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Keywords: perceptual integration, salience, somatosensory aggregation, tactile, thermal

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Abstract: Psychological characterisation of sensory systems often focusses on minimal units of perception, such as thresholds, acuity, selectivity and precision. Research on how these units are aggregated to create integrated, synthetic experiences is rarer. We investigated mechanisms of somatosensory integration by asking volunteers to judge the total intensity of stimuli delivered to two fingers simultaneously. Across four experiments, covering physiological pathways for tactile, cold and warm stimuli, we found that judgements of total intensity were particularly poor when the two simultaneous stimuli had different intensities. Total intensity of discrepant stimuli was systematically overestimated. This bias was absent when the two stimulated digits were on different hands. Taken together, our results showed that the weaker stimulus of a discrepant pair was not extinguished, but contributed less to the perception of the total than the stronger stimulus. Thus, perception of somatosensory totals is biased towards the most salient element. 'Peak' biases in human judgements are well-known, particularly in affective experience. We show that a similar mechanism also influences sensory experience.

Suggested Reviewers:

London, UK, 03 May 2016

To: Prof. Natalie Sebanz

Associate Editor

Cognition

Dear Prof. Sebanz,

Enclosed please find the second revision of our manuscript entitled "Salience-driven overestimation of total somatosensory stimulation" (COGNIT-D-14-00756R2). We have updated the manuscript to address each of Reviewer 1's comments, including the addition of a Bayesian analysis of the data from Experiment 3 (see p.20, lines 478-489). We also address these comments on a point-by-point basis in the enclosed response letter.

We look forward to hearing your thoughts on the revised manuscript.

Yours sincerely,

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*Response to Reviewers

Reviewers' comments:

Reviewer #1: Major comments

1. The newly added Experiment 2 nicely demonstrates that the overall intensity judgment didn't solely based on the strongest stimulus in the discrepant pair. However, the authors should consider a better way to introduce the experiment in the manuscript. In its current form, it would be unclear to readers why the experiment is important and necessary. A way to improve it is to clearly state that Experiment 2 was done to check whether the results from Experiment 1 support the hypothesis of 'peak-biased' integration.

Authors: We agree that the rationale for Experiment 2 was not made clear enough. We have now revised the Introduction to clarify that Experiment 2 was done to check whether the overestimation bias we found in Experiment 1 was due to extinction of the weaker stimulus, or to peak-biased aggregation (p. 5, lines 137-141).

2. The major implication of Experiment 3 is based on null results and the authors couldn't directly show whether it is due to lack of statistical power. The authors should use Bayes factors (see the reference below) to check whether their non-significant results support the null hypothesis, or whether the data are just insensitive.

Dienes, Z. (2014). Using Bayes to get the most out of non-significant results. Frontiers in Psychology, 5, 781.

Authors: We thank the reviewer for this helpful suggestion. We have now re-run the analysis of the data from Experiment 3 using Bayesian statistics (p. 20, lines 478-489). The Bayes factor (null/alternative) is 4.00, indicating that our data are not under-powered, and do in fact support the null hypothesis that the overestimation bias does not occur when the two stimuli are delivered to different hands.

3. The structure of the Discussion should be revised. The authors should discussed about the three possible explanations to their findings sequentially. The ones that can't provide fully support to their results, such as filling-in in LN574-586 and lateral inhibition in LN 620-639 should come first and the most likely one, peak-bias integration in LN 562-573, should come last.

Authors: We again agree with the reviewer. We have now changed the structure of the Discussion according to the reviewer's suggestions, to provide a more readable and orderly explanation of our findings (pp. 24-25, lines 559-614).

4. LN603-619 If the authors want to discuss about thermal referral, they should provide a

better description on it and discuss its similarity to the overestimation effect that they found.

Authors: After carefully considering this point, we have decided that a comparison between thermal referral and our overestimation bias is not necessary, and makes the flow of our discussion difficult to follow. However, thermal referral is relevant for other reasons, as well. Thus, we now mention it in the Introduction (p. 4, lines 112-118), and we consider it in the context of a possible filling-in mechanism in the Discussion (p. 25, lines 593-595).

Minor comments

1. More details should be provided for 'peak' bias in the Introduction.

Authors: We have now added further description of affective peak biases to the Introduction (p. 4, lines 87-91).

2. LN 97-98 'Neurons capable of responding to inputs on any finger are present at later levels of the somatosensory hierarchy…' Please clarify what exactly those later levels are.

Authors: We now specify that those citations refer to the secondary somatosensory cortex (p. 4, line 102).

3. LN 522 Replace spatial summation with spatial integration. Spatial summation is typically used to refer to the dependence of apparent intensity on stimulated area or the trade-off between the physical intensity and the stimulated area to keep a constant apparent intensity.

Authors: We have replaced 'spatial summation' with 'spatial integration' throughout the manuscript (p. 13, line 333; p. 23, line 536).

4. Please explain what 'iconic' storage means.

Authors: Iconic storage refers to very short term memory in a sensory form (Sperling, 1960). We have added this classic definition to our discussion of somatosensory iconic memory (p. 24, line 564).

Reviewer #2: In the present version of the manuscript, the authors included an additional experiment and clarified their previous interpretations. In addition they have replied to all my previous concerns. Therefore, I feel that the current reviewed version of the manuscript has been improved and that it is now suitable for publication on Cognition.

Title: Salience-driven overestimation of total somatosensory stimulation

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* Equal Contribution

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Abstract

Psychological characterisation of sensory systems often focusses on minimal *units* of perception, such as thresholds, acuity, selectivity and precision. Research on how these units are *aggregated* to create integrated, synthetic experiences is rarer. We investigated mechanisms of somatosensory integration by asking volunteers to judge the total intensity of stimuli delivered to two fingers simultaneously. Across four experiments, covering physiological pathways for tactile, cold and warm stimuli, we found that judgements of total intensity were particularly poor when the two simultaneous stimuli had different intensities. Total intensity of discrepant stimuli was systematically overestimated. This bias was absent when the two stimulated digits were on different hands. Taken together, our results showed that the weaker stimulus of a discrepant pair was not extinguished, but contributed less to the perception of the total than the stronger stimulus. Thus, perception of somatosensory totals is biased towards the most salient element. 'Peak' biases in human judgements are well-known, particularly in affective experience. We show that a similar mechanism also influences sensory experience.

Keywords: perceptual integration, salience, somatosensory aggregation, tactile, thermal

Highlights

- Participants judged the total intensity of two somatosensory stimuli
- When stimulus intensities were discrepant, the total was overestimated
- These findings indicate a 'peak' bias in perceptual integration
- This process could contribute to somatosensory scene perception

Introduction

Our perception of the environment around us is fundamentally incomplete, yet it permits us to interact successfully with the world. Perception may be limited for two very different reasons. First, a stimulus may not generate an afferent signal to the brain, because sensory receptors are lacking, or too weakly activated. Second, a stimulus may be incorrectly perceived because the central capacity for conscious perception is not available to represent it. That is, perceptions can be affected by failures of transduction and afference, but also by limitations of central perceptual bandwidth. The latter are often discussed under the heading of 'selective attention'. The bandwidth of most perceptual channels is profoundly limited. For example, studies of touch suggest that it is effectively impossible to perceive three or more tactile stimuli simultaneously (Gallace, Tan, & Spence, 2006; Plaisier, Bergmann Tiest, & Kappers, 2009).

As a result, we generally perceive a small subset of the stimuli that impinge on the receptor surface. Many studies of perception focus on best-case processing performance for this selected subset (Paffen, Tadin, te Pas, Blake, & Verstraten, 2006; Sathian & Zangaladze, 1996; Tadin, Lappin, Gilroy, & Blake, 2003; Van Boven & Johnson, 1994). In this paper, we consider how a perceptual system with limited bandwidth can provide broad perception of entire stimulus sets. Specifically, we asked participants to report the *total* perceived intensity of a number of simultaneous stimuli. This situation represents a challenge for perceptual systems wired for selectivity.

Salient information from an unselected channel can sometimes enter consciousness, as in the cocktail party effect (Cherry, 1953). In the case of touch, Tinazzi, Ferrari, Zampini, and Aglioti (2000) described a patient with left tactile extinction. When simultaneously given a salient stroking stimulus on the left hand and a subtler touch stimulus on the right hand, the patient perceived a stroking stimulus on the right hand. Information from both left and right stimuli was clearly processed at some level, but a pathologically-limited bandwidth (Driver & Vuilleumier, 2001) led to the quality of the left-hand stimulus being incorrectly linked to the location of the right-hand stimulus. In healthy participants, a tactile distractor stimulus interferes with perception of a target stimulus in the same modality, both within and between hands (Tamè, Farnè, & Pavani, 2011). Thus, even when bandwidth limitations or selective attention prevent full processing, some features of an unselected stimulus may be perceived. Salience—whether defined by stimulus intensity, quality or affect—may play a key role in determining which elements of stimulation enter into conscious awareness. Moreover, the most salient stimuli may have a disproportionately large influence on the perceptual scene as a whole, similar to the 'peak' bias (Fredrickson & Kahneman, 1993) found in the literature on human affective judgements. In general, judgements of the overall affective intensity of a temporally extended event are biased towards the moments of strongest affect within the event period, rather than the average. Low-level perceptual judgements of intensity may be similarly biased towards ‘peaks’ of intense stimulation, but evidence in support of this claim is lacking.

