apparatus (Dolce et al., 1987; Thompson & Thompson, 1986), proprioceptive localization judgments (Longo & Holmes, 2020; Mora

et al., 2018), as well as several other tasks (Bianchi et al., 2008; D'Amour & Harris, 2017; Fuentes et al., 2013). The link between distortions of tactile distance perception and more explicit body size judgments remains uncertain, both in the case of the face specifically and of the body more widely. The qualitatively similar overestimation of body part width found in both cases, however, suggests that there may be important links between these aspects of body representation. That the body image of the tongue operates according to similar principles as for other body parts is supported by reports of phantom tongue experiences in people who have had their tongue removed (Drake et al., 2022; Hanowell & Kennedy, 1979), as well as reports of subjective tongue swelling in epileptic aura (Ionășescu, 1960; Penfield & Jasper, 1954). In both these cases, misperceptions of the tongue are highly similar to those reported for other body parts. To our knowledge, no studies have investigated explicit judgments of tongue size and shape. Future work should investigate whether the perceptual overestimation of face size found for external facial features also affects body image for the inside of the mouth, and how this is linked to the tactile distortions described in the present study.

In the present study, there was no correlation between hunger scores and tactile distance anisotropy on the tongue. This result contrasts with the study of Crutchfield et al. (2018) who found that hungry participants perceived the size of objects in their mouths as larger than sated participants. We can only speculate about the reasons for this difference between studies, but we wish to highlight four points relevant to this issue. First, this correlation in our study was based on a small sample ($N=18$), which makes the results tentative. Second, hunger was not explicitly manipulated in our study and the between-subjects variability in measured hunger was relatively small. Third, because we measured tactile distance *anisotropy*, rather than absolute perceived tactile distance, we would only expect a correlation between hunger and PSEs if hunger *differentially* influenced perceived size in the mediolateral and proximodistal axes of the tongue. If, as suggested by Crutchfield and colleagues, being hungry simply makes objects feel *larger*, no change in PSE would be expected, since this would affect both axes in the same way. Finally, there may also be important differences between the perception of the size of continuous objects (as in the study of Crutchfield and colleagues) and of the distance between two distinct touches (as in the present study). A recent study by Tamè et al. (2022) found qualitatively different patterns of anisotropy for these aspects of perceived size, and it is possible that they are differentially affected by hunger.

In conclusion, the present results generalize findings of tactile distance anisotropy beyond the body surface, showing anisotropy on the tongue similar to that found on several other parts of the body. These findings provide further

evidence that the overestimation of tactile distances aligned with body width is a consistent feature of touch across many parts of the body. The link between spatial distortions of touch on the tongue and clinical conditions such as ARFID and dysphagia is unclear. It is notable that while dysphagia is a common consequence of aging (Clavé & Shaker, 2015; Serra-Prat et al., 2011), there was no apparent correlation between age and anisotropy on the tongue in this study, though the sample size was comparatively small. It will be interesting in future research to investigate tactile distance perception on the tongue in clinical populations and in more elderly samples.


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