



BIROn - Birkbeck Institutional Research Online

Cataldo, A. and Ferrè, Elisa Raffaella and di Pellegrino, G. and Haggard, P. (2019) Why the whole is more than the sum of its parts: salience-driven overestimation in aggregated tactile sensations. *Quarterly Journal of Experimental Psychology* 72 (10), pp. 2509-2526. ISSN 1747-0218.

Downloaded from: <https://eprints.bbk.ac.uk/id/eprint/45537/>

Usage Guidelines:

Please refer to usage guidelines at <https://eprints.bbk.ac.uk/policies.html> or alternatively contact lib-eprints@bbk.ac.uk.

Why the whole is more than the sum of its parts: Saliency-driven overestimation in aggregated tactile sensations

Journal:	<i>Quarterly Journal of Experimental Psychology</i>
Manuscript ID	QJE-STD-18-107.R1
Manuscript Type:	Standard Article
Date Submitted by the Author:	07-Mar-2019
Complete List of Authors:	Cataldo, Antonio; University College London Institute of Cognitive Neuroscience, Ferrè, Elisa; Royal Holloway University of London, Psychology di Pellegrino, Giuseppe; University of Bologna, Psychology Haggard, Patrick; University College London Institute of Cognitive Neuroscience,
Keywords:	Somatosensory integration, nonlinear summation, digital nerve stimulation, perceptual saliency, tactile integration model, divisive normalisation

Article type

Original article

Corresponding Author

Patrick Haggard, Institute of Cognitive Neuroscience, 17 Queen Square,
London, WC1N 3AZ, United Kingdom.

Tel.: +44 (0)20 7679 1177

Email address: p.haggard@ucl.ac.uk

Article title

Why the whole is more than the sum of its parts: Saliency-driven overestimation
in aggregated tactile sensations

Short title

Saliency-driven overestimation in touch

Authors

Antonio Cataldo^{a b c}, Elisa Raffaella Ferrè^d, Giuseppe di Pellegrino^b, & Patrick
Haggard^{a c}

Abstract

Experimental psychology often studies perception analytically, reducing its focus to minimal sensory units, such as thresholds or just noticeable differences in a single stimulus. Here, in contrast, we examine a synthetic aspect: how multiple inputs to a sensory system are aggregated into an overall percept. Participants in three experiments judged the total stimulus intensity for simultaneous electrical shocks to two digits. We tested whether the integration of component somatosensory stimuli into a total percept occurs automatically, or rather depends on the ability to consciously perceive discrepancy among components (Experiment 1), whether the discrepancy among these components influences sensitivity or/and perceptual bias in judging totals (Experiment 2), and whether the saliency of each individual component stimulus affects perception of total intensity (Experiment 3). Perceptual aggregation of two simultaneous component events occurred both when participants could perceptually discriminate the two intensities, and also when they could not. Further, the actual discrepancy between the stimuli modulated both participants' sensitivity and perceptual bias: increasing discrepancies produced a systematic and progressive overestimation of total intensity. The degree of this bias depended primarily on the saliency of the stronger stimulus in the pair. Overall, our results suggest that important nonlinear mechanisms contribute to sensory aggregation. The mind aggregates component inputs into a coherent and synthetic perceptual experience in a saliency-weighted fashion that is not based on simple summation of inputs.

Keyword

Somatosensory integration, nonlinear summation, touch, digital nerve stimulation, perceptual saliency, tactile integration model.

Why the whole is more than the sum of its parts: Saliency-driven overestimation in aggregated sensations

Antonio Cataldo^{a b c}, Elisa Raffaella Ferrè^d, Giuseppe di Pellegrino^b, & Patrick Haggard^{*a c}

a. Institute of Cognitive Neuroscience, University College London, Alexandra House 17 Queen Square, London WC1N 3AZ, UK

b. Centre for Studies and Research in Cognitive Neuroscience, Alma Mater Studiorum - University of Bologna, Viale Europa 980, 47521 Cesena, Italy

c. Institute of Philosophy, School of Advanced Study, University of London, Senate House, Malet Street, London, WC1E 7HU

d. Department of Psychology, Royal Holloway University of London, Egham, Surrey TW20 0EX, UK.

* Corresponding author. Address: Institute of Cognitive Neuroscience, 17 Queen Square, London, WC1N 3AZ, United Kingdom. Tel.: +44 (0)20 7679 1177. Email address: p.haggard@ucl.ac.uk

Abstract

Experimental psychology often studies perception analytically, reducing its focus to minimal sensory units, such as thresholds or just noticeable differences in a single stimulus. Here, in contrast, we examine a synthetic aspect: how multiple inputs to a sensory system are aggregated into an overall percept. Participants in three experiments judged the total stimulus intensity for simultaneous electrical shocks to two digits. We tested whether the integration of component somatosensory stimuli into a total percept occurs automatically, or rather depends on the ability to consciously perceive discrepancy among components (Experiment 1), whether the discrepancy among these components influences sensitivity or/and **perceptual bias** in judging totals (Experiment 2), and whether the salience of each individual component stimulus affects perception of total intensity (Experiment 3). Perceptual aggregation of two simultaneous component events occurred both when participants could perceptually discriminate the two intensities, and also when they could not. Further, the actual discrepancy between the stimuli modulated both participants' sensitivity and **perceptual bias**: increasing discrepancies produced a systematic and progressive overestimation of total intensity. The degree of this bias depended primarily on the salience of the stronger stimulus in the pair. Overall, our results suggest that important nonlinear mechanisms contribute to sensory aggregation. The mind aggregates component inputs into a coherent and synthetic perceptual experience in a salience-weighted fashion that is not based on simple summation of inputs.

Keywords

Somatosensory integration, nonlinear summation, tactile perception, digital nerve stimulation.

Introduction

Most studies of tactile perception focussed on how *single tactile events* are detected (LaMotte & Whitehouse, 1986; Johansson, Vallbo, & Westling, 1980), localized (Sherrick, Cholewiak, & Collins, 1990; Harris, Thein, and Clifford, 2004; Porro, et al., 2007), and identified (Johnson & Phillips, 1981; Stevens & Patterson, 1995). Such isolated single stimuli are rare in daily life. Rather, we continually experience multiple, simultaneous, non-homogeneous stimuli spread across several skin locations, yet the brain may still generate a single, coherent percept. For instance, when we hold an object between our fingertips we do not perceive five distinct sensations. Rather, we have an immediate and synthetic perception of the whole grasped object.

Simultaneous inputs coming from each finger must be combined along the somatosensory pathways to generate such coherent, multi-touch percepts (Gallace & Spence, 2014; Martin, 1992; MacKay, 1967). This process is limited by both intersensory interactions and by bandwidth (Gallace & Spence, 2014; Cohen, Dennett, & Kanwisher, 2016). For example, two or more somatosensory stimuli may interact, rather than simply sum linearly. Studies on *vibro-tactile masking* (Craig, 1976; von Békésy, 1967) and the *double simultaneous stimulation paradigm* (Sherrick, 1964; Tamè, Farnè, & Pavani, 2011), show that tactile detection drastically deteriorates when the stimulus is presented in spatial and temporal proximity with a distractor. Second, studies on *tactile subitizing* (Gallace, Tan, & Spence, 2006a; Plaisier, Bergmann Tiest, & Kappers, 2009; Riggs et al., 2006; for a review see Gallace, Tan, & Spence, 2008) show that both errors and response times in an enumeration task dramatically increase when two or more vibro-tactile stimuli are delivered simultaneously.

Intensity is a fundamental dimension of all perceptual channels (Bensaïa, 2008), and has been widely explored (Gescheider et al., 2004; Gibson & Tomko, 1972; Marks,

1
2
3 1979; Verrillo & Gescheider, 1975; Bolanowski et al 1988; Craig, 1972, 1974). Yet,
4
5 perception of the overall intensity of combined multi-touch stimuli has rarely been studied
6
7 (Tamè, Moles & Holmes, 2014; Walsh et al., 2016). Walsh and colleagues (2016) asked
8
9 participants to judge the overall intensity of electro-tactile stimulation simultaneously
10
11 delivered to two fingers of the same hand. The intensity of each stimulus in the pair was
12
13 manipulated in order to obtain different levels of discrepancy in the percept, while
14
15 keeping the overall physical intensity constant. If somatosensory intensity perception is
16
17 based on linear summation of component stimuli, uneven distribution of physical
18
19 intensity across the fingers should not affect perception of total intensity. In fact, Walsh
20
21 et al. (2016) found that participants' accuracy in judging the total intensity drastically
22
23 decreased as the discrepancy between the two stimuli increased. In particular, the total
24
25 intensity of discrepant stimuli was systematically overestimated, suggesting that the
26
27 mechanism for aggregating the component stimuli was strongly biased by the peak
28
29 stimulus. That is, the most salient input (i.e. the strongest stimulus in a discrepant pair)
30
31 made a disproportionately strong contribution to the perception of the total. Importantly,
32
33 Walsh et al., (2016) ruled out the possibility that the weak stimulus in the pair was simply
34
35 extinguished, suggesting that the overestimation bias is an effect of stimuli's aggregation.
36
37
38
39
40
41

42 The mechanisms underlying this interesting perceptual nonlinearity remain
43
44 unclear. Such effects could reflect perceptual interactions between component stimuli,
45
46 limited bandwidth for transmitting multiple stimuli to awareness, or both of these factors.
47
48 Therefore, we used discrepant and non-discrepant electro-tactile patterns to investigate
49
50 how the intensity of multiple simultaneous somatosensory events is integrated into a
51
52 holistic percept. First, Experiment 1 tested whether individuals' ability in judging the
53
54 overall intensity of two simultaneous stimuli was related to the ability to consciously
55
56 perceive discrepancy between the component stimuli. Our results indicate that
57
58
59
60