Here we investigate these processes in the context of somatosensory stimuli delivered to multiple digits in parallel. Everyday interactions with objects, such as grasping a piece of fruit, involve simultaneous contact between the object and several digits. The rich innervation of all the fingertips ensures that salient inputs, such as object slip, are rapidly and appropriately processed (Johansson & Westling, 1984; Lemon, Johansson, & Westling, 1995). At the same time, perceptual bandwidth is too low to support parallel percepts at each finger individually (Gallace, Tan, & Spence, 2006; Plaisier, Bergmann Tiest, & Kappers, 2009). Indeed, the normal phenomenological content gives a single tactile experience of the object we are holding, rather than individual contact sensations at each digit (Martin, 1992). Neurons capable of responding to inputs on any finger are present at later levels of the somatosensory hierarchy, such as the secondary somatosensory cortex (Fitzgerald, Lane, Thakur, & Hsiao, 2006; Robinson & Burton, 1980; Sinclair & Burton, 1993).

Previous studies have used perceptual illusions to investigate the mechanisms that integrate multiple, simultaneous tactile or thermal stimuli. In the *funneling illusion* two closely-spaced tactile stimuli are perceived as a single, more intense stimulus at the centroid of the actual stimulation points (Gardner & Spencer, 1972). Activation in primary somatosensory cortex also reflects the illusory location of stimulation, rather than the true locations of the individual stimuli (Chen et al., 2004). In the *tactile continuity illusion*, Kitagawa and colleagues (2009) showed that brief vibrotactile stimuli interspersed with low amplitude noise are perceived as continuous stimulation. Gaps in tactile perception are filled in with illusory sensations sharing the same attributes (e.g., intensity level) as the surrounding physical stimuli. In *thermal referral illusions*, warm or cold thermal stimulators are applied to the ring and index fingers of one hand, and a neutral-temperature stimulator to the middle finger. In this configuration, all three fingers feel warm or cold (Green, 1977, 1978; Ho et al., 2010, 2011). Participants accurately perceive total thermal intensity, but distribute the perceived temperature evenly across the fingers rather than experiencing an exact copy of the intensity on the individual outer fingers referred to the neutral middle finger (Ho et al., 2011). Taken together, these illusions demonstrate an integrative quality in somatosensory processing, which acts to produce a coherent overall percept from multiple stimulations distributed in space and time. This integration might take place at multiple levels in the somatosensory pathway, from peripheral mechanisms (e.g., energy summation in skin receptors) to central mechanisms (e.g., Gestalt perceptual grouping principles).

Thus, the somatosensory system integrates sensations across digits to produce an overall percept, but this process remains poorly understood. Here, we investigated the impact of selectivity on these integration processes, by asking participants to judge the *total* intensity of discrepant somatosensory stimuli delivered to two fingers. Correctly computing the total stimulation involves summing the two individual stimuli, according equal weight to each. However, strong selectivity implies a higher weighting for the stronger stimulus in a pair – leading to an incorrect estimate of the total. Thus, errors in computing totals may provide important information about how selectivity mechanisms influence perceptual processing.

In Experiment 1, we tested participants' ability to judge the total intensity of two electrotactile stimuli delivered to two fingers on the same hand. We predicted that the total of two stimuli with discrepant intensities would be perceived differently than the same total intensity distributed uniformly across the two fingers, indicating imperfect aggregation mechanisms in the somatosensory system. We found that the stronger stimulus had disproportionate influence over judgements of total intensity. In Experiment 2, we investigated whether the inaccurate totalling of stimulus intensity found in Experiment 1 could reflect extinction of the weaker stimulus in the pair, or rather a peak-biased integration mechanism. Our findings support the latter hypothesis by showing that the weaker stimulus is not extinguished, but does make some contribution to perception of the total. Experiment 3 found peak-biased aggregation within hands but not between hands, showing that the effect occurs within a single hemisphere. Finally, Experiment 4 showed peak-biased aggregation in other somatosensory modalities, namely, innocuous warm and cold processing, suggesting a general feature of somatosensory processing.

Methods

Twenty-one healthy right-handed human volunteers (mean age: 26, range: 19-39, 12 female) participated in Experiment 1. Two were excluded because they did not perceive any electrical stimuli on one of their fingers. A further six were excluded because suitable detection and pain thresholds to electrical stimulation of the digital nerves could not be established (see Methods, Experiment 1). The final sample size was 13. A group of twenty new participants (mean age: 22, range: 18-30, 7 female) took part in Experiment 2. Four were excluded because suitable detection and pain thresholds to electrical stimulation could not be established (see Methods, Experiment 2), leaving a final sample size of 16. Ten new volunteers (mean age: 21, range: 18-24, 7 female) participated in Experiment 3. Lastly, sixteen new participants (mean age: 24, range: 18-33 years, 11 female) took part in Experiment 4. One was excluded because of chance performance overall (mean 50% correct), leaving 15 participants in the final sample. Experimental procedures were fully explained to the participants before they provided informed written consent, but participants were kept naïve to the scientific hypotheses tested. The University College London Research Ethics Committee approved this study and experimental procedures conformed to the Declaration of Helsinki.

Experiment 1

Experimental setup

A pair of stainless steel ring electrodes (Technomed Europe, Netherlands) was placed on the right index finger of the participant. Electrode gel was used between the electrode and the skin. A second pair of ring electrodes was placed on either the middle finger (Fig. 1A) or the little finger (Fig. 1B). Transcutaneous electrical stimuli were delivered using a pair of Digitimer DS5 constant current stimulators (Digitimer Ltd., United Kingdom), controlled by a computer. Visual stimuli were generated using Psychophysics Toolbox v3 (http:// http://psychtoolbox.org/) for MATLAB.

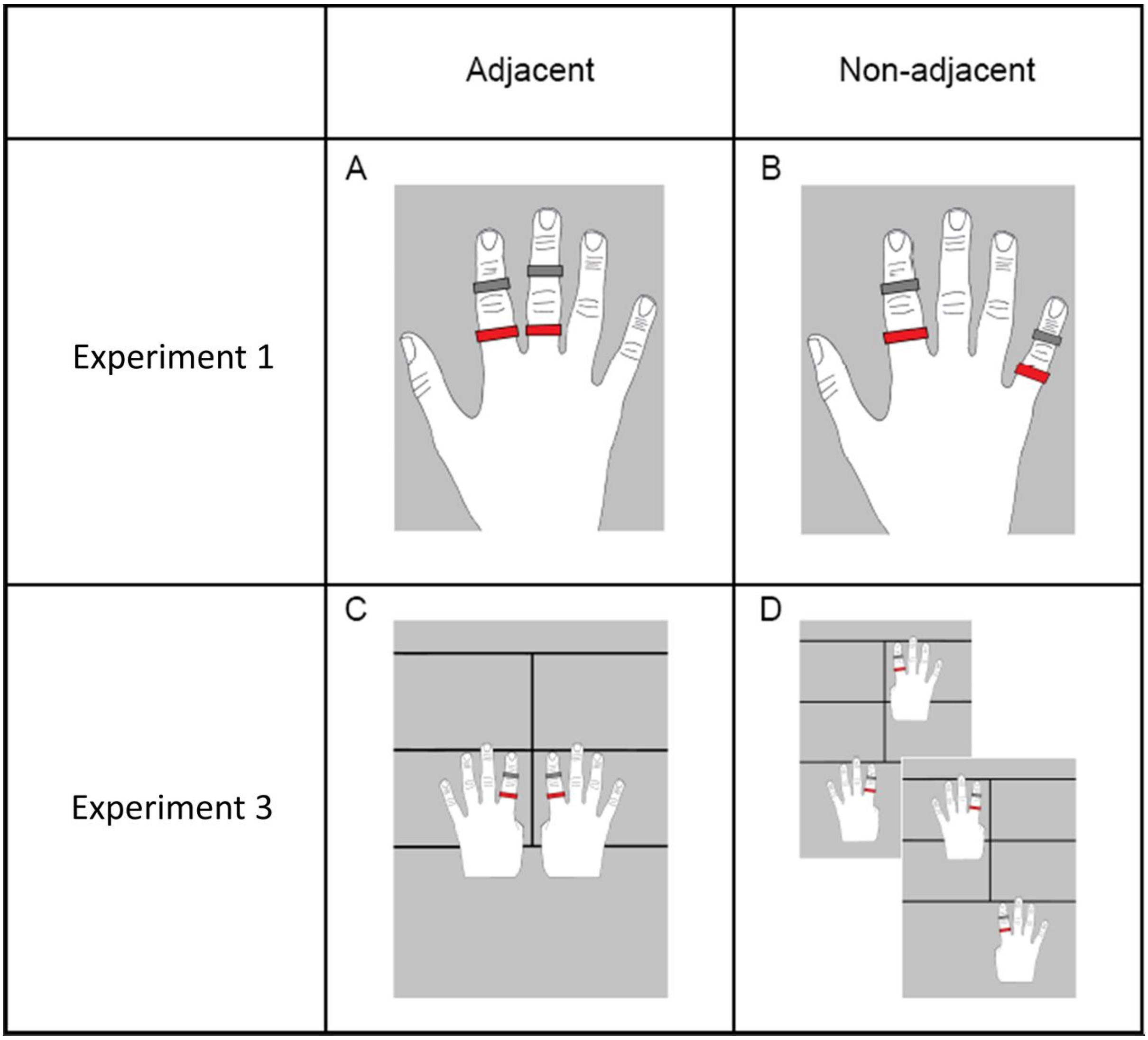


Figure 1. Electrode placement in Experiments 1 and 3. In Experiment 1 (top row), electrodes were placed on adjacent digits (A) or non-adjacent digits (B). In Experiment 3 (bottom row), electrodes were placed on the index fingers of both hands. In the 'adjacent' condition (C) the hands were placed 4 cm apart and symmetrically in front of the body midline. In the 'non-adjacent' condition (D), one hand was displaced proximally 12.5 cm and the other distally 12.5 cm.

