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Examining central biases in somatosensory localization: Evidence from brain-damaged individuals

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ABSTRACT

How does the brain localize touch under conditions of uncertainty caused by brain damage? By testing single cases, previous work found mislocalization of touch toward the center of the hand. We investigated whether such central bias changes as a function of uncertainty in somatosensory system. Fifty-one brain-damaged individuals were presented with a tactile detection task to establish their tactile threshold, and a tactile localization task in which they localized suprathreshold stimuli presented at different locations on the hand. We predicted that with increased somatosensory uncertainty, indexed by higher detection thresholds, participants would more likely to localize the stimuli toward the center of the hand. Consistent with this prediction, participants' localization errors were biased towards the center of the hand and, importantly, this bias increased as detection threshold increased. These findings provide evidence that instead of showing random errors, uncertainty leads to systematic localization errors toward the center of the hand or the center of the stimulus distribution, which overlapped in the present study. We discuss these findings under different frameworks as potential mechanisms to explain biases in tactile localization subsequent to brain damage.

1. Introduction

After tactile stimulation, somatosensory system activity leads to a percept at a particular location on the skin surface (Longo et al., 2010; Medina and Coslett, 2010). This process, which involves converting information from distorted somatosensory maps to a veridical representation of the skin surface, often results in biased responses (Taylor-Clarke et al., 2004; see Medina and Coslett, 2016 for a review). Furthermore, tactile acuity varies widely by body part (Johnson and Phillips, 1981; Van Boven and Johnson, 1994), with two-point discrimination threshold ranging from approximately 1 mm on the tongue to 50 mm on the back (Peters and Schmidt, 1991; Sato et al., 1999). These differences in acuity can result in variability regarding the uncertainty of sensory input for different skin surfaces. Do differences in uncertainty also lead to systematic *biases* in tactile localization?

In previous research, this question has been examined by manipulating signal strength in neurologically intact individuals. For example, Steenbergen et al. (2014) examined tactile localization of electrical stimuli presented to the forearm at different intensity levels. Participants were asked to localize the stimuli by pointing at a picture of their forearm presented on a tablet over the stimulated arm. As expected, they observed that variability in localization judgments increased as stimulus intensity decreased, indicating higher uncertainty with weaker stimuli. Along with this, participants also demonstrated a systematic bias toward the center of the arm that increased as stimulus intensity decreased, suggesting that the brain relies on additional information under sensory uncertainty. In a different study, weaker stimuli were localized not only toward the center of the body part (i.e., forearm), but also toward the center of the stimulus distribution, demonstrating multiple sources of information contributing to localization bias (Brooks et al., 2019).

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Localization biases have also been reported in individuals with increased somatosensory uncertainty due to brain damage (Rapp et al., 2002; also see Paillard et al., 1983). Rapp et al. (2002) tested two left hemisphere damaged individuals on a tactile localization task on the dorsal and ventral hand surfaces. Interestingly, both participants showed a systematic bias on both surfaces for tactile localization: near the actual stimulus, but consistently shifted towards the center of the hand, demonstrating shrinkage in perceived tactile space relative to the hand surface. Other reports of tactile localization due to brain damage also show central biases of varying amounts (Birznieks et al., 2016; Medina and Rapp, 2014). These findings provide evidence for systematic directional localization bias rather than random errors after brain damage, indicating common mechanisms underlying tactile localization under central somatosensory noise.

In the present study, we investigated whether central bias in tactile localization increases as a function of somatosensory uncertainty due to brain damage. A group of unselected brain-damaged individuals underwent a tactile detection and localization task. The detection task was designed to assess noise in the somatosensory system, with increasing thresholds corresponding to increasing noise. Next, we examined localization biases for suprathreshold tactile stimuli presented to the hand. If central bias observed in tactile localization is related to the degree of uncertainty of the somatosensory system, we expect central bias to increase as a function of higher detection thresholds.

2. Materials and methods

2.1. Participants

Sixty-nine individuals with brain-damage due to stroke with heterogeneous lesions took part in the present study. Exclusion criteria of this study were: i) severe motor impairment that prevented the execution of motor response on the tactile localization task; ii) a false alarm rate (i.e., participants reported a stimulation in catch trials) above 30% in the tactile detection task (see Tactile detection task below). Eighteen participants did not meet these criteria and were excluded from the study. The final sample was composed of 51 individuals (23 left hemisphere lesions; 20 females; age $M = 64.1$ years, $SD = 10.8$ years). All participants were consented, and the study was approved by the Institutional Review Board at the University of Delaware.