1
2
3 participants made accurate overall intensity judgements despite a surprisingly poor ability
4
5 to detect intensity discrepancy between the component stimuli, suggesting an automatic
6
7 process of aggregation.
8
9

10 Second, we investigated whether the intensity overestimation described by Walsh
11
12 at al. (2016) is a genuine perceptual process or alternatively is driven by changes in
13
14 response bias (Experiment 2). Our results indicate that as the intensity discrepancy
15
16 between two stimuli increased, perceptual sensitivity to total intensity decreased, and
17
18 participants' **perceptual bias** become more liberal, leading to overestimates of total
19
20 intensity.
21
22

23
24 Experiment 3 compared the perceived intensity of double stimuli to that of single
25
26 stimuli. We found that the perceived overall intensity of two discrepant stimuli was
27
28 almost entirely explained by the intensity of the strongest component stimulus. The peak
29
30 intensity of a multi-touch somatosensory stimulation has a disproportionate influence on
31
32 judgements of total intensity.
33
34
35
36
37

38 39 Methods

40 41 Experiment 1. Aggregation and discrimination of the parts for the 42 43 perception of the whole

44
45 Experiment 1 aimed to compare participants' accuracy in aggregating versus
46
47 discriminating the intensity of two tactile stimuli. In addition to this, we used less-
48
49 frequent "rating trials" to investigate whether information about the intensity of the
50
51 individual components was affected by the context of global judgements regarding
52
53 aggregates or discriminanda.
54
55
56
57
58

59 60 Participants

1
2
3 Twenty healthy right-handed volunteers (10 female, mean age \pm SD: 25.5 \pm 4.1 years)
4 participated in Experiment 1. Two of them were excluded because the tactile stimulation
5 range (i.e. the range between the detection threshold and the pain threshold to electrical
6 stimulation of the digital nerves) was too small to generate the whole set of experimental
7 stimuli required by our design (stimulation range $<$ 2 mA; see below). Data from two
8 further participants were lost due to a technical error. The final sample size of Experiment
9 1 (n = 16) was decided *a priori*, on the basis of previous similar studies (Walsh et al.,
10 2016). The experimental protocol was approved by the research ethics committee of
11 University College London, and adhered to the ethical standards of the Declaration of
12 Helsinki.

23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60

Transcutaneous electrical tactile stimuli were delivered through a Digitimer DS5 constant current stimulator (Digitimer, Ltd., United Kingdom), controlled by a computer. A pair of stainless digital ring electrodes (Technomed Europe, Netherlands) was applied to the proximal and intermediate phalanges of index and middle fingers of the right hand. Electrical impedance between each electrode and the skin was kept below 5k Ω throughout the experiment by means of self-adhesive conductive gel patches. Participants were asked to rest their right-hand palm downwards on a table. Particular care was taken to make sure that the ring electrodes did not touch each other, and that the only points of contact between the hand and the surface of the table were the thenar and hypothenar eminences, the distal finger pads of digits 2–5 and the lateral side of the thumb pad. Vision of the hand was blocked by a screen. Instructions before and during the task were presented using the Psychophysics Toolbox v3 (<http://psychtoolbox.org>) for MATLAB.

1
2
3 Before the experiment started, detection and pain thresholds were established for
4 each participant. The procedure was based on the methods described by Walsh and
5 colleagues (2016). In a staircase procedure, the same stimulation intensity was delivered
6 simultaneously to both fingers starting from 0.5 mA and increasing in steps of 0.5 mA
7 until the participant perceived the stimulus. After the first detection, the current was
8 reduced in steps of 0.5 mA until the stimulus was no longer perceived, and then increased
9 once again. The current intensity able to evocate the second detection was taken as
10 participant's detection threshold. Pain threshold was established with the same
11 procedure, but in this case, participants were asked to report whether the stimulation was
12 painful or not. In order to set stimulus values within the participants' tactile range only,
13 we selected current intensities that were clearly above detection threshold (floor: 1.5 x
14 detection threshold), yet below pain threshold (ceiling: 90% of pain threshold). Then,
15 small and large total intensities were set at 37.5% and 62.5% of the stimulation range for
16 each participant.
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33

34
35 Next, in a pre-testing phase, we verified that participants' accuracy in judging the
36 total intensity of non-discrepant pairs would avoid ceiling and floor effects when testing
37 our experimental hypotheses. A series of non-discrepant pairs with small or large
38 intensity were simultaneously delivered on the index and middle fingers, and participants
39 were asked to judge the overall intensity of each pair by pressing one of two keys
40 corresponding to "small"/"large" total. At the beginning of the block, participants were
41 presented with a small and a large total example. Performance was checked after 20
42 trials. If accuracy was below 60% or above 80%, the difference between the two totals
43 was increased or decreased respectively, and the block was repeated until performance
44 lay between these limits. The group mean final accuracy \pm SD was: 75.6% \pm 6.8%.
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Finally, from each non-discrepant pair, we derived a discrepant pair characterized by the 70% of the maximum possible discrepancy within the stimulation range (see Figure 1).

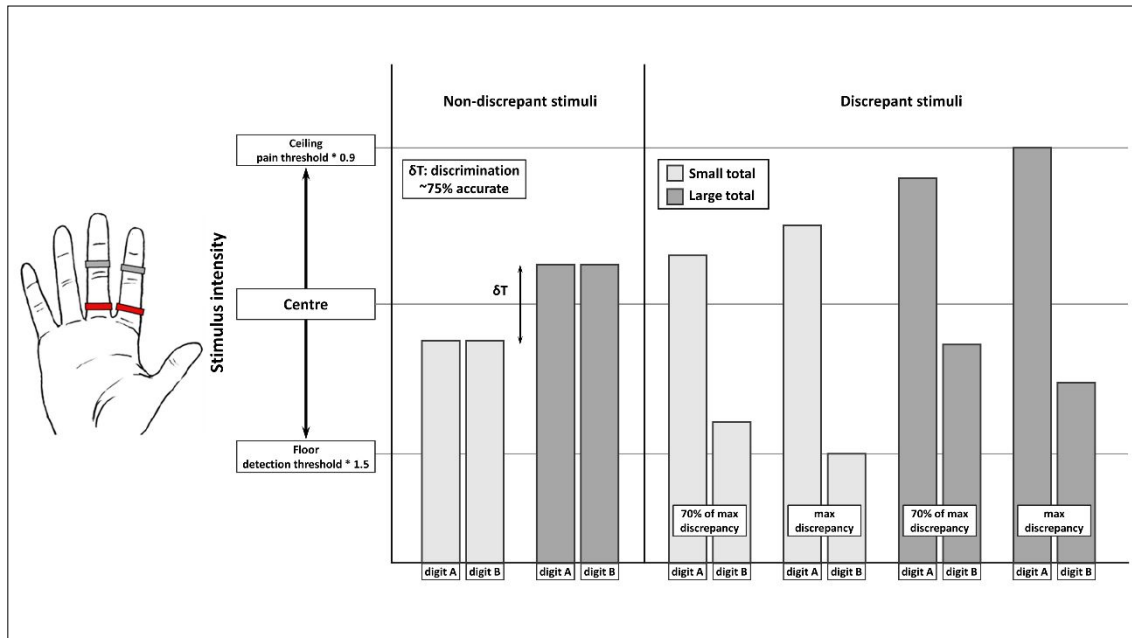


Figure 1. Stimulation levels for Experiment 1 (non-discrepant stimuli and 70% discrepant stimuli) and Experiment 2 (all the stimuli). In both experiments, electrodes were placed on participants' right index and middle fingers. The intensity of the electro-tactile stimulation in each condition was established on the basis of individual detection and pain thresholds. For non-discrepant stimulus pairs, intensities were chosen so that participants discriminated small from large stimuli at approximately 75% correct. In Experiment 1 stimulus pairs were based on 70% of this maximal discrepancy. In Experiment 2, aside the 70% discrepant stimuli, maximally discrepant stimuli spanned the range from detection to pain thresholds, and were total-matched to non-discrepant stimuli.

Procedure

In two separate blocks, participants performed either an aggregation (“judge the total intensity of the pair”) or a discrimination (“judge the discrepancy of the pair”) task on exactly the same combination of stimuli. We decided to test participants' aggregation/discrimination ability in two separate blocks (1) to prevent potential errors

1
2
3 due to the continue task-switching required by a full-randomisation paradigm, and (2) to
4
5 prevent cognitive and perceptual overload.
6

7
8 Participants were delivered with both a discrepant and a non-discrepant pair,
9
10 separated by 1s delay. One of the pairs had the large total intensity and the other the small
11
12 total intensity. Participants performed a two-interval forced choice task, judging which
13
14 pair had the larger overall intensity (aggregation task) or the larger discrepancy between
15
16 the two intensity (discrimination task). The stimuli in both tasks were identical. In a
17
18 small subset of trials (rating trials: 17%), randomly distributed across each block,
19
20 participants were instead presented with a single discrepant pair, and were asked to rate
21
22 the intensity of either the strong stimulus or the weak stimulus in the pair between 1 (very
23
24 weak) to 10 (very strong). These rating trials allowed us to assess how well the
25
26 component stimuli within a pair were perceived. We specifically aimed to compare
27
28 perception of individual component stimuli between blocks where the primary task was
29
30 either aggregation or discrimination. To anchor their magnitude estimation on rating
31
32 trials, participants were presented with the limits (floor and ceiling) of their stimulation
33
34 range, at the beginning of each block and after every 20 trials.
35
36
37
38
39