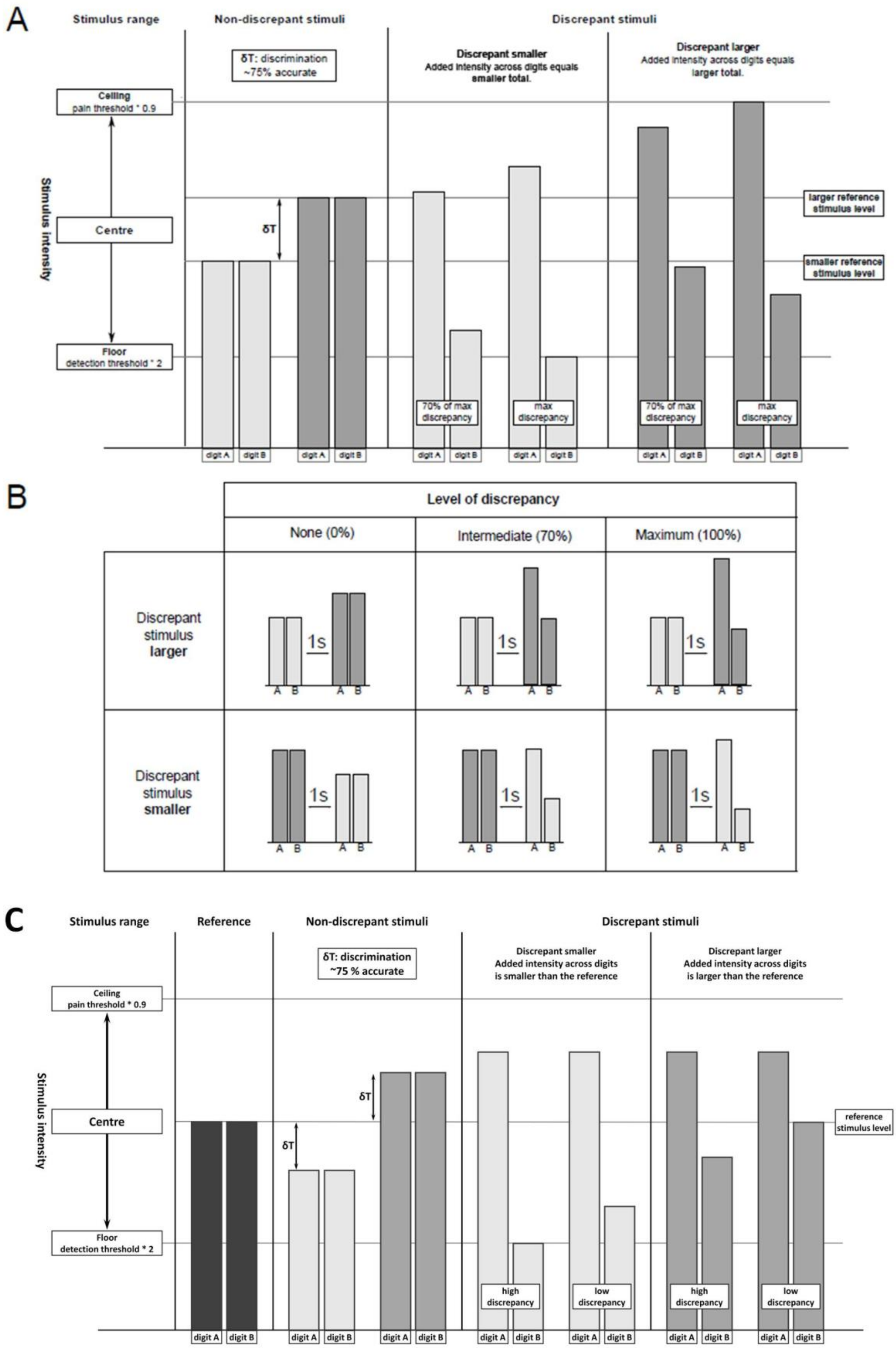
The participant rested their hand palm down on a table, with the thenar and hypothenar eminences, the distal finger pads of digits 2-5 and the lateral side of the thumb pad touching the table surface. Vision of the right hand and wrist was blocked with a screen. Detection and pain thresholds for electrical stimulation of the digital nerves were measured prior to the experiment. Both fingers were stimulated simultaneously with the same current intensity, starting at 0.5 mA and then increasing in steps of 0.5 mA until the participant perceived a stimulus. The current was then reduced in 0.5 mA steps until the stimulus was no longer detected, and then increased again until the stimulus was again perceived. This second value was used as an estimate of the detection threshold. Next, the current was increased rapidly to near pain threshold, and then the same 'up, down, up' procedure was used to measure the pain threshold. The stimulation floor for the experiment was set to double the participant's detection threshold, and the ceiling was set to 90% of the pain threshold. Six participants were excluded at this stage because double their detection threshold was greater than 90% of their pain threshold.

Next we selected the stimulus values. In each trial of this pre-test, two pairs of stimuli were delivered, each consisting of one stimulus on the index finger and another on the middle finger. There was an interval of 1 s between the first pair and the second pair. The same stimulus intensity was delivered to the middle and index fingers within each pair, and the total of the two pairs presented in each trial could differ by 0%, 25%, 50%, 75% or 100% of the stimulation range (ceiling minus floor). Each pair was accompanied by an audible beep. After the second pair, the participant saw the question "Which beep contained the larger total shock (the first or the second)?" on a computer display, and made a button press response with the left hand. The purpose was to identify the difference in total intensity between the two stimulation pairs needed for the participant to answer correctly approximately 75% of the time. Piloting on 11 participants consistently found this difference to be 25% of the stimulus range. Therefore, for subsequent participants the stimulus selection procedure began with an intensity difference of 25% of the stimulus range. However, the pre-test was still used in each participant as screening tool, confirming the 75% correct level for total intensity discrimination. Two participants could not feel any stimulus on one finger, due to suspected peripheral neuropathy. One was detected at the setup/screening stage. The other participant reported being unable to detect stimuli on the little finger, and was excluded at this point in the experiment.

Data collection

In the main experiment, the participant performed a two interval forced choice task. Two pairs of stimuli were delivered to the participant's fingers, separated by an interval of 1 s. In the *non-discrepant reference pair* the currents on the two fingers were equal. In the other pair the currents on the two fingers could be unequal, making this the *discrepant test pair*. Three levels of discrepancy were used for the test pair: the maximum possible discrepancy within the stimulation range, 70% of the maximum and zero (i.e., non-discrepant stimuli). In all discrepant test pairs, one finger was stimulated with a current larger than the current used for each finger of the non-discrepant reference pair, even when the discrepant pair had the smaller total intensity (see Fig. 2A and B). In a similar fashion, the smaller current in the discrepant pair was always smaller than the current used for each finger in the non-discrepant pair, even when the discrepant pair had the larger total intensity. Importantly, these constraints meant that a participant who attempted to judge total intensity by relying only on the most strongly stimulated single finger would give incorrect responses when the discrepant pair had the smaller total, but correct responses when the discrepant pair had the larger total.

Each stimulus pair was accompanied by an audible beep. After both pairs were delivered, the question “Which beep had the larger total shock (the first or the second)?” appeared on a computer monitor in front of the participant. The participant then responded by button press with the left hand.