2.2. Procedure

2.2.1. Tactile detection task

The participant was seated in front of a table with the tested hand aligned with the body midline, placed on the table and palm facing up. Tactile detection was measured using a set of 20 Semmes-Weinstein monofilaments (North Coast Medical Inc., CA, USA, ranging from 0.008 to 300 g force) presented on the palmar side of the distal segment of the middle finger of each hand. Testing on the more sensitive skin palmar surface allowed us to best index differences in tactile detection due to stroke.

To determine detection threshold, we used a weighted 1-down, 1-up staircase procedure (Liu et al., 2020). In each block, participants were first touched with the thickest filament; if they were able to detect the stimulus, they were presented with a filament two levels thinner in the next trial. If participants did not detect the stimulus, they were then presented with a filament one level thicker. After each stimulation, the experimenter asked "Did you feel anything?" and participants verbally responded Yes or No. Participants had their eyes closed during the entire block. To differentiate hits from false alarms, catch trials where the experimenter approached without touching the hand were randomly interspersed on an average of 16.3% of trials (range 9.1%–20%). Each block ended after at least 10 reversals, though a few blocks ended early due to participant fatigue or related issues. In cases where the participant failed to respond to the heaviest filament (300 g) on four consecutive trials, the experiment ended and the participant's threshold was considered as 300 g (filament No. 20). On average, participants performed the task with 14 reversal points (range 5–24). Each hand was tested in one block. The first hand to be tested was counterbalanced across participants.

2.2.2. Tactile localization task

Participants placed the tested hand on a table, aligned with their body midline and palm facing down. A filament three intensities above the participant's detection threshold was manually presented by an experimenter at 22 different locations on the hand dorsum (see Rapp et al., 2002; Liu et al., 2020; see Fig. 2, black dots). These locations were pre-defined and were marked on a hand template. We tested on the dorsum as individuals suffering from stroke present different degrees of muscle tone that can make presenting stimuli to multiple locations on the palmar surface difficult. Furthermore, localization biases are more consistent and likely to be observed on the dorsum than palmar surface of the hand (Mancini et al., 2011). Participants kept their eyes closed during stimulus presentation; immediately after the stimulation, participants opened their eyes and pointed with the index finger of the untested hand at the location on the tested hand where they felt the touch. A second experimenter recorded the participant's response on a standardized hand template (i.e., a drawing of the hand with basic hand landmarks) on a piece of paper (Rapp et al., 2002; Liu et al., 2020). This method has been used in previous work to test tactile localization abilities in stroke individuals (Paillard et al., 1983; Rossetti et al., 1995; Rapp et al., 2002; Liu et al., 2020). The second experimenter was blind to the expected pattern of results. All testing sessions were videotaped and recorded, and responses on the hand drawing were confirmed with the videos offline. To ensure that participants were able to make accurate motor responses, the experimenter asked the participant to point to various locations on their own hand and on the table before testing each hand. All analyzed participants were competent in making motor responses.

For each hand, participants were presented with two blocks of 22 trials in randomized order (one trial for each location in each block; two trials for each location in total). The order of blocks was counterbalanced using ABBA design, with the starting hand counterbalanced across participants. Trials in which the participant did not perceive any stimulation were excluded from the analysis.

2.3. Data analysis

2.3.1. Tactile detection

Tactile detection threshold was computed as the average filament number (1–20) across all reversal points. We ran a mixed-design ANOVA on tactile detection threshold, with damaged hemisphere (left brain damage LBD, right brain damage RBD) as a between-subjects factor and hand side (contralesional hand, ipsilesional hand) as a within-subjects factor.

2.3.2. Tactile localization

To quantify mislocalization, we first calculated *overall localization error* as the straight-line distance between perceived and actual stimulus location (Fig. 1). Overall localization error was analyzed using a mixed-design ANOVA with damaged hemisphere (LBD, RBD) as a between-subjects factor and hand side (contralesional hand, ipsilesional hand) as a within-subjects factor.