40 Participants performed two blocks (Aggregation task, Discrimination task). Each
41
42 block consisted of 192 trials (160 main trials plus 32 rating trials), for a total of 384 trials.
43
44 The order of the task (aggregation/discrimination) was counterbalanced between
45
46 participants. The presentation order of small/large and discrepant/non-discrepant pairs,
47
48 the localization of the strong stimulus in discrepant pairs (index/middle), and the target
49
50 of the rating trials (strong/weak stimulus) were counterbalanced within participants.
51
52
53
54
55
56

57 Experiment 2. Sensitivity and perceptual bias in judgements of
58 total tactile intensity
59
60

1
2
3 Experiment 2 aimed to investigate whether the tendency to overestimate the total
4 intensity of discrepant stimuli (Walsh et al., 2016) reflects a change in participants'
5 sensitivity and/or **perceptual bias**.
6
7
8
9

10 11 12 Participants

13
14
15 Twenty participants (10 female, mean age \pm SD: 25.7 ± 2.4 years) took part in Experiment
16
17 2. The experimental protocol was approved by the research ethics committee of the
18
19 Department of Psychology of the University of Bologna. The study adhered to the ethical
20
21 standards of the Declaration of Helsinki. Participants provided their written informed
22
23 consent before the beginning of the experiment.
24
25
26
27
28

29 30 31 Experimental setup

32
33 Transcutaneous electrical nerve stimulation was delivered by means of a Digitimer DS7
34
35 constant current stimulator (Digitimer, Ltd., United Kingdom). Two pairs of self-
36
37 adhesive surface electrodes (SU15N1 electrodes, SEI EMG, Padova) connected to the
38
39 stimulator were applied to the hairy skin of proximal and intermediate phalanges of
40
41 participants' index and middle fingers. Instructions before and throughout the experiment
42
43 were presented using the E-Prime 2.0 software (Psychology Software Tools, Pittsburgh,
44
45 PA), while stimulation was delivered using custom software. Participants rested their
46
47 right hand palm down on a table. Vision of the stimulated hand was blocked with a
48
49 screen.
50
51

52
53 The procedure for establishing tactile detection and pain thresholds was the same
54
55 as Experiment 1. The floor and ceiling levels were set at 2 x detection threshold and 90%
56
57 of the pain threshold, respectively. Again, we selected the 37.5% and 62.5% of the
58
59 stimulation range as small and the large total intensities. Next, we subdivided each total
60

1
2
3 in three different levels of discrepancy: 0% (no discrepancy between the two stimuli),
4
5 70% (low discrepancy) and 100% (maximum discrepancy) (see Figure 1).
6
7

8 Participants performed a brief familiarization task where 30 non-discrepant small
9
10 and large pairs were sequentially presented in random order. Each stimulus was
11
12 associated to an audible beep. Participants were asked to judge the overall intensity of
13
14 each pair by pressing one of two keys corresponding to “small”/“large” total. At the end
15
16 of the task, accuracy was checked (group mean accuracy \pm SD: 81.6% \pm 7.6%).
17
18
19
20

21 Procedure

22
23
24 The procedure of the main experiment was identical to the familiarization task
25
26 described above, with the only exception that each small/large total was delivered at one
27
28 out of the three different levels of discrepancy (0%, 70%, and 100%). The presentation
29
30 order of the stimuli and the localization of the strongest stimulus in the discrepant trials
31
32 (index/middle finger) were randomized within participants. Each stimulus was repeated
33
34 40 times, giving a total of 240 trials. Participants were given a short break every 60 trials.
35
36
37
38
39
40

41 Experiment 3. Perceived intensity of discrepant and non- 42 discrepant double tactile stimulations

43
44
45 Experiment 3 aimed to compare directly the perceived intensity of double simultaneous
46
47 stimulations, either discrepant or non-discrepant, with the perceived intensity of single
48
49 stimuli.
50
51
52
53

54 Participants

55
56
57 Fourteen participants (10 female, mean age \pm SD: 23.9 \pm 4.1 years) participated in
58
59 Experiment 3. Four of these were excluded because their electro-tactile stimulation range
60

1
2
3 was too small (i.e. < 3 mA), leaving a final sample size of $n = 10$. The experimental
4
5 protocol was approved by the research ethics committee of University College London.
6
7 The study adhered to the ethical standards of the Declaration of Helsinki. Participants
8
9 provided their written informed consent before the beginning of the experiment.
10
11
12
13

14 Experimental setup

15
16
17 We used the same experimental setup as in Experiment 1. However, three fingers (index,
18
19 middle and ring fingers) were stimulated during the experiment. Detection and pain
20
21 threshold were assessed separately for each digit in order to level out any eventual
22
23 difference in the perception of electro-tactile stimulation due to physical difference
24
25 between the fingers.
26
27

28
29 In order to extend the range of tactile stimuli deliverable, we established the floor
30
31 at $1.2 \times$ detection threshold, and the ceiling at $90\% \times$ pain threshold of the index finger.
32
33 Then, we set the intensity of the non-discrepant stimulus at 37.5% of participants'
34
35 stimulation range. We calculated the intensities at 70% of the maximum possible
36
37 discrepancy for the same total intensity. Then, for each of the three stimulation levels
38
39 established for the index finger we used a staircase procedure to find the corresponding
40
41 perceived isointensities for the middle and ring fingers, separately. In each staircase, one
42
43 of the three reference intensities was delivered to the index finger first. After 500msec ,
44
45 a comparison stimulus was presented on the target digit (middle or ring finger).
46
47 Participants were asked to press a key to adjust the physical intensity of the second
48
49 stimulus until it matched the intensity of the reference stimulus. At the beginning of the
50
51 staircase procedure, the step size was set at 10% of participant's maximal stimulation
52
53 level for their ring finger (i.e. their pain threshold for ring finger). After the first reversal,
54
55 the step size was reduced from 10% to 5% of participant's pain threshold for ring finger.
56
57
58
59
60

1
2
3 The staircase procedure ended after seven reversals, and the average of the last three
4
5 reversals was taken as the stimulation level for the target finger.
6
7
8
9

10 Procedure

11
12 Experiment 3 aimed to compare the perceived intensity evoked by single (small/large)
13
14 and double (non-discrepant/discrepant) tactile stimulations.
15
16

17 The experiment was divided in four blocks. In each block, participants were
18
19 presented with one ascending and one descending staircase for each of four experimental
20
21 conditions: (1) single small stimulation, (2) single large stimulation, (3) double non-
22
23 discrepant stimulation, and (4) double discrepant stimulation (see Figure 2). The single
24
25 small stimulus corresponded to the intensity of one stimulus of the non-discrepant pair,
26
27 while the single large stimulus corresponded to the strongest stimulus of a discrepant pair.
28
29 The position of the strong stimulus (index/middle finger) in condition 4 (double
30
31 discrepant stimulation) was counterbalanced across two separate staircases, and the
32
33 results from the two staircases were pooled together. The staircase procedure was similar
34
35 to that described above for the pre-testing phase. In each trial, a reference stimulus was
36
37 presented on the index finger alone (single stimulation) or on index and middle fingers
38
39 simultaneously (double stimulation). The comparison stimulus, instead, was always
40
41 delivered on the ring finger. The four blocks were presented in a counterbalanced order
42
43 across participants. In each block, the two staircases (starting from the floor or the ceiling
44
45 level of the ring finger) were randomly interleaved. Each staircase ended after seven
46
47 reversals, and the average of the last three reversals was taken as a measure of the
48
49 perceived intensity in each condition (Levitt, 1970).
50
51
52
53
54
55
56
57
58
59
60

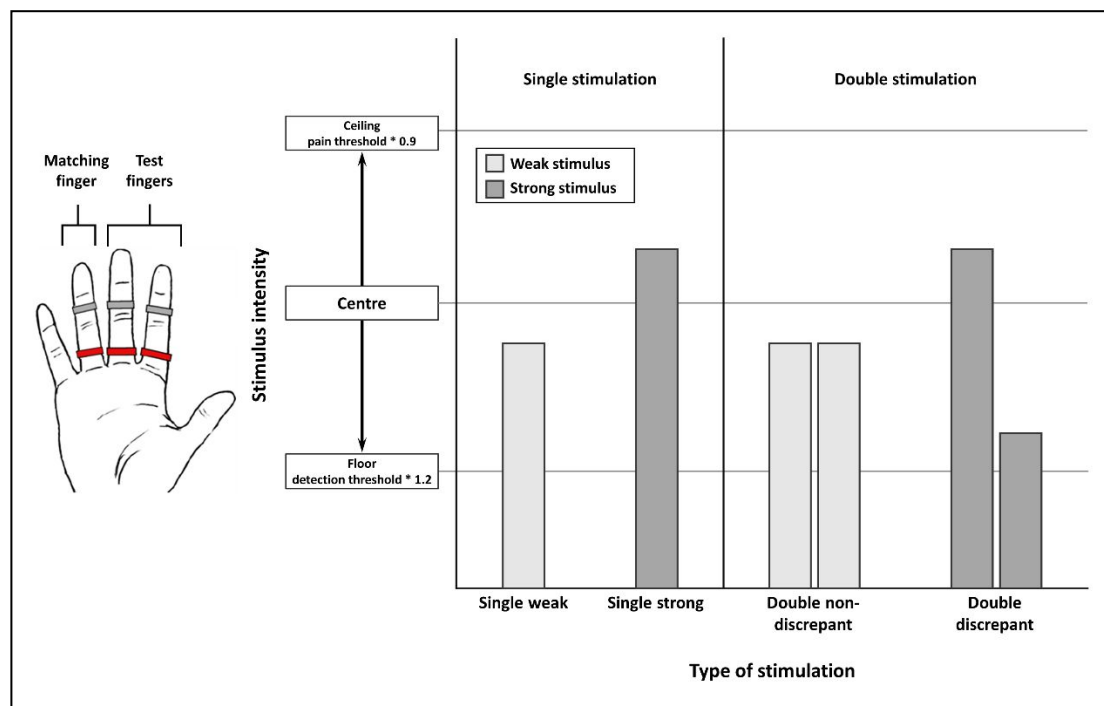


Figure 2. Stimulation of index and middle fingers in Experiment 3, was discrepant or non-discrepant as in Experiment 1. Additional trials delivered weak or strong stimuli either to index or middle fingers alone, matching the intensity of component stimuli in stimulus pairs. Participants adjusted shocks to ring finger to have the same perceived intensity of the stimuli delivered to index and middle fingers.