A
Stimulus range
Non-discrepant stimuli
Discrepant stimuli
δT: discrimination ~75% accurate
Discrepant smaller
Added intensity across digits equals smaller total.
Discrepant larger
Added intensity across digits equals larger total.
Ceiling
pain threshold * 0.9
Centre
Floor
detection threshold * 2
Stimulus intensity
δT
larger reference stimulus level
smaller reference stimulus level
70% of max discrepancy
max discrepancy
digit A
digit B
B
Level of discrepancy
None (0%)
Intermediate (70%)
Maximum (100%)
Discrepant stimulus larger
Discrepant stimulus smaller
1s
A
B
C
Stimulus range
Reference
Non-discrepant stimuli
Discrepant stimuli
δT: discrimination ~75 % accurate
Discrepant smaller
Added intensity across digits is smaller than the reference
Discrepant larger
Added intensity across digits is larger than the reference
Ceiling
pain threshold * 0.9
Centre
Floor
detection threshold * 2
Stimulus intensity
δT
reference stimulus level
high discrepancy
low discrepancy
digit A
digit B

233

Figure 2. A) All stimuli in Experiments 1 and 3 consisted of simultaneous electrical stimulation to two digits. Overall stimulus intensity either equalled the smaller total (light grey shading) or the larger total (dark grey shading). The difference between the higher and lower totals, δT, was set to a level at which subjects scored approximately 75% correct when all stimulus pairs were non-discrepant. B) The 3x2 design of Experiment 1. Trials consisted of two paired electrical stimulations of the digits, separated by an interstimulus interval of 1 s. Critically, all three levels of discrepancy involved the same total intensity. See main text for further details. C) In Experiment 2, the intensity of the strongest stimulus in the discrepant pairs was kept constant, and the intensity of the weaker stimulus was varied to produce different amounts of discrepancy. Any difference in accuracy between conditions would then be due to the contribution of the weaker stimulus to the perceived total intensity.

We used a factorial within-participants design with three independent factors. The first factor was which stimulus pair had the larger *total* (test or reference). The second factor was the level of *discrepancy* in the test pair (0, 70% max. or 100% max.) and the third factor (*adjacency)* was whether the stimulated fingers were adjacent (index and middle) or non-adjacent (index and little). The first and second factors were randomised, while the third was blocked. The order of blocks was counterbalanced across participants. Within each block, half of the trials delivered the discrepant test pair first, and the other half delivered the non-discrepant reference pair first. Furthermore, in half of the trials the index finger received the larger stimulus for the discrepant pair, and this was reversed for the other half. Each trial was repeated 10 times, and the order of trials within a block was randomised. This made a total of 240 stimulus pairs for each experimental block. The participant was given a 1-minute break every 60 trials and a 5-minute break halfway through.

Experiment 2

Experiment 1 manipulated the discrepancy between two transcutaneous electrical stimuli, while keeping the total intensity of the pair constant (Fig. 2A and B). Discrepancy was thus confounded with the intensity of each individual stimulus in the discrepant pair; a highly discrepant pair necessarily involved one stimulus with very high intensity and another with very low intensity. Consequently, effects of discrepancy could alternatively be explained by a strategy in which participants processed only the strongest stimulus in the discrepant pair, comparing it to the intensity of either stimulus in the non-discrepant pair. That strategy would rely on processing a single stimulus rather than aggregation of the two stimuli to produce a percept of total intensity.

Experiment 2 tested this possibility by holding the intensity of the strongest stimulus in the discrepant pair constant, and varying the intensity of the weaker stimulus. If participants disregarded the weaker stimulus, and considered only the stronger stimulus in their judgements of total intensity, then no effect of discrepancy should be found in this experiment.

Experimental procedures were broadly similar to Experiment 1. In each trial, participants received both a non-discrepant pair of electrical stimuli (the reference pair) and a discrepant pair of electrical stimuli (the test pair), separated by an interval of 1 s. However, the method used to set stimulus intensities differed from Experiment 1. In particular, the intensity of the non-discrepant pair was always set at the midpoint of each participant's stimulation range (i.e., the range between double the detection threshold and 90% of the pain threshold). For the discrepant pair, the intensity of the stronger stimulus was invariably set at 70% of the stimulation range, while the intensity of the weaker stimulus varied between four possible intensities (0%, 15%, 45% and 60% of the stimulation range). These proportions were chosen as the most suitable for each discrepant pair to meet the following constraints: 1) to have either a smaller or larger total intensity than the non-discrepant reference pair, 2) to have the total intensities of the discrepant pairs equally spaced around the total intensity of the non-discrepant reference pair, 3) to set the intensity of the stronger stimulus in the discrepant pair higher than the intensity of each individual stimulus in the non-discrepant reference pair, 4) to hold the intensity of the stronger stimulus constant across all discrepant pairs, and 5) to vary discrepancy level (Fig. 2C).

Moreover, to prevent floor/ceiling effects, we used a pre-test to check that accuracy in discriminating the non-discrepant reference pair from non-discrepant versions of the test pairs with the smallest and largest totals lay between 65% and 85%, over 40 trials. If accuracy was higher than 85%, the test pair total was adjusted to be more similar to the reference pair total (i.e., increased if it was the smaller total, or decreased if it was the larger total). If accuracy was lower than 65%, then the pre-test was simply repeated, because it was not possible to make the test pair total less similar to the reference pair total under the constraints described above. Participants were excluded from participating in the experiment if their performance was still not within the specified range after three successive adjustments (4 exclusions out of 20 participants recruited).

The main experiment consisted of a 2 (discrepant pair total: larger vs. smaller) x 2 (discrepancy: low vs. high) within-participants design. Both the presentation order of non-discrepant and discrepant pairs and the location of the strongest stimulus in the discrepant pair (right index or middle finger) were fully counterbalanced across trials. Each comparison between the non-discrepant reference pair and each type of discrepant pair was repeated 10 times, giving a total of 160 trials. Vision of the right hand was blocked by a screen for the duration of the experiment**.**

Experiment 3

The experimental setup was the same as in Experiment 1 with two key exceptions. First, the stimulation electrodes were placed on the left and right index fingers. Thus, participants determined the total of two stimuli delivered simultaneously to different hands. Second, the spatial distance between the fingers was controlled by moving the hands on the table between three spatial configurations. In the first condition, the hands were adjacent on the table, and the inter-index distance approximated the index-middle distance from the first experiment (Fig. 1C). The other two conditions separated the tips of the index fingers by 25 cm in the sagittal plane (Fig. 1D). The experiment was performed in four blocks of 120 trials each: two identical ‘hands adjacent’ blocks, one ‘hands apart’ block with left hand forward, and one ‘hands apart’ block with right hand forward. The two hands-apart blocks were combined, because our predictions concerned only the distance between the hands, not the position of either hand. For efficiency, stimulus setup used a single block of 120 trials in the ‘hands adjacent’ condition to confirm that total intensity could be discriminated with approximately 75% accuracy (see Experiment 1). Finally, the same trial structure and randomisation was used as in Experiment 1 with the exception that the order of blocks was randomised.

Experiment 4

The fourth experiment investigated perception of total thermal stimulation rather than electrical stimulation. Pairs of thermal stimuli were delivered via two computer-controlled Peltier-type thermodes with 13-mm diameter pen-shaped probes (Physitemp NTE-2A, Clifton, NJ). The two probes were fixed to a bar, approximately 2.5 cm apart. Stimulus delivery was controlled by a high-power servo motor (Hitec HS-805BB, Poway, CA) which moved the bar carrying the probes into contact with the index and middle fingers.

The purpose of this experiment was to test spatial integration of innocuous warm and cold stimuli to produce percepts of total thermal energy. Warm and cold temperatures were always tested in separate blocks. The temperature ranges for warm and cold stimuli were chosen to activate specific physiological pathways associated with warm and cold sensation (Hensel & Iggo, 1971; Morin & Bushnell, 1998; Schepers & Ringkamp, 2010). Extreme hot and cold temperatures were avoided, as we did not want to stimulate nociceptors, nor produce pain. These multiple constraints meant that we could not set stimulation levels individually as in Experiment 1. Instead, we set fixed levels of thermal stimulation based on the physiological ranges of target receptors reported in the literature (see above), and a pilot study of 9 volunteers who did not participate in the main study. From the pilot data, we determined warm and cold stimulation levels that were not painful and that yielded, on average, 65-75% accuracy in discriminating total intensity of non-discrepant stimulus pairs (Table 1). Discrimination of total temperature was better in the warm than in the cold range, so we used smaller temperature differences in the warm condition than in the cold condition, but the *relative* temperature discrepancy levels of the discrepant stimulus pairs were the same in both temperature ranges (medium discrepancy level 75% of high discrepancy level). Participants judged which stimulus pair had the greater total warmth/coldness (as appropriate), the first or the second.

		Warm range		**Cold range**	
		Test pair warmer	**Test pair less warm**	**Test pair colder**	**Test pair less cold**
Reference pair: Non-discrepant	**Stimulus 1**	37.00°C	38.00°C	21.00°C	19.00°C
	Stimulus 2	37.00°C	38.00°C	21.00°C	19.00°C
Test pair: Non-discrepant	**Stimulus 1**	38.00°C	37.00°C	19.00°C	21.00°C
	Stimulus 2	38.00°C	37.00°C	19.00°C	21.00°C
Test pair: Discrepant (75% max.)	**Stimulus 1**	35.75°C	34.75°C	22.00°C	24.00°C
	Stimulus 2	40.25°C	39.25°C	16.00°C	18.00°C
Test pair: Discrepant (100% max.)	**Stimulus 1**	35.00°C	34.00°C	23.00°C	25.00°C
	Stimulus 2	41.00°C	40.00°C	15.00°C	17.00°C

Table 1. Warm and cold stimulation levels used in Experiment 4.