We next examined whether localization bias occurred toward the center of the hand. For this purpose, we first calculated *directional bias* as signed distance between the perceived and actual stimulus location along the proximodistal and mediolateral axes separately (Fig. 1). Positive values indicate distal (towards the fingers) and lateral (away from the body midline) bias, negative values indicate proximal (towards the wrist) and medial (towards the body midline) bias. Next, we tested whether *directional bias* changed as a function of actual stimulus location

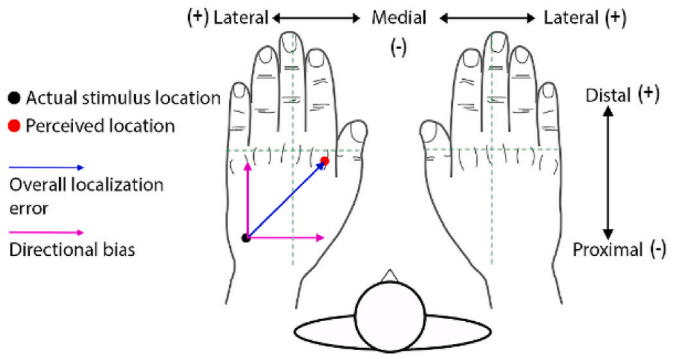

Fig. 1. Illustration of dependent variables of tactile localization: overall localization error and directional bias. Signs denote the direction of direction bias. The intersection between the dotted green lines is defined as the geometric center of the hand. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

relative to the geometric center of the hand (defined as the midpoint between the most distant points on the hand template along the mediolateral and distal-proximal axes, Fig. 1). If tactile localization was biased toward the center of the hand, there would be more *medial* bias for stimuli on more *lateral* locations and vice versa. Similarly, there would be more *proximal* bias for stimuli at more *distal* locations and vice versa. Importantly, if central bias is caused by uncertainty in sensory information, there would be a stronger central bias as tactile detection threshold increased.

We ran linear mixed-effects models to test these predictions. In a linear mixed model, participant is treated as a random factor by modelling random intercepts and random slopes, allowing baseline performance and the effect of fixed factors to vary across individuals. As a result, linear mixed model is more powerful in capturing the variability in the performance within and across individuals compared to ANOVA (Kliegl et al., 2011). Confidence intervals were computed using the model_parameters function of parameters package in R.

Mediolateral and proximodistal biases were analyzed separately. The dependent variable was directional bias in each dimension, and the fixed factors of interest were actual stimulus location relative to the center of the hand in the corresponding dimension (named "centered stimulus location" hereafter), detection threshold, and hand side (contralesional hand or ipsilesional hand). All factors inserted in the model were mean-centered such that each score was recoded as the difference from the mean, except for affected side which was dummy coded. We used a stepwise approach in which we created a series of models by sequentially adding one or more factor(s) of interest and their interactions. Specifically, we created a null model with no fixed factors and only random intercepts of participants. We first compared a model containing a single fixed factor with this null model. If the fixed factor improved the model fit, it was kept in the final model. Another factor was then added to this model and its contribution was tested by comparing this new model with the previous best model. In all models, participants were inserted as random intercepts. To maximize model fit, each factor of interest was also included as a random slope unless the model did not converge (Barr et al., 2013). Models were compared with a log-likelihood ratio test using the ANOVA function in R. This function was also used to estimate the F-statistics of the final model. To explore the observed significant interactions from linear-mixed models, we used the simple slope method (Aiken et al., 1991; West et al., 1996) for post-hoc tests. All analyses were conducted on trial-by-trial data without averaging trials within a condition, and were implemented using the lmer function in the lme4 package in R (version 3.6.2).

For illustrative purpose, detection thresholds were recoded as a categorical variable following guidelines for Semmes-Weinstein monofilaments (North Coast Medical Inc., CA, USA): Normal performance (score ≤ 4; contralesional n = 19; ipsilesional n = 33); diminished light touch ($4 <$ score ≤ 6; contralesional n = 15; ipsilesional n = 15); diminished protective sensation ($6 <$ score ≤ 10; contralesional n = 7; ipsilesional n = 3); loss of protective sensation ($10 <$ score ≤ 19; contralesional n = 5); deep protective sensation only (score >19; contralesional n = 5). Detection threshold was treated as a continuous variable in data analyses.

3. Results

3.1. Tactile detection

Tactile detection threshold was analyzed in a mixed-design ANOVA with damaged hemisphere as a between-subjects factor and hand side as a within-subjects factor. As expected, we found a main effect of hand side ($F_{1,49} = 14.8$, $p < .001$): tactile detection thresholds were higher on the contralesional hand ($M = 6.80$, $SD = 5.38$, 95% CI = [5.32, 8.27], than ipsilesional hand ($M = 3.70$, $SD = 1.25$, 95% CI = [3.35, 4.04]. Neither the main effect of damaged hemisphere ($F_{1,49} = 1.6$, $p = .20$; RBD: $M = 5.68$, $SD = 4.86$, 95% CI = [4.40, 6.95]; LBD: $M = 4.74$, $SD = 3.15$, 95% CI = [4.27,7.08]) nor the interaction ($F_{1,49} = 1.7$, $p = .19$) were significant.