Results

Experiment 1

To assess whether discrimination of the parts is required in for total intensity perception, we performed a 2 (judgement: aggregation/discrimination) x 2 (total intensity: small/large) repeated measures ANOVA on the accuracy level showed in each condition (see Figure 3). We found a significant main effect of judgement ($F(1, 15) = 14.357$; $p = 0.002$; $\eta^2 = 0.489$). Participants' accuracy in the aggregation task was significantly higher (mean \pm SD: $81.5\% \pm 13.3\%$) than that in the discrimination task (mean \pm SD: $61.88\% \pm 22.4\%$). The main effect of total intensity ($F(1, 15) = 0.122$; $p = 0.732$) and the interaction between factors ($F(1, 15) = 1.115$; $p = 0.308$) were both non-significant. If

aggregation were to depend critically on discrimination, then aggregation performance could not exceed discrimination performance. In fact, the converse was found. Therefore, accurate judgements of total intensity (i.e. aggregation) were possible even for some stimuli that were not readily discriminable.

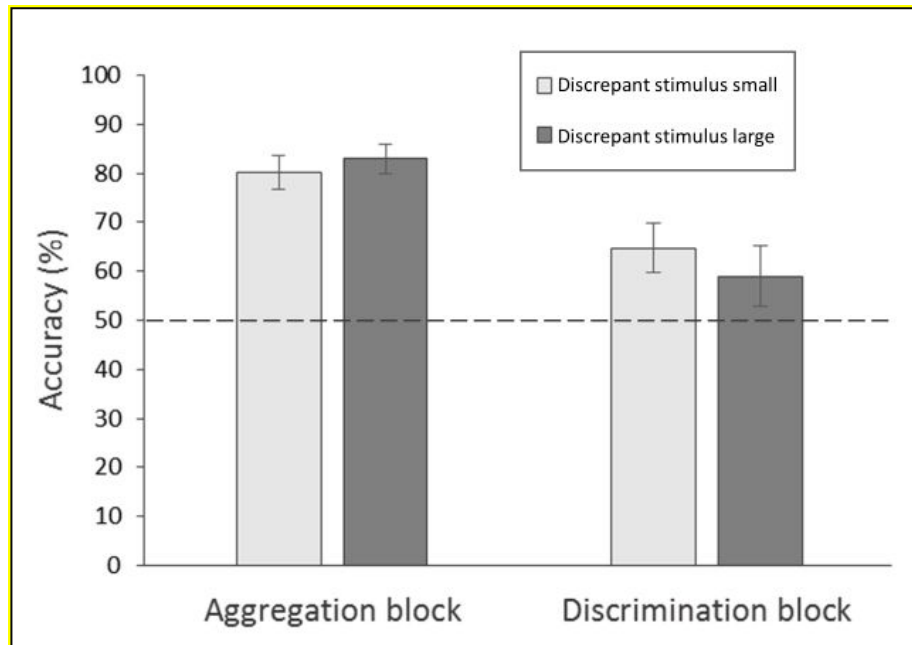
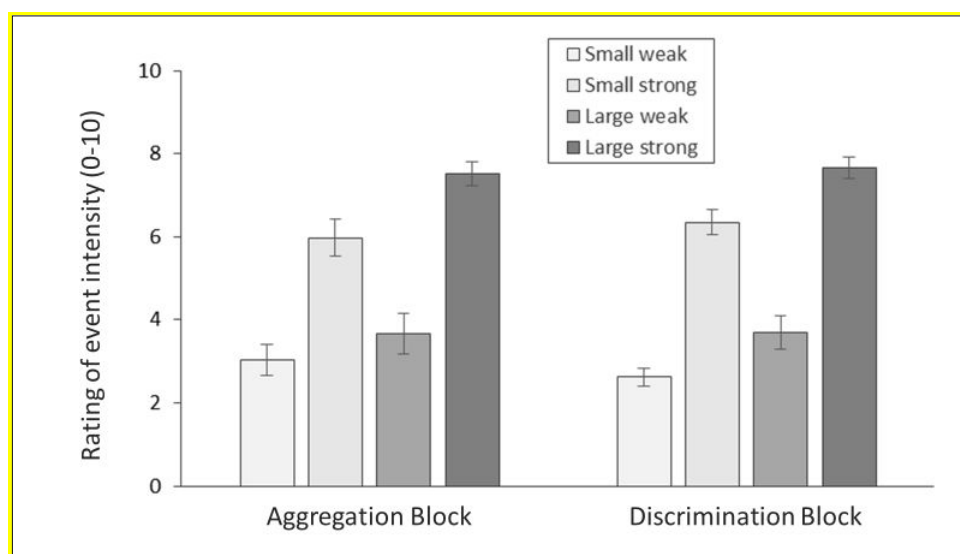


Figure 3. Accuracy in the Aggregation/Discrimination blocks in Experiment 1. Participants' performance was significantly higher in the Aggregation block compared to the Discrimination block. Accurate judgement of total intensity was possible even if discrimination of the overall discrepancy between the stimuli was just slightly above chance level. The dashed line represents the chance level (50%). Error bars show standard error of the mean.

Next, we tested whether the intensity of each single event in a discrepant pair could be retrieved even when participants' attention was mainly directed toward the global features of the percept (i.e. overall intensity or overall discrepancy). To this purpose, we run a 2 (judgement: aggregation/discrimination) x 2 (total intensity: small/large) x 2 (event intensity: weak/strong) repeated measures ANOVA on participants' magnitude estimation in the rating trials. We found no main effect of judgement ($F(1, 15) = 0.086$;

1
 2
 3 $p = 0.774$), but a significant main effect of total intensity ($F(1, 15) = 13.476$; $p = 0.002$;
 4
 5 $\eta^2 = 0.473$) and event intensity ($F(1, 15) = 65.352$; $p < 0.001$; $\eta^2 = 0.813$). No interaction
 6
 7 was significant (all $p > 0.077$). Overall, large totals induced higher magnitude estimation
 8
 9 ratings (mean \pm SD: 5.639 ± 0.273) than small totals (mean \pm SD: 4.498 ± 0.209).
 10
 11 Moreover, regardless of the block and the total intensity, the strong event in the pair was
 12
 13 rated as greater (mean \pm SD: 6.879 ± 0.254) than the weak stimulus (mean \pm SD: $3.256 \pm$
 14
 15 0.325) (see Figure 4). Thus, participants were equally accurate in perceiving the intensity
 16
 17 of single events when the context required them to focus primarily on discrepancies or
 18
 19 totals of stimulus pairs. Put another way, information about the intensity of individual
 20
 21 components was not lost when participants attended to total intensity.
 22
 23
 24
 25
 26
 27
 28
 29
 30
 31
 32
 33
 34
 35
 36
 37
 38
 39
 40
 41
 42
 43
 44
 45
 46



47 Figure 4. Magnitude estimate of single events **in the rating trials presented** in Experiment
 48 1. Participants showed accurate perception of the intensity of each stimulus (weak/strong
 49 event, small/large total) in both the Aggregation and the Discrimination block. Error bars
 50 show standard error of the mean.
 51
 52
 53
 54
 55
 56
 57
 58
 59
 60

Experiment 2

1
2
3 We tested whether our results replicated the nonlinear overestimation bias described by
4 Walsh and colleagues (2016). A 2 (total intensity: small/large) x 3 (discrepancy: 0%,
5 70%, or 100%) repeated measures ANOVA was applied to participants' performance in
6 each condition (see Figure 5a). When the data violated the assumption of sphericity, a
7 Greenhouse-Geisser correction was applied. The analysis revealed no significant effect
8 of total intensity ($F(1, 19) = 0.196; p = 0.663$), but a significant main effect of discrepancy
9 ($F(1.5, 28.8) = 6.509; p = 0.008; \eta^2 = 0.255$). Pairwise comparisons between each level
10 of discrepancy showed that accuracy was significantly lower in the 100% discrepant
11 condition compared to 70% discrepant condition (mean difference: $-6.650; p = 0.021$; CI
12 $-12.182, -1.118$) and 0% discrepant condition (mean difference: $-11.411; p = 0.010$; CI
13 $-19.73, -3.091$). The interaction between total intensity and discrepancy was also
14 significant ($F(1.3, 24.9) = 20.189; p < 0.001; \eta^2 = 0.515$). Pairwise comparisons showed
15 that all discrepancy conditions were significantly different from each other in the small
16 total ($p < 0.001$ in all cases), but not in the large total ($p > 0.232$ in all the cases). Finally,
17 a significant difference between the totals was found both in the 0% and the 100%
18 discrepant condition ($p < 0.014$ in both cases) (see Figure 5a). Overall, participants'
19 accuracy in total intensity judgements significantly decreased as discrepancy increased.
20 Thus, participants showed a systematic overestimation error in judging the total of
21 discrepant stimuli.