Each participant completed three blocks of 24 trials each in the warm temperature range and another three blocks in the cold temperature range. Blocks of the same temperature range were done consecutively, and the order of warm/cold conditions was counterbalanced across participants (e.g. WWWCCC or CCCWWW). Additionally, a short practice block (10 trials) was given before the first warm block and before the first cold block to familiarise participants with the task and the temperature range. A rest period of at least three minutes was given before switching temperature ranges, and the skin surface temperature was checked with an infrared thermometer at the end of the rest period to ensure that it had returned to baseline.

Participants sat at a table with their left hand placed palm-up. On each trial, the thermode probes would descend and touch the participant's index and middle fingers for 1 s, and then retract. After a 3 s delay, the probes would descend and touch the participant's fingers again, retracting after 1 s. The participant would then press a button with the right hand to indicate whether the first or second pair was warmer (in the warm condition) or colder (in the cold condition) *in total*. Each trial contained one stimulus pair with the same temperature on both probes (the non-discrepant reference pair) and a test pair that could be discrepant. As in Experiment 1, the test pair could either have the same temperature on both probes (i.e., non-discrepant), an intermediate difference in temperature between the two probes (medium-discrepant), or a larger difference in temperature between the two probes (highly-discrepant). Levels of discrepancy were set so that the temperatures in the highly-discrepant stimulus pairs fell within the range of innocuous warm/cold sensation. The medium discrepancy level was set to 75% of the high discrepancy level. The interval containing the discrepant pair (first or second) was counterbalanced within blocks, as was the site of the more extreme temperature in discrepant pairs (index or middle finger). To avoid peripheral effects such as receptor adaptation, vascular responses and persistent changes in skin temperature, the first and second stimulus pairs were delivered to different parts of the fingers (one pair to the distal finger pads and the other to the middle finger pads). Half the participants received the first stimulus pair on the distal pads and the second on the middle pads, and the other half received the reverse order of finger pad stimulation. The inter-trial interval was 5 s.

Results

Experiment 1: Total intensity judgements

A 2 (finger adjacency: adjacent or non-adjacent) x 2 (test pair total: larger or smaller) x 3 (discrepancy level: none, 70%, or maximum) within-participants ANOVA was performed on percentages of correct responses. The data violated the assumption of sphericity, so a

Greenhouse-Geisser correction was applied where necessary. There was a significant main effect of discrepancy ($F_{1.35,17.53} = 6.44$, $p = 0.014$). Accuracy at judging total intensity decreased monotonically as discrepancy increased. The ANOVA showed neither a main effect of finger adjacency ($F_{1,13} = 0.003$, $p = 0.961$), nor an interaction between adjacency and discrepancy ($F_{2,26} = 0.84$, $p = 0.445$).

Figure 3 separately plots data from the blocks with stimulation on adjacent and non-adjacent fingers. Because our test pair was sometimes non-discrepant, we arbitrarily and equally divided such trials into the 'test pair smaller' and 'test pair larger' categories. Discrepancy only affected participants' performance when the discrepant test pair had a smaller total than the non-discrepant reference pair. The ANOVA showed a main effect of test pair total, ($F_{1,13} = 14.48$, $p = 0.002$) and a significant interaction with discrepancy level ($F_{1.43,18.56} = 8.03$, $p = 0.006$). Simple effects contrasts were used to clarify this interaction. Discrepancy affected accuracy at judging total intensity when the test pair was the smaller total ($F_{1.15,14.90} = 10.62$, $p = .004$), but not when the test pair was the larger total ($F_{2,26} = 0.32$, $p = .726$).

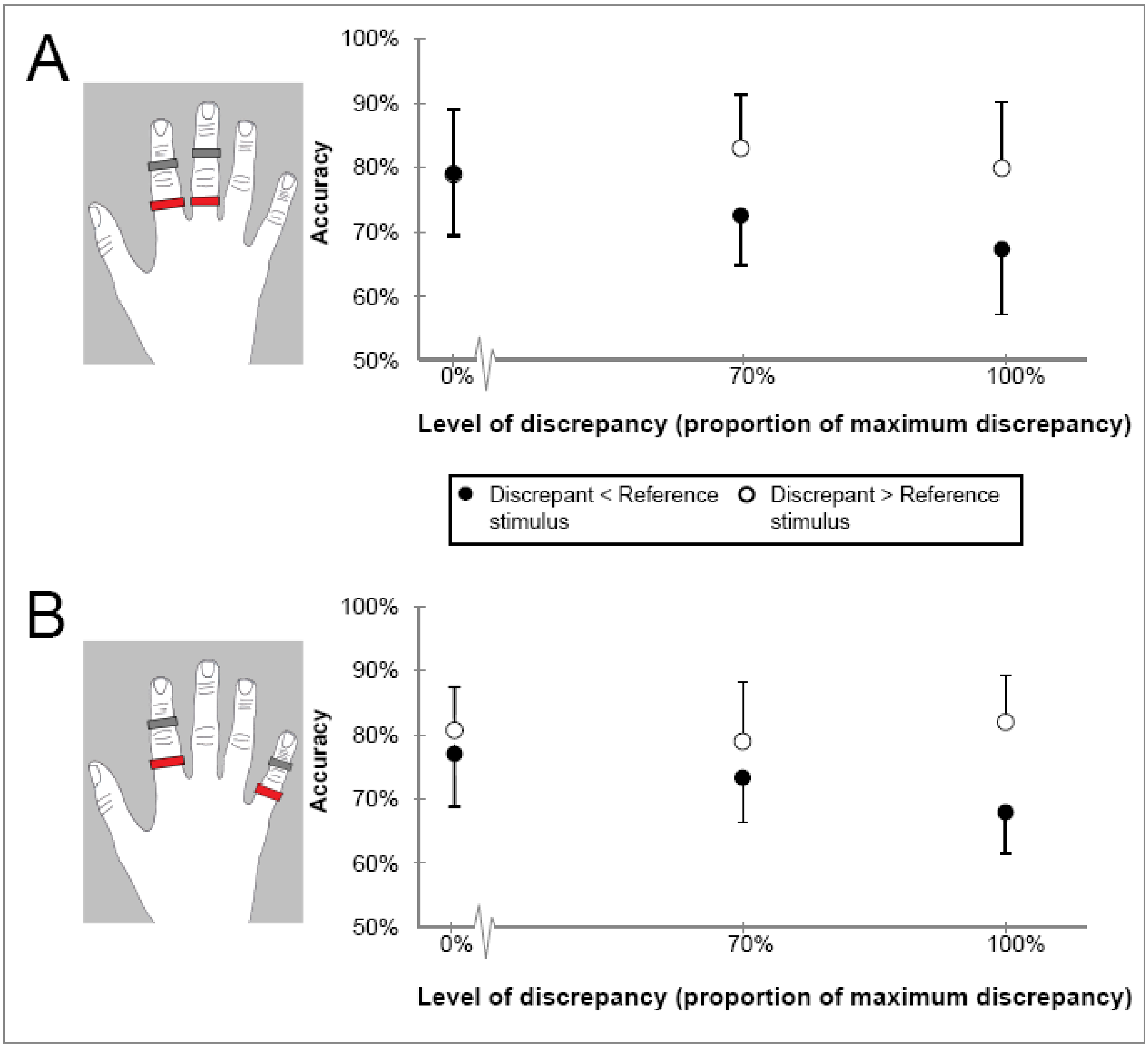


Figure 3. Accuracy of intensity judgements decreased with discrepancy when the discrepant stimulus had a smaller total intensity, but not when the discrepant stimulus had a greater total intensity. Note similar effects when stimulated fingers are adjacent (A) or non-adjacent (B). Error bars show standard error of the mean.

Experiment 2: Contribution of the weak stimulus to total intensity judgements

First, to determine whether Experiment 2 replicated the effect of discrepancy found in Experiment 1, we compared participants' performance in the pre-test, where they compared non-discrepant versions of the smallest and largest test pair totals to the non-discrepant reference pair total, with their accuracy in judging the discrepant versions of the same totals in the main experiment. The 2 (test pair total: smaller or larger) x 2 (discrepancy level: non-discrepant or discrepant) repeated measures ANOVA showed no main effect of test pair total ($F_{1,15}$ = 0.35, p = 0.564), but a significant main effect of discrepancy ($F_{1,15}$ = 9.49, p = 0.008). Accuracy was higher overall when test pairs were non-discrepant (73.3% correct; CI:

70.3%, 76.2%) rather than discrepant (66.5% correct; CI: 62.1%, 70.9%; Fig. 4). Crucially, the interaction between test pair total and discrepancy level was significant ($F_{1,15}$ = 8.24, p = 0.012). Simple effects contrasts showed that discrepancy did not affect judgements of the larger totals ($F_{1,15}$ = 0.47, p = 0.505). The smaller test pair was incorrectly judged to have the larger total intensity more often when it was discrepant (63.1% correct; CI: 57.1%, 69.2%) than when it was non-discrepant (75% correct; CI: 71%, 79%) ($F_{1,15}$ = 14.60, p = 0.002). Consistent with Experiment 1, participants overestimated the total intensity of discrepant stimulus pairs.