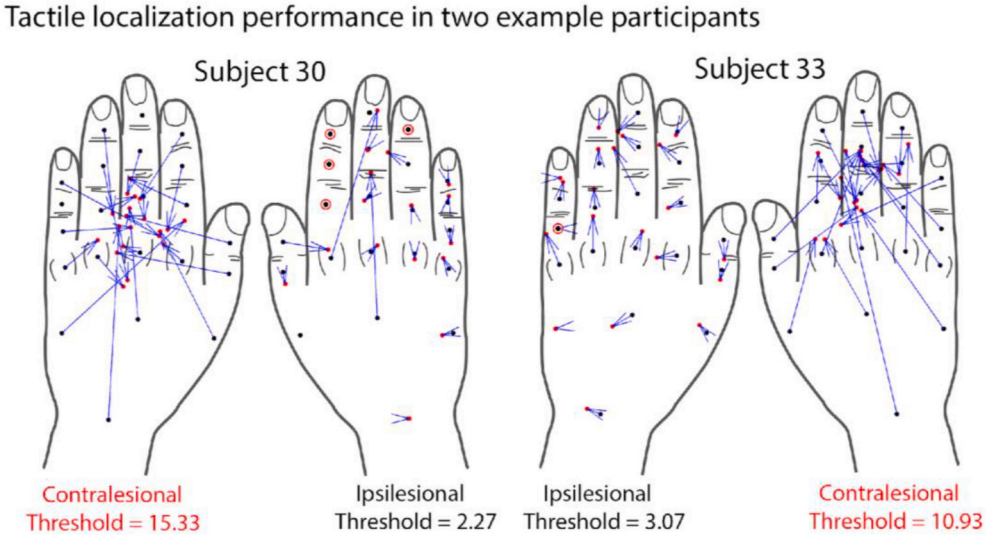

Fig. 2. Localization bias in two selected participants with right (Subject 30) and left (Subject 33) hemisphere lesion respectively. Black dots denote actual stimulus locations; mean localization judgments for each location are shown in red. Blue arrows points from the stimulus location to the mean localization judgment. Red circles around black dots denote accurate judgments. Detection thresholds (in filament number) are reported for the contralesional and ipsilesional hand. Both participants show a strong localization bias toward the center of the hand along with a higher tactile detection threshold on the contralesional hand compared to the ipsilesional hand. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2. Tactile localization

Overall, participants felt the stimulus on 78% of trials (74% on the left and 81% on the right hand; 83% of trials on the fingers, 67% on the palms).

We first performed a mixed-design ANOVA on overall localization error, with damaged hemisphere as a between-subjects factor and hand side as a within-subjects factor. As expected, the analysis showed a significant main effect of hand side ($F_{1,49} = 12.9$, $p < .001$), with a greater error on the contralesional ($M = 16.1$ mm, $SD = 20.1$ mm, 95% CI = [10.5 mm, 21.6 mm]) than the ipsilesional hand ($M = 8.6$ mm, $SD = 11.9$ mm, 95% CI = [5.3 mm, 11.8 mm]). The main effect of the damaged hemisphere ($F_{1,49} = 1.7$, $p = .19$; RBD: $M = 14.4$, $SD = 13.7$, 95% CI = [10.89 mm, 18.06 mm]; LBD: $M = 13.09$, $SD = 9.82$, 95% CI = [10.25 mm,15.92 mm]) or the interaction between damaged hemisphere and affected side ($F_{1,49} = 1.8$, $p = .18$) was not significant.

Next, we examined directional bias using linear mixed models, with centered stimulus location, tactile detection threshold, and hand side as fixed factors. If participants made responses towards the center of the hand, a relationship between directional bias and stimulus location would be predicted – more proximal bias for more distal targets and vice versa, and more medial bias for more lateral targets and vice versa. Moreover, we predicted a stronger central bias with higher detection thresholds and on the contralesional hand when compared to the ipsilesional hand. Therefore, an interaction between centered stimulus location and tactile detection threshold, and between centered stimulus location and hand side was expected. Finally, given a higher tactile detection threshold on the contralesional versus ipsilesional hand, a three-way interaction between centered stimulus location, tactile detection threshold, and hand side was expected. Specifically, we predicted a larger bias toward the center of the hand for stimuli that occurred further from the hand center, and this relationship would be more prominent for higher detection thresholds on the contralesional hand. Fig. 2 shows localization judgments of two participants with high detection thresholds and a stronger central bias on the contralesional hand compared to the ipsilesional hand.