22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Next, we used a **Signal Detection Theory (SDT)** approach to investigate whether such overestimation bias was due to a genuine perceptual process and/or to a change in **perceptual bias**. We arbitrarily defined a hit as a "large" response when the large total was presented, and a false alarm as a "large" response when the small total was delivered. Sensory discriminability (d'), calculated as $z(pHIT) - z(pFA)$ **perceptual bias (B)**, calculated as $0.5 * [z(pHIT) + z(pFA)]$, were then estimated from the hit rate and false

1
2
3 alarm rate. First, to compare the perceptual discriminability of double tactile stimulations
4
5 at increasing levels of discrepancy (discrepancy: 0%, 70%, and 100%), we performed a
6
7 one-way repeated measures ANOVA on participants' d' values. Data violated the
8
9 assumption of sphericity, therefore Greenhouse-Geisser correction was applied.
10
11 Discrepancy produced a significant effect on participants' sensitivity (d') ($F(1.5, 29) =$
12
13 $5.446; p = 0.015; \eta^2 = 0.223$). Pairwise comparisons showed that participants' sensitivity
14
15 was significantly higher in the 0% discrepancy condition (mean \pm SD: 2.026 ± 0.86)
16
17 compared to both the 70% (mean \pm SD: $1.614 \pm 0.76; p = 0.029$) and 100% (mean \pm SD:
18
19 $1.472 \pm 0.66; p = 0.017$) discrepancy condition (see Figure 5b). Second, we ran another
20
21 one-way repeated measures ANOVA on the participants' perceptual bias (B) comparing
22
23 the three levels of discrepancy. Although many SDT paradigms cannot distinguish
24
25 between perceptual and decision-based biases (Witt et al., 2015), in our task participants
26
27 could not have a decision-based bias, because the different conditions were presented in
28
29 a completely random fashion. Therefore, we believe we can safely interpret our results
30
31 as a case of perceptual bias. Again, analyses were Greenhouse-Geisser corrected. The
32
33 effect of discrepancy was highly significant ($F(1.3, 25) = 60.907; p < 0.001; \eta^2 = 0.762$).
34
35 Pairwise comparisons showed that as discrepancy increased, participants' perceptual bias
36
37 significantly shifted, producing a higher number of "large" responses ($p < 0.001$ in all
38
39 comparison) (0% discrepancy condition, mean \pm SD: 0.522 ± 0.42 ; 70% discrepancy,
40
41 mean \pm SD: -0.17 ± 0.38 ; 100% discrepancy, mean \pm SD: -0.432 ± 0.42) (see Figure 5c).
42
43 Thus, as discrepancy between the two single intensities increased, the sensitivity to total
44
45 intensity decreased and participants tended to perceive every stimulation as a large total
46
47 (i.e. overestimation bias), regardless of the actual total stimulus intensity.
48
49
50
51
52
53
54
55
56
57
58
59
60

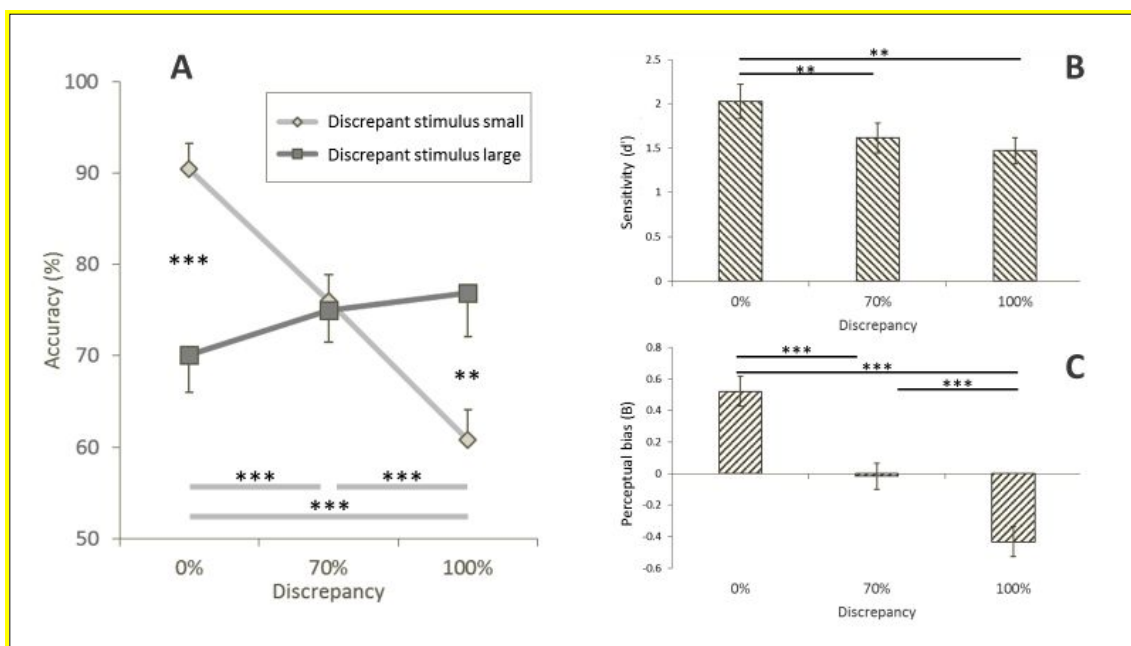


Figure 5. Accuracy, sensitivity, and perceptual bias along discrepancy in Experiment 2. Participants' accuracy (A) decreased along with discrepancy when the discrepant pair had a small total intensity, but not when the discrepant stimulus had a large total intensity. Both sensitivity (B) and perceptual bias (C) were significantly modulated by the discrepancy between the two simultaneous stimuli in the pair. Error bars show standard error of the mean.

Experiment 3

First, as a sanity check for the psychophysical method, we tested whether the results from low- and high-starting staircases converged to similar values. Paired t-tests analyses showed no statistical difference between both measurements in each condition ($p > 0.110$ in all comparisons), confirming convergence of the two staircases.

Hence, the values from ascending and descending staircases were averaged together and analysed in a 2 (number of stimuli: single/double) \times 2 (intensity: small/large) repeated measures ANOVA to evaluate any difference in perceived intensity among the four experimental conditions. We found a significant main effect of intensity ($F(1, 9) = 10.638$; $p = 0.010$; $\eta^2 = 0.542$), but no effect of number of stimuli ($F(1, 9) = 1.758$; $p =$

0.218) nor interaction between the factors ($F(1, 9) = 0.468$; $p = 0.511$). In particular, regardless of the number of fingers stimulated (one or two), participants reported a higher perceived total intensity when a large stimulus was present in the stimulation (mean \pm SD: 6.464 ± 2.04) compared to when the single/double stimulation was composed by the small stimulus/i only (mean \pm SD: 5.738 ± 1.98) (Figure 6). To check whether our non-significant results were due to a lack of statistical power, we conducted a post hoc power analysis using GPower (Faul & Erdfelder, 1992; Erdfelder, Faul, & Buchner, 1996) with power ($1 - \beta$) set at 0.80 and $\alpha = 05$. This showed us that sample size would have to increase up to $n = 46$, far beyond the range of the sample sizes used in previous studies (e.g., Walsh et al., 2016: $n = 10-16$) in order for the main effect of number of stimuli to reach statistical significance at the .05 level. Thus, it seems unlikely that our negative result was due to a limited sample size. Finally, non-significant result was further investigated through a Bayesian analysis, using JASP (version 0.9.2.0; JASP Team 2016, University of Amsterdam) to determine whether results supported the null hypothesis, or could alternatively reflect insufficient statistical power (Rouder et al., 2009; Wetzels, Grasman, & Wagenmakers, 2012). We found that the data about number of stimuli were 2.6 times more likely under the null hypothesis than the alternative hypothesis ($BF_{01} = 2.591$, error = 1.348%), suggesting that the absence of difference between single and double stimuli conditions was not simply due to a lack of statistical power.

Therefore, rather than relying on the actual (physical) total intensity, participants' perception was strongly influenced by the most salient stimulus in the pair only.

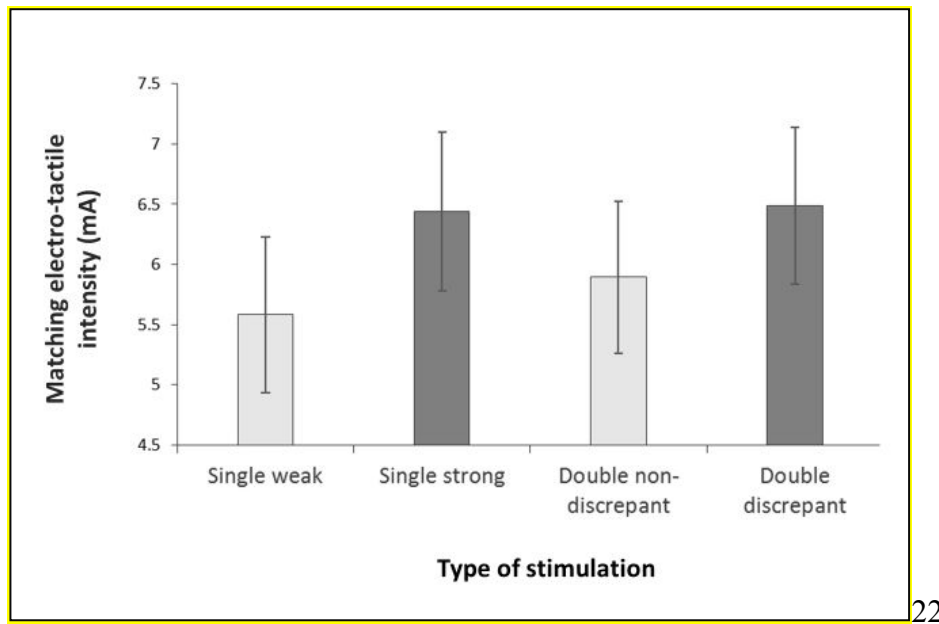


Figure 6. Matching electro-tactile intensity of single/double weak/strong stimuli in Experiment 3. Participants perceived a larger total intensity when a strong stimulus was present in the stimulation, compared to when the single or double stimulation was composed by the small stimulus/i, suggesting that the perception of double discrepant stimulation is strongly biased towards the more salient stimulus in the pair.