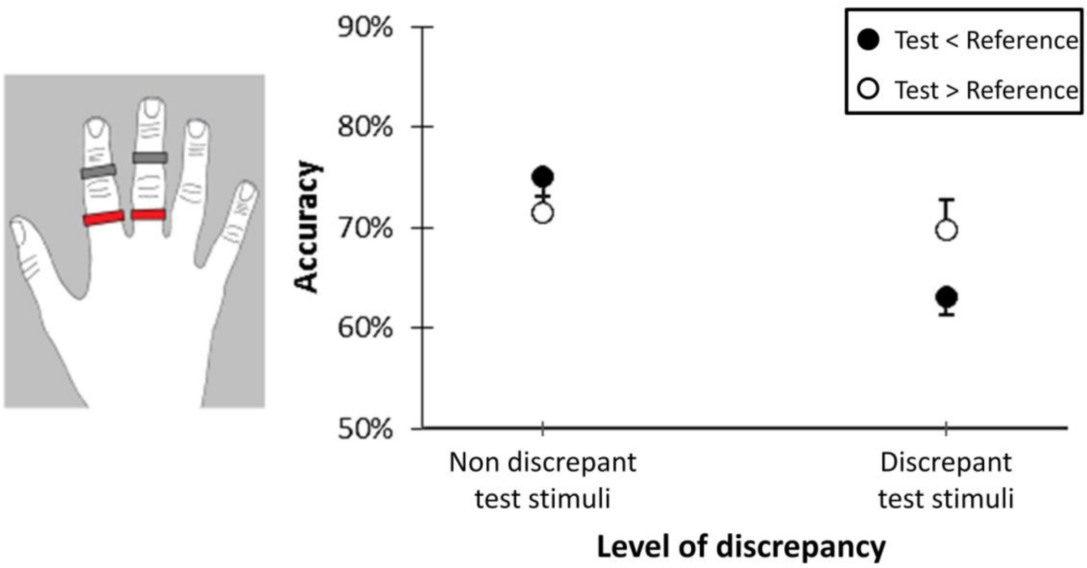


Figure 4. Accuracy in judging total intensity decreased with discrepancy when the discrepant stimulus had a smaller total intensity, but not when the discrepant stimulus had a larger total intensity. Note the similarity to Experiment 1. Error bars show standard error of the mean.

Next, we tested whether this overestimation occurred because participants based their judgements entirely on the intensity of the strongest stimulus in each pair. If this were the case, then there should be no main effect of discrepancy level, nor interaction between discrepancy level and discrepant pair total, because these effects depended only on the level of the weaker stimulus. Instead, there should only be a main effect of discrepant pair total. That is, a participant considering only the stronger stimulus in the discrepant pair would tend to be more accurate when the discrepant pair is, in fact, the larger total, and less accurate when the discrepant pair is actually the smaller total, *irrespective of discrepancy level*.

A 2 (discrepant pair total: smaller or larger) x 2 (discrepancy level: low or high) within-participants ANOVA on percentages of correct responses showed a significant main effect of discrepant pair total ($F_{1, 15} = 5.34$, $p = 0.036$), but no main effect of discrepancy level ($F_{1, 15} = 71.19$, $p = 0.341$). Overall, accuracy was lower when the discrepant pair was smaller in total (58.8% correct; CI: 53.1%, 64.5%) than when it was larger in total (67.7% correct; CI: 62.9%, 72.4%). Importantly, there was a significant interaction between discrepant pair total and discrepancy level ($F_{1, 15} = 11.65$, $p = 0.004$). Simple effects contrasts showed that accuracy was not affected by discrepancy when the discrepant pair was larger in total than the non-discrepant reference pair ($F_{1, 15} = 2.19$, $p = 0.159$). However, when the discrepant pair was smaller in total, accuracy at judging total intensity *increased* with discrepancy. That is, participants made more accurate total intensity judgements when the actual difference between the discrepant and non-discrepant pair totals was larger (63.1% correct; CI: 63.6%, 69.2%), compared to when this actual difference was smaller (54.5% correct; CI: 47.7%, 61.3%; $F_{1, 15} = 9.58$, $p = 0.007$; Fig. 5). This result confirms that participants indeed processed the weaker stimuli of discrepant pairs, and considered both the stronger stimulus and the weaker stimulus when judging the total intensity of the pair.

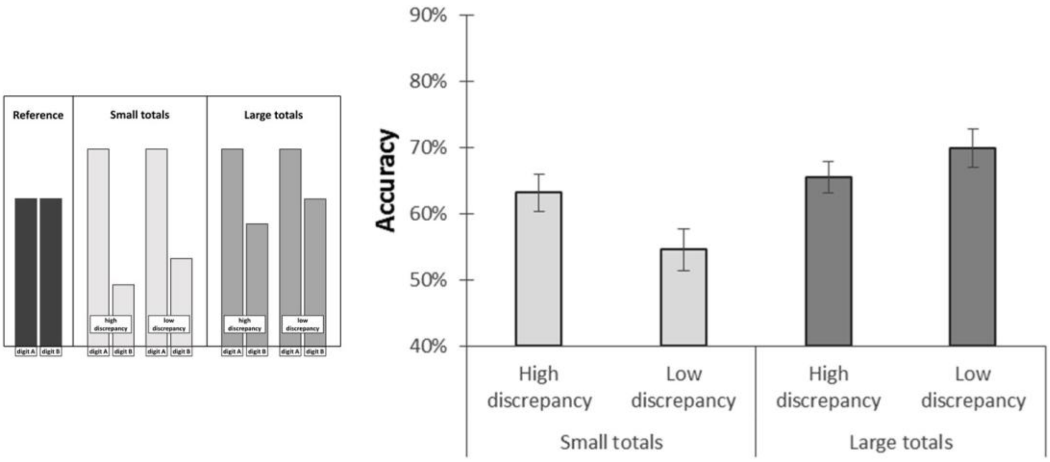


Figure 5. When the intensity of the strong stimulus in the discrepant pair was held constant and only the weak stimulus varied, accuracy increased with the actual difference in total intensity between the two stimulus pairs, confirming that the weak stimulus contributed to the perception of the discrepant pair total. Error bars show standard error of the mean.

Experiment 3: Total intensity judgements between hands

A 2 (spatial proximity: hands together or hands apart) x 2 (test pair total: larger or smaller) x 3 (discrepancy level: none, 70%, or maximum) within-participants ANOVA was performed on percentages of correct responses when participants judged the total intensity of two stimuli delivered to different hands. No Greenhouse-Geisser corrections were necessary. We did not observe any significant effects of discrepancy on total intensity judgements (Fig. 6). With hands together, participants' mean performance was 82.1% (CI: 75.2%, 89.1%) correct with zero discrepancy and 78.8% (CI: 73.0%, 84.5%) with maximum discrepancy. The main effects of discrepancy ($F_{2,18} = 2.72$, p = 0.093) and discrepant pair total ($F_{1,9} = 0.60$, $p = 0.459$) were both non-significant. The spacing between the index fingers did not have an effect ($F_{1,9} = 0.05$, $p = 0.835$). Furthermore, none of the interactions between these factors were significant ($p \geq 0.10$ in all cases).

We additionally used Bayesian analysis to determine whether our data actually supported the null hypothesis, or were merely insufficiently powered for detecting an effect of discrepancy on perception of total stimulation intensity. In the previous experiments, discrepancy only had an effect when the discrepant pair was smaller in total than the reference pair. Therefore, the key finding would be an interaction between discrepancy level and test pair total. We conducted a Bayesian ANOVA (JASP 0.7.5.5) comparing the null model to an alternative model with the factors test pair total (larger or smaller), discrepancy level (none, 70%, or maximum), and the interaction between test pair total and discrepancy. The Bayes factor (null/alternative) showed that the data were 4 times more likely to occur under the null model than under the alternative model, $BF_{01} = 4.00$, error = 2.98%. This indicates that the data are not under-powered, and they provide substantial evidence for the null hypothesis.