Fig. 3 displays directional bias as a function of centered stimulus location and tactile detection threshold for each hand, with detection threshold recoded as a categorical variable for illustrative purposes. Results from linear mixed models supported our predictions. As predicted, a main effect of centered stimulus location was found for both mediolateral ($F_{1,3394} = 165$, $p < .001$) and proximodistal bias ($F_{1,3412} = 263$, $p < .001$). Specifically, there was a stronger medial bias for more lateral stimulus locations and vice versa (Fig. 3, top) and a stronger proximal bias for more distal stimulus locations and vice versa (Fig. 3, bottom). These findings demonstrate a general tendency of localizing touch toward the hand center.

Next, we also found an interaction between centered stimulus location and tactile detection threshold for both mediolateral ($F_{1,3388} = 44.9$, $p < .001$) and proximodistal ($F_{1,3407} = 42.6$, $p < .001$) bias. Specifically, the effect of centered stimulus location was stronger for higher detection thresholds (Fig. 3, red and purple lines), demonstrating more central bias with larger somatosensory noise. In addition, interaction between centered stimulus location and hand side was significant for both mediolateral ($F_{1,3395} = 21.9$, $p < .001$) and proximodistal ($F_{1,3413} = 20.1$, $p < .001$), with a stronger effect of centered stimulus location on contralesional versus ipsilesional hand (Fig. 3).