Discussion

The sense of touch must deal with multiple, highly diverse stimuli impinging simultaneously on the cutaneous receptors. Psychology of perception has classically studied touch through the presentation of artificially isolated events. The question of why some components of total tactile stimulation are perceptually dominant, while others are neglected, has rarely been addressed. Most discussions invoke peripheral or central adaptation, selective attention, and low bandwidth of tactile perception (see Gallace & Spence, 2014 for a review). Here we investigated the mechanisms underlying the somatosensory integration of double discrepant electro-tactile stimuli.

Across three experiments, we replicated and extended previous findings of nonlinear aggregation of multiple tactile intensities (Walsh et al., 2016). Those authors

1
2
3 suggested that perception of total tactile intensity involves a salience-based
4 overestimation bias: the strongest component stimulus has a disproportionate weighting
5 in the perception of the total. Our study adds several new pieces of knowledge. First, in
6
7
8
9
10 Experiment 1 we showed that (1) the intensity of each component event in a double
11
12
13 stimulation can be correctly perceived (rating trials), and yet, (2) somatosensory
14
15
16 aggregation does not rely on the prior discrimination and separate perception of the
17
18
19 intensity of each independent stimulus component, followed by the simple summation of
20
21
22 those components. Rather perception of total intensity appears to involve specific
23
24
25 processes that occur in addition to the perception and summation of individual component
26
27
28 stimuli. Second, in Experiment 2 we extended the results on the overestimation bias
29
30
31 described by Walsh and colleagues (2016), using a different psychophysical approach.
32
33
34 We found that participants' accuracy in judging the total intensity of increasingly
35
36
37 discrepant pairs significantly decreased when the total was small, but not when the total
38
39
40 was large, confirming the unidirectionality of the overestimation effect found by Walsh
41
42
43 et al. (2016). Small discrepant totals were (mis-)perceived as larger than reality, while
44
45
46 large totals were not affected or, if anything, were also felt as larger than their physical
47
48
49 intensity. Importantly, we also found that sensitivity to overall intensity significantly
50
51
52 decreases as the discrepancy between two events in a tactile percept increases, thus
53
54
55 increasing the probability of perceiving the total as larger than its actual physical
56
57
58 intensity. Last, in Experiment 3, we quantified the extent to which the intensity of a single
59
60
strong stimulus contributes to the perception of the overall intensity of a discrepant pair,
showing that judgements of total intensity of multiple stimulations strongly rely on the
intensity of the most salient stimulus in the percept.

Perception of the single events forming a total tactile percept

1
2
3 Results in Experiment 1 showed that participants accurately perceived intensity of each
4 component in a discrepant double tactile stimulation. Thus, judging the properties of the
5 whole percept (i.e. overall intensity or overall discrepancy) did not affect perception and
6 retrieval of information about the parts. This is in apparent contrast with previous reports
7 about holistic perception in other sensory modalities (Nelson, 1993). Poljac and
8 colleagues (2012), for example, reported that the ability to detect colour changes in a
9 pattern of scrambled dots dramatically drops when the dots can be integrated into a
10 meaningful Gestalt, suggesting that the construction of a visual whole comes at the cost
11 of reduced access to information about its constituent parts. Similarly, Mathis and Kahan
12 (2014) showed that the holistic perception of Kanizsa figures reduces the identification
13 of local-level elements such as edges. Auditory studies (Wile & Balaban, 2007;
14 Schneider & Wengenroth, 2009) suggest that the perception of a holistic virtual pitch (an
15 illusory tone derived by the nonlinear integration of multiple simultaneous pure tones)
16 prevents the detection of changes in some of its components, giving rise to several illusory
17 phenomena such as the *Shepard scale illusion* (Shepard, 1964), the *phantom fundamental*
18 (Turner, 1977), and the *tritone paradox* (Deutsch, 1986). Although still in debate
19 (Nelson, 1993; Cacciamani et al., 2014), these findings are often quoted as evidence that
20 when stimuli are processed as integrated wholes, access to the component parts is lost or
21 reduced.

22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
Increasing evidence suggests that grouping of multiple stimuli in a unitary Gestalt
can also occur for somatosensory stimuli (Kitagawa et al., 2009; Chang et al., 2007;
Carter et al., 2008; Serino et al., 2008; for a review see Gallace & Spence, 2011),
However, to our knowledge this is the first attempt to investigate how the properties of a
tactile whole relate to the perception of its parts. In Experiment 1 (rating trials), we
unpredictably asked participants to report the intensity of a single event while they

1
2
3 performed a task requiring perception of multiple stimuli (overall intensity/discrepancy).
4
5 An account of somatosensory integration based on the effects described above for visual
6
7 and auditory modalities would predict that judging a compound tactile stimulus for either
8
9 total intensity or discrepancy, should produce the loss of specific information regarding
10
11 each individual component. However, participants remained accurate in magnitude
12
13 estimations of single stimuli in Experiment 1. This demonstrates that the perception of
14
15 the single stimuli was not affected by the holistic judgements required by the main tasks.
16
17

18
19 A crucial difference between our paradigm and the studies above (Poljac et al.,
20
21 2012; Mathis and Kahan, 2014) is that our whole/part judgements were given in separate
22
23 trials, rather than together. This might have potentially brought to a situation in which
24
25 participants switched very rapidly from a “holistic mode” to an “analytic mode” (Foard,
26
27 and Nelson, 1984), instead of processing the information in parallel. Yet, such a
28
29 possibility seems unlikely for at least **three** reasons. First, rating trials were significantly
30
31 rarer than main trials in Experiment 1. Therefore, it seems quite reasonable to assume
32
33 that participants maintained a “holistic mode” during the entire course of each block, as
34
35 a strategy based on attending to both tasks simultaneously would have been overly slow
36
37 and effortful. Second, **the rating trials occurred in a completely unpredictable fashion**
38
39 **throughout the experiment, and participants were not informed about the type of trial until**
40
41 **its very presentation. Thus, it was virtually impossible for the participants to adjust their**
42
43 **strategy in function of the type of trial. Finally,** studies using the *global-local task* in
44
45 visual perception (Navon, 1977; Kimchi, 1992; for a review, see Kimchi, 2015) show that
46
47 global features have precedence over local features, such that perception of the whole
48
49 typically recruits attentional resources more readily and automatically than perception of
50
51 the constituent parts (but see also Davidoff et al., 2008).
52
53
54
55
56
57
58
59
60

1
2
3 Thus, our results suggest that the intensity of single stimuli in a tactile whole can
4 be successfully retrieved in spite of the fact that attention is directed towards the global
5 characteristics of the percept. The somatosensory system may be relatively exempt from
6 the 'global dominates local' phenomena in other sensory modalities. Importantly,
7 therefore, information about individual component stimuli could remain available for
8 further computations, such as the estimation of the salience of each stimulus in the
9 percept.
10
11
12
13
14
15
16
17
18
19
20
21
22

23 Aggregation versus discrimination of multiple stimuli

24 Perception of total intensity could rely on two alternative processes. One possibility is
25 that aggregation involves first perceiving each individual stimulus, and subsequently
26 summing all the individual components. Alternatively, aggregation of intensity could
27 rely on a specific module, independent from the precise discrimination of single events.
28 Previous results suggest that this module would be strongly influenced by the salience of
29 stimuli (Walsh et al., 2016).
30
31
32
33
34
35
36
37
38

39 On the first account, information about single intensities is indeed available (as
40 suggested by rating trials in Experiment 1). Therefore, a simple comparison could
41 compute the discrepancy between one stimulus and another. On this view, the
42 discrepancy between any pair of inputs should remain available for report. Yet, our
43 results from the discrimination block in Experiment 1 showed that discrepancy perception
44 was surprisingly poor, even when information about individual component intensities was
45 fully processed (as shown by rating trials). The comparative information about the
46 difference between their intensities was either lacking or inaccessible to perceptual
47 awareness.
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 Conversely, results from the aggregation block (Experiment 1) show that the total
4
5 intensity of a tactile stimulation was above 80% even if the single parts composing it
6
7 could not be separated and discriminated equally well (~60% accuracy). This finding
8
9 clearly supports the idea that somatosensory aggregation occurs automatically and
10
11 without requiring individuated perception of each component. Therefore, total intensity
12
13 of multiple inputs must be computed through perceptual mechanisms of weighted
14
15 summation which are independent from the perceptual individuation of component
16
17 stimuli, yet are related to their relative intensities.
18
19