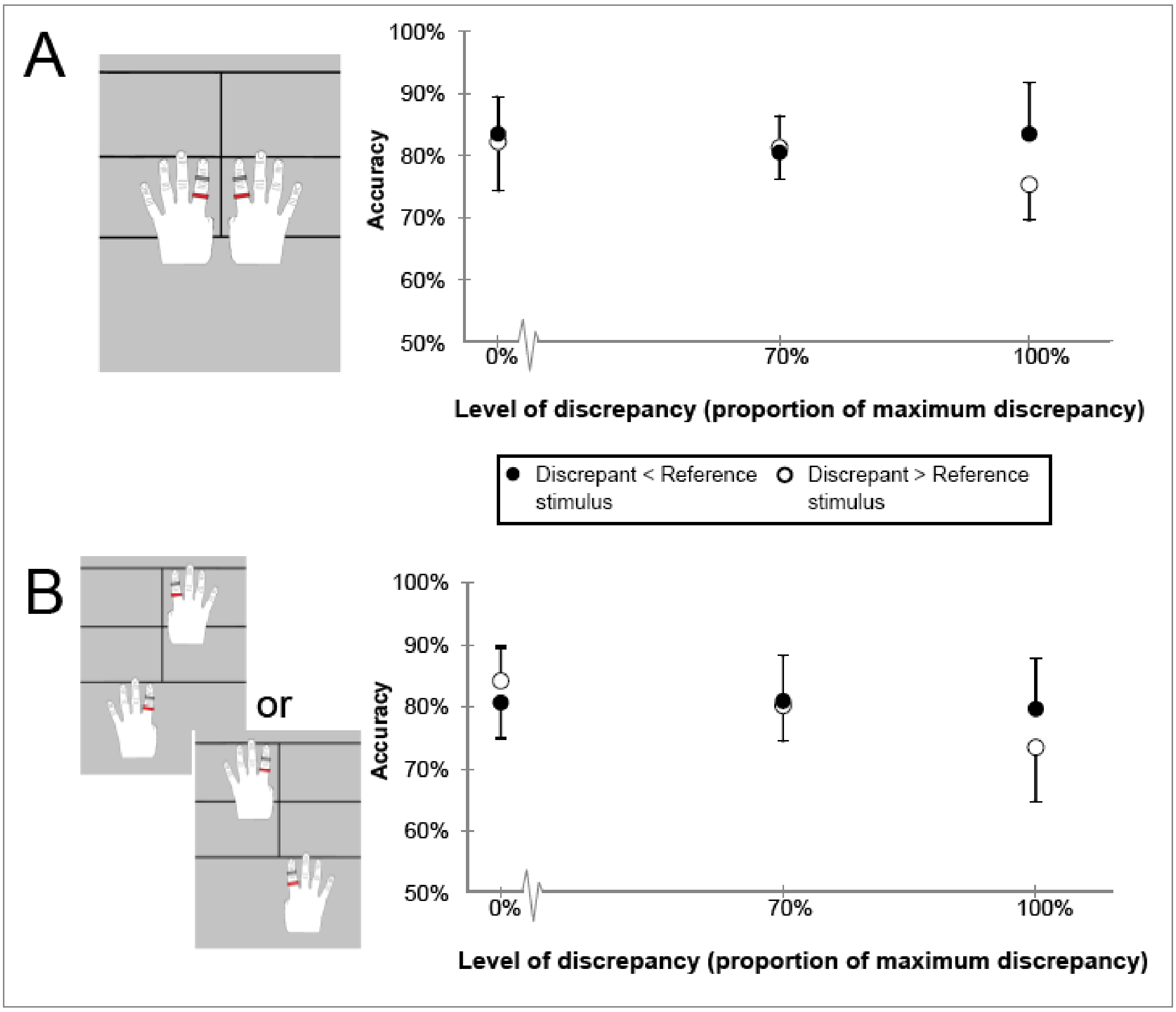


Figure 6. Results of Experiment 3. Discrepancy does not affect perception of total intensity for stimuli distributed across two hands. Note similar results when hands are together (A) versus apart (B). Error bars show standard error of the mean.

Experiment 4: Total thermal intensity judgements

Responses to thermal stimulation were analysed with a 2 (temperature range: warm or cold) x 2 (test pair total: more or less extreme temperature) x 3 (discrepancy level: zero, 75% or maximum) within-participants ANOVA. The assumption of sphericity was violated, so a Greenhouse-Geisser correction was applied where necessary. There was a main effect of temperature range ($F_{1,14}$ = 11.01, p = 0.005), with a mean of 73.5% correct (CI: 68.3%, 78.8%) in the cold condition and 64.2% correct (CI 61.5%, 66.8%) in the warm condition. This indicates that the task was easier in the cold condition than in the warm condition, despite our attempts to balance difficulty across temperature ranges. Note that smaller temperature differences were used in the warm temperature range than in the cold temperature range based on the pilot study. This adjustment was necessary to avoid near-ceiling performance in the warm condition. Importantly, performance was well above chance and well below ceiling in both cases.

There was also a main effect of test pair total ($F_{1,14}$ = 37.05, p = 0.00003). Accuracy was higher when the total of the test pair was a more extreme temperature (warmer in the warm condition or colder in the cold condition) than the non-discrepant reference pair (73.2% correct; CI: 70.3%, 76.1%) compared to when the test pair was less extreme (64.4% correct; CI: 60.9%, 68.0%). Moreover, the interaction between test pair total and discrepancy level was significant ($F_{2,28}$ = 8.99, p = 0.001). Simple effects contrasts were used to clarify this interaction. There was an effect of discrepancy when the test pair total was the less extreme temperature ($F_{2,28}$ = 6.38, p = 0.005). Accuracy at judging total intensity decreased as discrepancy increased (Fig. 7). In contrast, discrepancy did not significantly affect accuracy at judging total intensity when the test pair total was the more extreme temperature ($F_{2,28}$ = 2.53, p = 0.097).

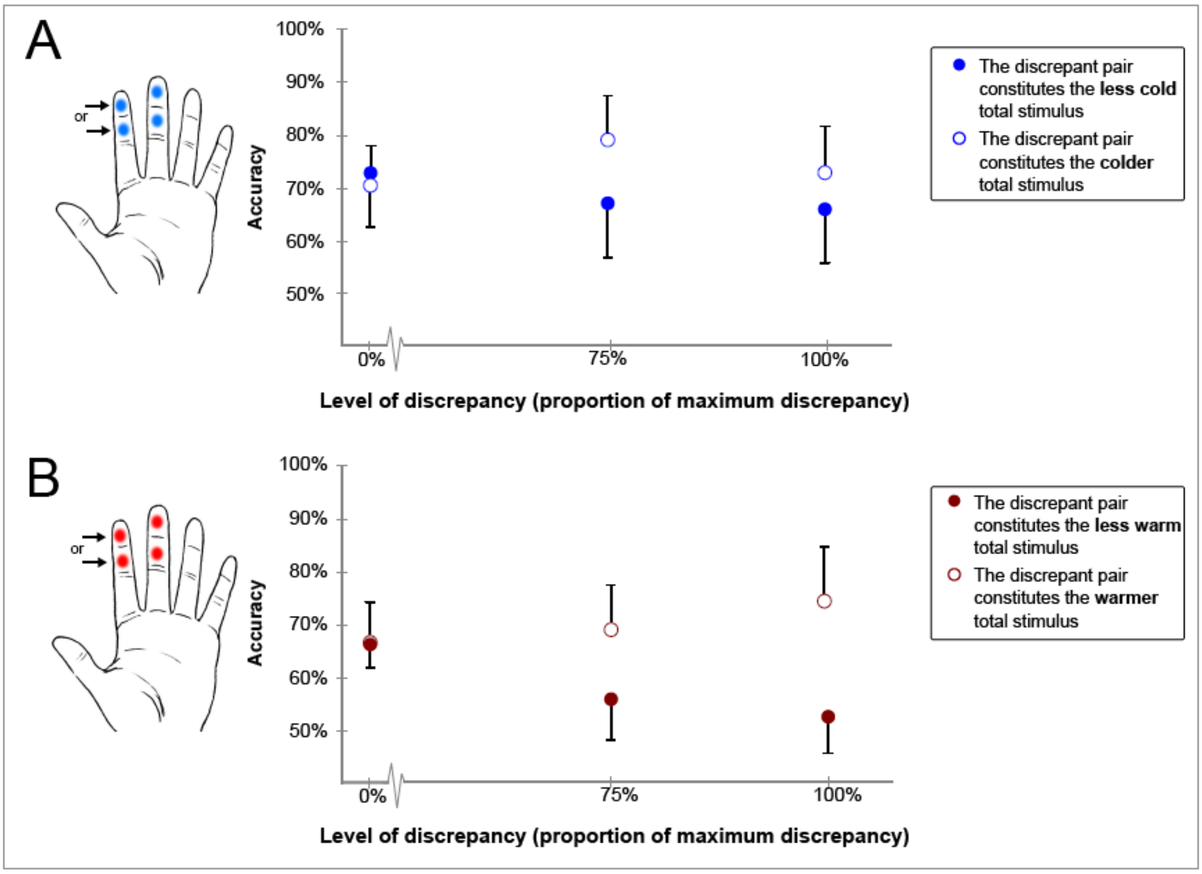


Figure 7. Results of Experiment 4. Accuracy decreased with discrepancy when the discrepant stimulus had the smaller total intensity. Note similarity between cold range (A) and warm range (B), and with Experiment 1. Error bars show standard errors of the mean.

Discussion

Our somatosensory experience of the surrounding world emerges from continual integration of multiple, individual points of stimulation. Here we investigated this integration process by asking healthy volunteers to judge the total intensity of two somatosensory stimuli delivered simultaneously to two different digits. We found a strong and reliable overestimation bias in judging the total of discrepant stimulus pairs, indicating a biased somatosensory aggregation mechanism.

Across our four experiments, we investigated effects of discrepancy on total intensity judgements of transcutaneous electrical stimuli (Experiments 1-3), contact-heat stimuli and contact-cold stimuli (Experiment 4). Despite the fact that these three kinds of stimulation activate distinct peripheral receptor types and afferent fibres (Desmedt & Cheron, 1980; Hensel & Iggo, 1971; Schepers & Ringkamp, 2010; Yarnitsky & Ochoa, 1991), we observed the same overestimation bias in all three cases. Our results therefore suggest that such a bias may be a general principle underlying spatial integration in the somatosensory domain.