The final model included a three-way interaction between centered

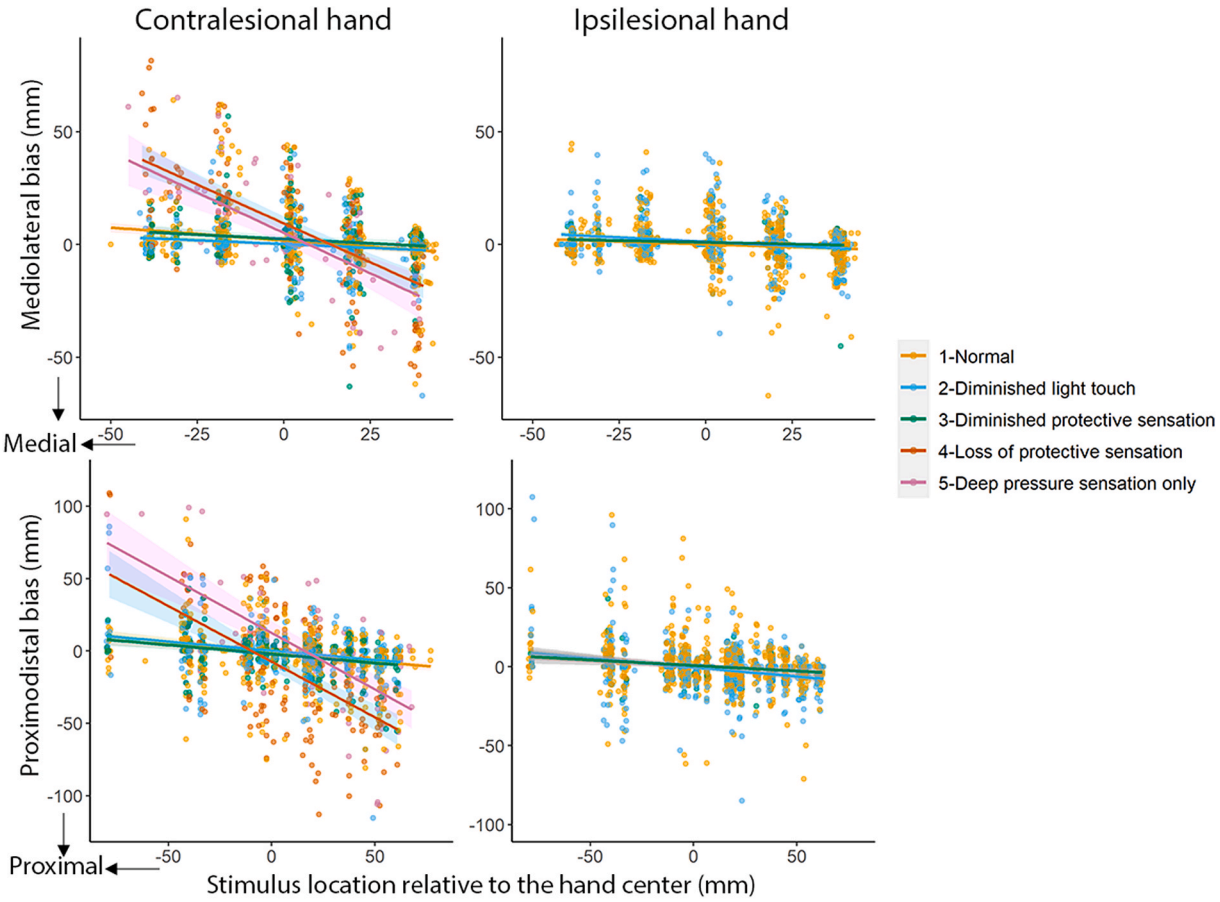

Fig. 3. Directional bias (on the y-axis) as a function of centered stimulus location (x-axis) and participants' threshold (categorized and shown in lines of different colors) for the contralesional (left panel) and ipsilesional (right panel) hand. Larger negative slope represents stronger central bias. Each dot represents a trial. Shadowed areas surrounding the regression lines represent 95% CI.

stimulus location, tactile detection threshold, and hand side for both mediolateral ($F_{1,3406} = 27.09$, $p < .001$; in comparison with a model including the interaction between affected side and centered stimulus location and the main effect of tactile detection threshold: logLik = −12948, χ^2 (3) = 312.87, $p < .001$; see Table S1 in Supplementary Materials for all model comparisons) and distal-proximal ($F_{1,3388} = 22.7$, $p < .001$; in comparison with a model including the interaction between affected side and centered stimulus location and the main effect of tactile detection threshold: logLik = −14179, χ^2 (3) = 373.9, $p < .001$) dimensions. As stated in the Methods, we investigated the three-way interactions using the simple slope methods (see Supplementary Materials for a complete report of this analysis). Overall, the main result of this analysis was that localization bias was deviated toward the center of the hand (i.e., significant effect of centered stimulus location) when the tactile threshold was high, and this effect occurred for both contralesional ($t > 25$, $p < .001$) and ipsilesional hand ($t > 1.8$, $p < .01$). This effect was also observed with low threshold only when tested with the ipsilesional hand ($t > 1.2$, $p < .01$). These findings are further captured in Fig. 4, with mean localization judgments more clustered toward the hand center for higher detection thresholds and contralesional hand.

Taken together, these findings demonstrate a central tendency in tactile localization toward the center of the hand. Importantly, central bias increased with higher detection thresholds and on the contralesional hand, providing evidence for systematic localization bias as a result of somatosensory uncertainty.

4. Discussion

This study examined the tendency to mislocalize tactile stimuli towards the center of the hand in a large sample of brain-damaged individuals, and whether central tendency increases as a function of somatosensory uncertainty. First, directional localization bias changed as a function of stimulus location relative to the hand center, e.g., stronger proximal bias for more distal locations, demonstrating central bias. Importantly, this central bias increased with tactile detection threshold, indicating a relationship between central bias and somatosensory noise. Past studies investigated tactile localization under different levels of input noise. For example, studies of neurologically-intact individuals showed that central bias on the forearm increases as stimulus intensity weakens (Brooks et al., 2019; Steenbergen et al., 2014). We examined tactile localization under another source of noise, i.e., the level of noise in the participants' somatosensory system subsequent to brain damage. Interestingly, previous work has reported central bias in single cases with parietal lesions affecting the somatosensory cortex (Birznieks et al., 2016; Rapp et al., 2002; Medina and Rapp, 2014). Our work shows that this central bias can be observed in an unselected sample of individuals with stroke presenting a heterogeneous pattern of lesions, suggesting that localization toward the center of the hand is a common mechanism under uncertainty after central changes.