20
21 Our result indicates that the intensity of two simultaneous events is poorly
22
23 discriminated. This is in line with previous studies investigating masking tasks (Craig,
24
25 1976; von Békésy, 1967) and double simultaneous stimulation tasks (Sherrick, 1964;
26
27 Tamè, Farnè, & Pavani, 2011). In such paradigms, the *detection* of a tactile event
28
29 drastically deteriorates when the stimulus is presented in spatial and temporal proximity
30
31 with a distractor. Even though in our task participants were asked to judge the *intensity*
32
33 of the single events, rather than simply detecting the stimuli, it is possible that the same
34
35 mechanisms of competition and limited sensory bandwidth described for masking and
36
37 DSS are responsible for the relatively low accuracy in this task. In contrast, our finding
38
39 that the same double simultaneous stimuli are more accurately aggregated than
40
41 discriminated is entirely novel for at least two reasons. First, while an ever-increasing
42
43 number of studies focus on the integrative effects taking place between different sensory
44
45 modalities (e.g. Redundant Target Effect, Foster et al., 2002; Crossmodal Congruency
46
47 Effect, Spence, Pavani, Maravita, & Holmes, 2008), our aggregation task required the
48
49 integration of multiple *unimodal* (i.e. purely tactile) stimuli. Second, while most of the
50
51 paradigms mentioned above are based on reaction times and stimulus detection, in our
52
53 task, participants were instead asked to judge the *total intensity* of multiple touches.
54
55
56
57
58
59
60

1
2
3 Memory for somatosensory stimuli is reportedly very short, lasting for about 700ms
4
5 (Harris et al., 2002). However, in the two-alternative forced choices paradigm used in
6
7 Experiment 1 there was a 1s interval between the first and the second pair of stimuli.
8
9 Therefore, one may argue that an alternative explanation for participants' scarce accuracy
10
11 in discrepancy detection might be ascribed to limited mnemonic resources. Although our
12
13 data cannot entirely rule out this possibility, it is important to note that the same 1s delay
14
15 was present in the aggregation block, where participants showed significantly higher
16
17 performance. Our results show a distinctive limitation of tactile information-processing
18
19 in comparing two distinct simultaneous sensations, even under circumstances where
20
21 those sensations can be successfully aggregated. This finding is consistent with the low
22
23 bandwidth or perceptual capacity reported for touch (Gallace & Spence, 2014).
24
25
26
27
28
29
30

31 Mechanisms underlying overestimation of multiple discrepant 32 stimuli 33 34

35
36 In line with Walsh and colleagues (2016), our findings from Experiment 2 show a
37
38 characteristic error in aggregation of multiple somatosensory stimulation. The total
39
40 intensity of discrepant stimuli is systematically overestimated. Walsh and colleagues
41
42 (2016) proposed that the overestimation of discrepant stimuli is driven by a perceptual
43
44 peak-bias mechanism relying on the salience of each stimulus. However, such a
45
46 hypothesis was not yet properly supported by a model describing how salience is first
47
48 computed, and then used in subsequent weighted summation.
49
50

51
52 First, one might ask whether overestimation of discrepant intensities reflects an
53
54 inherent property of the somatosensory system, or is rather a cognitive strategy. Peak-
55
56 biased judgements have been described in social, affective, and cognitive psychology for
57
58 a variety of situations (Carmon & Kahneman, 1996; Morewedge, Gilber, & Wilson, 2005;
59
60

1
2
3 Kemp, Burt, & Furneaux, 2008). We used a signal-detection paradigm to dissociate
4 perceptual sensitivity to total stimulation intensity from decision biases (Green & Sweets,
5 1996). We found that as the discrepancy between the two stimuli increased, participants'
6 sensitivity to total intensity decreased significantly. That is, discrepant pairs were
7 perceived as more intense than non-discrepant pairs having the same total intensity.
8 Interestingly, the decrease in d' was accompanied by a significant change in **perceptual**
9 **bias**. Participants **perception of the small/large totals significantly shifted as discrepancy**
10 **increased, inducing participants to judge** all double stimulations as 'large', irrespective of
11 their actual total intensity.
12
13
14
15
16
17
18
19
20
21
22

23
24 Thus, Experiment 2 suggests that overestimation of discrepant intensities depends
25 on a genuinely perceptual process. Yet, it still remains unclear what kind of sensory
26 mechanism could lead to such a supra-additive effect. Nonlinear interactions between
27 multiple unimodal somatosensory stimuli have been previously described. However,
28 they traditionally refer to sub-additive phenomena attributable to lateral inhibition.
29 Lateral inhibition is a well-known form of interaction between multiple somatosensory
30 stimuli (von Békésy, 1967; DiCarlo & Johnson, 1999, 2000; DiCarlo, Johnson, & Hsiao,
31 1998). This mechanism tends to suppress the response to a stimulus when another, nearby
32 region of the receptor surface is strongly stimulated. Therefore, lateral inhibition
33 increases contrast sensitivity and sharpens tactile discrimination between multiple
34 simultaneous stimuli: only the strongest signal is available for further analysis, while the
35 surrounding signals are damped.
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50

51
52 Our results from Experiment 3 are consistent with a strong effect of lateral
53 inhibition: adding an additional stimulus did not significantly increase perceived total
54 intensity. However, lateral inhibition alone appears unable to account for the
55 overestimation of discrepant stimuli, since discrepant pairs were perceived as larger than
56
57
58
59
60

1
2
3 equally-intense non-discrepant pairs (see also Walsh et al., 2016). In other words, lateral
4 inhibition might reduce, but should never boost, total perception, therefore an additional
5 process is needed to explain our overestimation result.
6
7
8

9
10 Figure 7 schematically depicts a scenario for comparing the total intensity of two
11 different tactile pairs. Crucially, as in our task, the overall physical intensity of the two
12 pairs is comparable. Within each pair, however, the distribution across the fingers varies,
13 providing non-discrepant (A) or discrepant (B) conditions.
14
15
16
17

18
19 First, when two stimuli (x_1 and x_2) are simultaneously delivered on adjacent fingers,
20 lateral inhibition produces a mutual reduction of both signals. The effect of this inhibition
21 on each individual digit (l_i) is assumed to depend on the stimulation of the fingers
22 adjacent to it:
23
24
25
26
27
28

$$l_i = (x_{i-1} + x_{i+1}) \cdot c$$

29
30 Thus, for each finger (i), the sum of the physical intensity delivered to the fingers adjacent
31 to it (x_{i-1}, x_{i+1}) is multiplied by a constant value (c). For non-discrepant stimulus pairs,
32 lateral inhibition affects both component stimuli equally. In contrast, for discrepant pairs,
33 the stronger stimulus will produce a stronger inhibition on the weaker stimulus, and will
34 itself be less inhibited by the weaker stimulus. **Importantly, given that lateral inhibition**
35 **linearly depends on the intensity of the two adjacent fingers, if the same overall intensity**
36 **is redistributed across fingers, then the overall lateral inhibition is also invariant.** That is,
37 lateral inhibition enhances discrepancies between individual component stimuli, but,
38 other things being equal, has no net effect on total intensity.
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53

54 The rating trials from Experiment 1 show that, at this stage, the intensity of each
55 event in the discrepant pair (B) can be correctly detected and reported. Importantly,
56 results from our Experiment 3 provide a direct measure of the parameter c . Comparing
57
58
59
60

1
2
3 the perceived intensity of a single stimulus with its double, non-discrepant version, we
4
5 found that the latter was perceived only slightly (and non-significantly) larger than the
6
7 former. This suggests that our paradigm produced strong lateral inhibition. We estimated
8
9 the value of c in our data using a version of the interaction ratio (Ruben et al., 2006; Hsieh
10
11 et al., 1995). This measure of lateral inhibition computes the normalised difference
12
13 between the perceived intensity of a double stimulation and the linear summation of each
14
15 single event:
16
17
18
19
20

$$21 \quad c = \frac{[perceived\ int(x_1) + perceived\ int(x_2)] - perceived\ overall\ int}{22 \quad [perceived\ int(x_1) + perceived\ int(x_2)]}$$

23
24
25
26
27
28 In particular, in line with previous results (Ruben et al., 2006) in our data from
29
30 Experiment 3, c was 0.46 ± 0.07 SD.
31
32

33 At the second stage of somatosensory integration, the *salience* of each stimulus is
34
35 computed, and then forwarded to the next module, for the appropriate weighted
36
37 summation. We suggest that the *salience* of each event (w_i) is calculated after the lateral
38
39 inhibition stage, as a function of the ratio between each single event and the average
40
41 intensity of all the concurrent stimulations.
42
43
44
45

$$46 \quad w_i = \frac{x_i}{\bar{X}}$$

47
48
49
50 On this view, a salient signal is one that stands out from the average intensity of
51
52 concurrent, irrelevant, stimulations (noise). According to this definition, in the case of
53
54 the non-discrepant pair, the weighting factor for each stimulus will obviously be always
55
56 equal to one. Crucially, in the case of the discrepant pair, instead, the stronger stimulus
57
58
59
60

1
2
3 will receive a weight above unity. This effectively amplifies the intensity of this
4
5 component, and biases the perception of the whole percept.
6