Experiment 2 clearly shows that the overestimation bias cannot be explained by participants simply relying on the strongest stimulus, without attempting to perceive the total of both stimuli. Judgements of total intensity were influenced by varying the intensity of the weaker stimulus in the discrepant pair, even when the intensity of the stronger stimulus was held constant. Indeed, participants were more likely to correctly perceive the discrepant pair as smaller in total when the weaker stimulus itself was smaller (and, thus, there was a larger difference between the totals of the discrepant and non-discrepant pairs). This means that participants must have registered both individual intensities, and attempted to sum them, rather than simply attending to the stronger stimulus only. Our pattern of results therefore reflects a mechanism that attempts to total multiple stimuli, but does so in a manner biased by the stronger stimulus.

This is the first investigation of a key form of neural integration in the somatosensory system, namely, the capacity to perceive the total of a number of simultaneous stimuli. Perceptual psychology has traditionally studied *minimal* units of somatosensation, focussing on thresholds, acuity, selectivity and precision (e.g., Graziano, Alisharan, Hu, & Gross, 2002). However, there is growing evidence that somatosensory bandwidth is deeply limited, and, as a consequence of this limitation, perception of whole somatosensory scenes is imperfect. Gallace and colleagues (2006) showed that only 2 or 3 simultaneous tactile stimuli can be individually perceived. Extinction of double simultaneous stimulation (Driver & Vuilleumier, 2001) suggests that brain damage can reduce this bandwidth to just 1. Our findings are perfectly in line with this growing literature, extending the effects of bandwidth limitations in the somatosensory system to judgements of total intensity.

Studies of visual search (Treisman & Gelade, 1980) have indicated two distinct ways that perceptual systems can function despite capacity limitations. First, serial sampling strategies can shift selective attention from one stimulus to another. Such strategies can build up a representation of the total over time, through a series of glimpses. However, the stimuli in our experiment were brief and simultaneous. Moreover, somatosensory 'iconic' storage – i.e., very short term memory in a sensory form (Sperling, 1960) – is around 700 ms (Harris, Miniussi, Harris, & Diamond, 2002). Serial sampling is therefore not a viable strategy for brief stimuli. Second, the perceptual system can attempt to process multiple stimuli in parallel, despite limited bandwidth. Below we discuss in turn some of the most likely somatosensory mechanisms relevant to parallel processing, which may be relevant to our findings. These include lateral inhibition, filling-in, and peak biases based on stimulus salience.

Lateral inhibition is an important form of interaction between stimuli at several levels in the somatosensory system, including primary somatosensory cortex (DiCarlo, Johnson, & Hsiao, 1998; DiCarlo & Johnson, 1999, 2000). This mechanism tends to suppress the response to a stimulus when another, nearby region of the receptor surface is strongly stimulated. A strong hypothesis of reciprocal inhibition between stimulated fingers in our task, weighted by individual stimulus intensities, would predict that the weaker stimulus in a discrepant pair should be partly or wholly extinguished, prior to perceiving the total. However, lateral inhibition alone appears unable to account for our results for three reasons. First, lateral inhibition would tend to produce underestimation of the totals of discrepant stimuli, while we found overestimation. Second, lateral inhibition classically operates between adjacent digits, in a strict spatial gradient (Buonomano & Merzenich, 1998). It is a principle of operation of early somatosensory areas (Gandevia et al., 1983). In our design, lateral inhibition would lead to stronger effects of discrepancy when stimulating adjacent, as opposed to non-adjacent digits. While caution is clearly required in interpreting null results, we saw no evidence for such a difference (Experiment 1). Third, judgements of total intensity were affected when the intensity of the weaker stimulus in the discrepant pair was varied, but the intensity of the stronger stimulus was held constant (Experiment 2). This result clearly demonstrates that the concurrent weak stimulus was not extinguished, nor disregarded in judgements of total intensity. Rather, both the stronger stimulus and the weaker stimulus contributed to the perceived total intensity of a discrepant pair.

Alternatively, participants may have “filled in” information about the intensity of the weaker stimulus in the discrepant pair, based on the intensity of the stronger stimulus. This could produce the observed overestimate. Such filling-in effects have previously been demonstrated for tactile (Kitagawa et al., 2009) and thermal stimulation (Green 1977, 1978; Ho et al., 2010, 2011). The results of Experiment 2, however, do not support a filling-in mechanism. When the discrepant test pair was smaller in total than the non-discrepant reference pair, and the intensity of the stronger stimulus in the discrepant pair was held constant, the intensity of the weaker stimulus influenced estimations of the total. Because the stronger stimuli were constant, reducing the intensity of the weaker stimulus resulted in a lower total intensity for the discrepant test pair, and thus better discrimination from the non-discrepant reference pair. Experiment 2 therefore shows that information about the intensity of the weaker stimulus was not lost. In fact, the intensity of the weaker stimulus informed participants’ judgements of total intensity, in a manner consistent with a genuine attempt at integration.

A third possible explanation for our findings could be a form of peak bias, based on stimulus salience. Salience is a term widely used in psychology. It may involve a number of factors, including intensity, quality or affect (Fecteau & Munoz, 2006; Vuilleumier, 2005; Wolfe, 1992). In a perceptual system with parallel rather than strictly serial organisation, percepts of the total may depend strongly on the most salient part, as salient stimuli may be selected for more detailed perceptual analysis, leaving fewer resources for processing less salient stimuli. In the case of our discrepant stimulus pairs, which were uniform in quality and lacking in affective valence, intensity would determine stimulus salience. Therefore, a mechanism sensitive to stimulus salience might account for the overestimation bias we found in judging the total of discrepant stimuli.

This overestimation followed the pattern of a peak bias, with judgements of total intensity being driven towards the most intense and salient element of stimulation. Peak biases are well established within the literature on memory for affective experiences (for a review, see Fredrickson, 2000). Overall judgements of affect are disproportionately influenced by moments of peak affect. Similarly, comparisons of moment-to-moment pain ratings with retrospective judgements of overall pain show that memories for both acute and chronic pain are driven by moments of peak pain intensity (Redelmeier & Kahneman, 1996; Stone, Schwartz, Broderick & Schiffman, 2005). All our stimuli were set below pain thresholds, and had no affective valence or special meaning for the participants. Nevertheless, our data were consistent with the notion that the salient peak serves as a proxy for an overall experience. We thus provide novel evidence that peak biases occur in low-level perceptual experiences, and not merely in higher-level affective judgements.

Our data provide additional information about the spatial organisation of the somatosensory peak bias. First, Experiment 3 showed that the mechanism operates within a single brain hemisphere. We found strong overestimation for discrepant pairs of stimuli on the same hand, but not when the two stimuli in the pair were delivered to homologous digits on different hands. Second, it appears to be independent of selective *spatial* attention. In Experiment 1, we found no difference between judging the total of adjacent and non-adjacent fingers. Additionally, in Experiment 3, we found no effect of the distance between the hands on the ability to judge the total intensity of stimuli delivered to both hands. Although caution is required in drawing conclusions from these null results, our findings are unlikely simply to reflect lack of power, since spatial attention effects are common in somatosensory perception (e.g., Eimer & Forster, 2003; Forster & Eimer, 2005) Attentional studies report a perceptual cost to dividing attention between two spatial locations (Forster & Eimer, 2005; Posner, 1978), yet our task of judging total intensity appeared not to reflect this cost. Furthermore, a Bayesian analysis of the data from Experiment 3 indicated that the study was not under-powered, and that the results do, in fact, support the null hypothesis that the overestimation bias does not occur when two stimuli are delivered to different hands. Thus, spatial proximity does not seem to play a major role in combining stimulus intensities to form a total, either in somatotopic space within a single hemisphere (no effect of fingers stimulated in Experiment 1) or in external space (no effect of hand positions in Experiment 3). Taken together, these results suggest the bandwidth limitation occurs at early, lateralised levels of somatosensory representation, rather than in a single, central channel of awareness (Broadbent, 1982). Judgements of total stimulation depend on a process of aggregation located prior to the remapping of tactile signals into external space (Azañón, Longo, Soto-Faraco, & Haggard, 2010; Azañón & Soto-Faraco, 2008); which is thought to occur in the parietal cortex.

Together, our four experiments demonstrate a mechanism of biased aggregation within the somatosensory system. Specifically, the most salient element (i.e., the most intense point of stimulation) makes a larger contribution to judgements of the total than less salient elements. This overestimation bias does not bear the hallmarks of lateral inhibition, namely, a strict spatial gradient and extinction of weak stimuli. Moreover, the bias does not seem to arise from a filling-in process, as information about the individual intensity of the weaker stimulus in the pair is not lost. Rather, our findings appear to reflect a peak bias in somatosensory perception, by which the contribution of each individual stimulus to perception of the total is weighted by its salience, or intensity. This process occurred independently within each hemisphere, but was otherwise unaffected by the spatial locations of the stimuli. We thus provide the first evidence for a peak bias in a purely perceptual judgement.

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