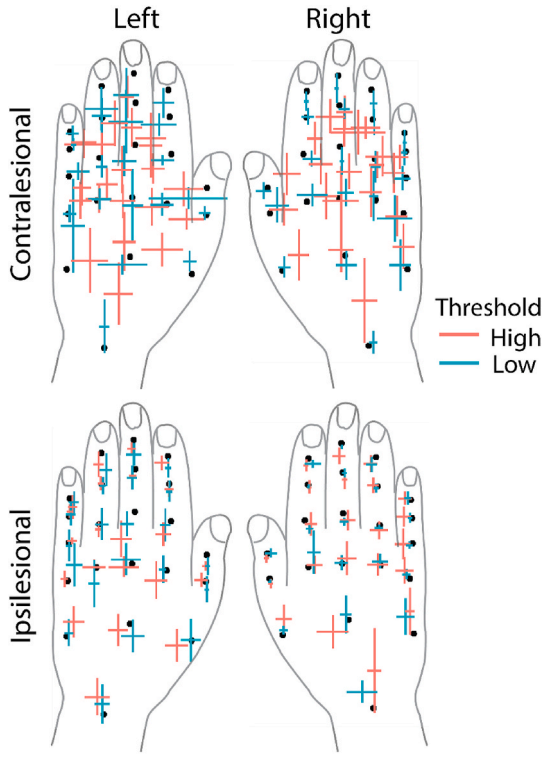

Fig. 4. Mean localization judgments across participants for each location on each hand and side. Black dots denote actual stimulus locations. For illustrative purposes, we used a median split to divide participants into high and low threshold groups. Crosses denote 95% CI. Localization judgments for higher detection thresholds (red markers) are more clustered toward the center of the hand compared with lower detection thresholds (blue markers), especially in contralesional hands. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

What mechanism could underlie this central tendency in both neurologically intact and brain-damaged individuals? One possibility is that these errors reflect a process in which the brain relies on prototypical information under stimulus uncertainty. Huttenlocher, Hedges & Duncan (1991) proposed a category adjustment model to explain biases in memory. In this model, spatial information is represented at two levels: specific (fine-grain) and categorical. At the fine-grain level, the representation of the stimulus is an unbiased distribution of values centered around the actual stimulus location. The categorical level is the potential distribution of stimuli within a specific category. For example, the location of a dot in a circle will be represented in memory based on a distribution centered around its actual location (fine-grain coding), but also at a categorical level (e.g., the remembered quadrant of the circle). Boundaries across categories identify the range of values that are included or not in a specific category. For instance, in the example of the circle, the boundaries will be the delimitation of each quadrant that may vary across individuals. Within each category, a *prototype* is the most representative example of a category (e.g., the center of the quadrant). Importantly, selecting the remembered location involves a weighting of both fine-grain and prototype information that varies as a function of the precision of the fine-grain information. If the fine-grain information regarding the specific event is inexact, individuals would rely more on categorical representation to reconstruct the event and will rely more on a *prototype* response to minimize the error in the reconstruction of the event (Huttenlocher et al., 1991; Ernst and Banks, 2002). This computation can be instantiated by a Bayesian procedure in which the inferred location is a combination of current sensory information (fine-grain representation) and prior knowledge of the distribution of stimuli (i.e., most likely at the center of a category; Cheng et al., 2007).

To test this model, Huttenlocher et al. (1991) used a visual memory task in which participants were asked to remember the location of a stimulus (a dot) inside a circular shape and they varied the degree of noise of fine-grain information (e.g., using a distractor task). In line with the model prediction, participants showed a systematic bias toward the center of the circle quadrant where the dot was located. Importantly, the authors showed that this effect increased in conditions with high degree of uncertainty regarding the location of the dot, e.g., when the presentation of a visual distractor interfered with the encoding of the stimulus location (Huttenlocher et al., 1991; Huttenlocher et al., 1988: Huttenlocher et al., 2007).

Our findings can be accounted for by the category adjustment model (Huttenlocher et al., 1991). For a touch on the hand, tactile localization involves a fine-grain representation of the actual stimulus location and may also involve a categorical representation that the touch occurred within the hand boundary, with the putative prototype value being the center of the hand. The final judgment of spatial location is a weighted

sum of these two sources of information, with weighting proportional to their relative precision. As sensory noise increases, prototype information is more strongly weighted, and would result in more central localization bias on the hand.

How might categorical information influence tactile localization? It has been proposed that somatosensory information from primary somatosensory cortex is mapped onto a representation of body size and shape (body form representation, Medina and Coslett, 2010; see also Longo et al., 2010; Taylor-Clarke et al., 2004; Head and Holmes, 1911). One possibility is that the central bias occurred during this mapping process. When sensory information is less noisy, neural responses in primary somatosensory cortex are more fine-tuned, leading to a more precise mapping between S1 and body form representation, e.g., neurons representing the index finger in S1 map to the "index finger" in the body form representation. However, when sensory information is noisy, either due to reduced quality of input or central damage, mapping between S1 and the body form representation becomes less exact and only activate the representation of a categorical body part. We propose that in these cases categorical information is more strongly weighted.

If this is a potential mechanism, then how could a category be defined? Our experiment was not designed to address this question, but we propose two possibilities. First, a category may be defined by the boundaries of a specific body part. A number of studies show that body part boundaries influence tactile localization, with higher accuracy near body part boundaries (Hamburger, 1980; Cholewiak and Collins, 2003; Cody et al., 2008). More specifically, the wrist has been shown to be a body part boundary that influences tactile localization. Other studies have shown that tactile distance perception changes near joint boundaries (De Vignemont et al., 2009; Le Cornu Knight et al., 2014; Le Cornu Knight et al., 2017; Shen et al., 2018). It has been proposed that body part boundaries segment the body, and that these divisions influence tactile perception. In our initial analysis, we made an *a priori* assumption that the hand would be the categorical unit with the wrist as a boundary. However, it is also possible that there are other potential categorical distinctions. Because the fingers and the palm area have different anatomical structures and functions, it is possible that the brain represents the finger and palm areas as two categories. Under this hypothesis, localization judgments would form two clusters, one near the center of the fingers (i.e., around the center of the middle finger), the other near the center of the palm. Furthermore, given that each finger can move individually, it is possible that stimuli on each finger are represented as within a separate category. Unfortunately, our study was not optimally designed to address this question. As an exploratory analysis, we created a model in which there were two categories, one for the fingers and one for the palm (see Supplemental Section, Additional Analysis), and compared this model with the original model using hand center. Our current dataset does not distinguish which model is better, and more experiments that directly examine these hypotheses should be conducted.

An alternative, non-exclusive possibility is that the category is defined by the distribution of tactile stimuli. For instance, Brooks et al. (2019) showed a stronger tendency in healthy individuals to mislocalize tactile stimuli towards the center of the stimulated forearm for weaker versus stronger stimuli, generally consistent with our prototype account. However, in an additional experiment, they displaced the center of the stimulus distribution from the center of the arm to either the distal or proximal half of the forearm. They found that, in addition to a systematic shift towards the arm center, responses to weaker stimuli were biased toward the center of the stimulus distribution. These results indicate that stimulation history influences tactile localization, likely by forming a spatial prior of stimulus distribution (Tamè et al., 2019). Similarly, in two individuals who suffered from somatosensory cortical damage, Medina and Rapp (2014) showed that tactile localization judgments were biased in the direction of the preceding stimulus. Unfortunately, our experiment was not designed to differentiate between these two possibilities. Future work should address this point and investigate directly whether the prototypical response reflects the center of the stimulus distribution, body part, or both.

One limitation of our work is that information about brain lesions were not available for all participants and therefore the neuroanatomical basis of the central bias was not directly investigated. Our primary purpose was to test for possible relationships between the level of noise in the somatosensory processing and central bias and we did not aim to determine whether this 'noise' derived from a damage to the somatosensory system or other regions. However, we believe that this an important question and future studies should directly investigate the neuroanatomical underpinnings of the central bias.

Finally, we found no difference in tactile detection and overall localization error between left- and right-hemisphere damage. This is in contrast with right-hemisphere dominance in higher level visuospatial attention functions, with more frequently and severely caused spatial neglect by damage to parietal cortex in the right hemisphere (Albert, 1973; Weintraub and Mesulam, 1987; Karnath and Rorden, 2012). While neglect can also cause deficits in tactile perception on the contralesional side of the body (Moscovitch and Behrmann, 1994), our finding of an effect of hand side (contralesional, ipsilesional) without effects of damage side suggests that our tactile detection and localization tasks more likely involves basic sensory processes and are supported mainly by the contralateral hemisphere.

To summarize, our work demonstrates in a large sample of participants with brain damage that errors in tactile localization follow systematic patterns toward the center of the hand. Importantly, these biases depend on the level of impairment in the ability to detect tactile stimuli. These findings provide evidence that after brain damage, the brain relies on prior information in localizing touch rather than making random errors. Future studies are needed to identify different sources of prior information that contribute to central localization bias.

Author contributions

All authors developed the study question. J. Medina designed the experiments. M. Grzenda and J. Medina performed data collection. E. Ambron, Y. Liu, and M. Grzenda analyzed data under J. Medina's supervision. E. Ambron and Y. Liu drafted the manuscript under J. Medina's supervision. All authors approved the final version of the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2021.108137.

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