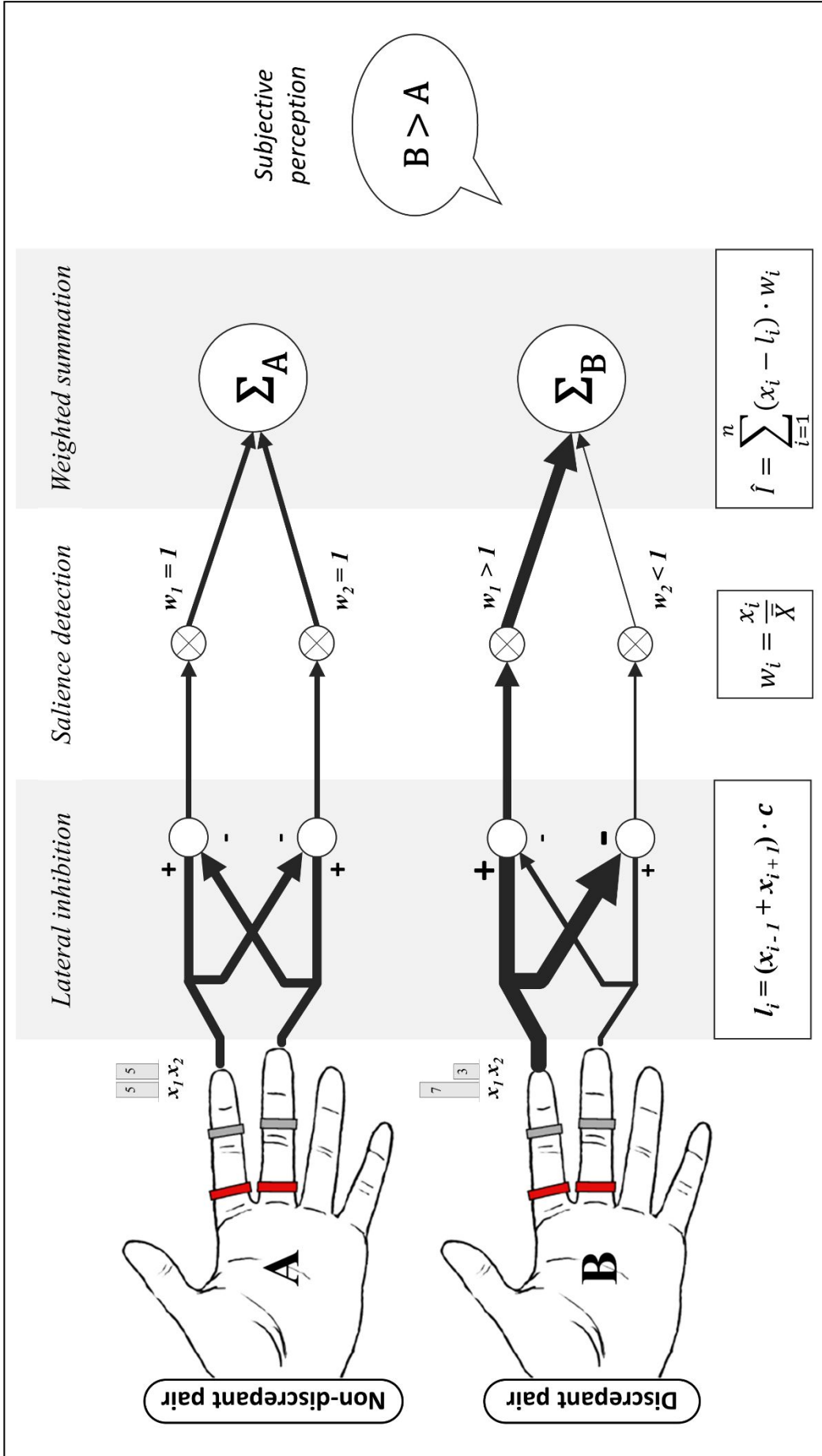
7
8 Finally, in a third stage, the estimation of the overall intensity of each pair can be
9
10 computed according to:

$$11 \quad \hat{I} = \sum_{i=1}^n (x_i - l_i) \cdot w_i$$

12
13
14
15
16
17 where the physical intensity of each event x_i – net of its corresponding lateral inhibition
18
19 value l_i – is multiplied by its respective weight w_i and summed across all components of
20
21 the total stimulation.
22
23

24
25 Our model of salience detection is coherent with the classical neural model of
26
27 *divisive normalisation* (Carandini & Heeger, 2011; Heeger, 1992; Carandini, Heeger, &
28
29 Movshon, 1997). According to the divisive normalisation model, the initial input-driven
30
31 activity of a neuron is divided by the summed activity of a large pool of neighbouring
32
33 neurons (Louie, Khaw, & Glimcher, 2013). Divisive normalisation has proven to be a
34
35 useful model to explain nonlinear responses in the visual (Heeger, 1991, 1992; Albrecht,
36
37 & Geisler, 1991), olfactory (Olsen, Bhandawat, & Wilson, 2010), and auditory system
38
39 (Rabinowitz, Willmore, Schnupp, & King, 2011; David, Mesgarani, Fritz, & Shamma,
40
41 2009), as well as multisensory (Ohshiro, Angelaki, & DeAngelis, 2011) and even
42
43 cognitive processes (Louie, Khaw, & Glimcher, 2013; Louie Grattan, & Glimcher, 2011;
44
45 Reynolds & Heeger, 2009). Although the divisive normalisation model has been
46
47 classically interpreted as a canonical mechanism for maximising sensitivity (Brouwer,
48
49 Arnedo, Offen, Heeger, & Grant, 2015) and reducing redundancy (Sinz & Bethge, 2013),
50
51 our results suggest it could also contribute to perceptual aggregation of multi-component
52
53 stimuli.
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



1
2
3 Figure 7. Putative model of somatosensory integration of multiple discrepant and non-
4 discrepant stimuli. A. When non-discrepant multiple simultaneous somatosensory
5 stimuli are aggregated in a total percept, the physical intensity delivered to each finger (i)
6 is first reduced by lateral inhibition (l_i) (top left of the scheme). Experiment 1 shows that
7 at this stage, the intensity of each input after lateral inhibition is retrievable. Next, in non-
8 discrepant pairs, the salience value is the same for both stimuli. Therefore, the weight
9 assigned to each stimulus (w_i) is 1 (top centre of the scheme), and the weighted summation
10 of the events only reflects the sub-additive effect of lateral inhibition (top right of the
11 scheme). B. Multiple discrepant stimuli are also subject to lateral inhibition from the
12 adjacent fingers. However, the amount of lateral inhibition is different among the stimuli,
13 with the weak stimuli producing less inhibition of the strong stimuli (bottom left of the
14 scheme). Single stimulus intensity of discrepant patterns after lateral inhibition is also
15 accessible. Next, as the strong stimulus is larger than the average intensity of the multiple
16 stimulation, the weight assigned to it is > 1 , while the weight of the weak stimulus is < 1
17 (bottom centre of the scheme). Finally, the weighted summation of the discrepant pair is
18 biased towards the strong stimulus in the pattern (bottom right of the scheme). As a result,
19 the comparison between equally-intense non-discrepant and discrepant pairs produces an
20 overestimation of the discrepant pattern, driven by the salience of the strongest stimulus
21 (far right of the scheme).
22
23
24
25
26
27
28
29

30 Interestingly, a recent fMRI study used *divisive normalisation* models to explain
31 the suppression of somatosensory responses during concurrent stimulations of different
32 digits (Brouwer, Arnedo, Offen, Heeger, & Grant, 2015). In particular, Brouwer and
33 colleagues (2015) speculated that interdigit suppression (i.e. lateral inhibition) may be
34 evident in the subregions of S1 in which each neuron responds to only one digit, while
35 normalization is stronger in subregions of S1 that have neurons with larger receptive
36 fields encompassing more than one digit (Krause et al., 2001; Besle et al. 2013, 2014).
37
38
39
40
41
42
43
44
45

46 All our experiments involved simultaneous double stimulation. Different salience
47 mechanisms apply when processing a series of stimuli. For example, in oddball tasks
48 (Squires, Squires, & Hillyard, 1975; Halgren, Marinkovic, & Chauvel, 1998), the oddball
49 is salient because it deviates from a predictive model learned from previous stimuli. Such
50 effects can also be described as a form of central adaptation. In principle, divisive
51 normalization mechanisms for simultaneous stimuli might interact with central adaptation
52 mechanisms. For example, Tamè and colleagues (2015) have shown that lateral
53
54
55
56
57
58
59
60

1
2
3 inhibition is responsible for a strong repetition suppression (i.e. a decrement of neuronal
4 responses for repeated presentation of a stimulus) during simultaneous tactile stimulation
5 of non-homologous fingers. In contrast, neural adaptation accounts for repetition
6 suppression effects for consecutive stimuli delivered to homologous fingers. Thus,
7 several mechanisms, both spatial and temporal, may contribute to salience, but our
8 investigation focusses particularly on lateral inhibition between simultaneous stimuli.
9
10
11
12
13
14
15
16
17
18
19

20 Simulations

21
22 We ran two separate simulations to test our salience model against a model based on
23 lateral inhibition only and against the actual data from Experiment 2 and 3, respectively.
24
25
26
27
28
29

30 Model comparison between the salience model and the lateral inhibition 31 model in Experiment 2

32
33
34 First, we used the formula for our salience model

$$35 \hat{I} = \sum_{i=1}^n (x_i - l_i) \cdot w_i$$

36
37
38
39
40
41
42
43
44 to estimate each participants' perceived total intensity (\hat{I}) in each condition of Experiment
45 2. For each individual participant, we fed the model with each stimulus intensity (x_i)
46 constituting either the small or the large totals along the three levels of discrepancy (0%,
47 70%, and 100%). Similarly, we estimated participants' perception as predicted by a
48 lateral inhibition model by simply removing the salience weighting parameter (w_i) from
49 our original formula, thus obtaining:
50
51
52
53
54
55
56
57
58
59
60

$$\hat{I} = \sum_{i=1}^n (x_i - l_i)$$

Then, to compare the output of either model with the experimental data from Experiment 2, we converted both measures into percentage change (in accuracy for performance data, or perceived intensity for model predictions) between each discrepant condition (70% and 100%) and the non-discrepant condition (0% discrepancy: baseline). That is, we computed $\Delta\%(\text{condition}) = (\text{condition} - \text{baseline}) / \text{baseline}$. This captures the fact that larger discrepancies should have greater effects on perception of the average. Figure 8 shows the percentage change for each total (small/large) in the experimental data and both models.

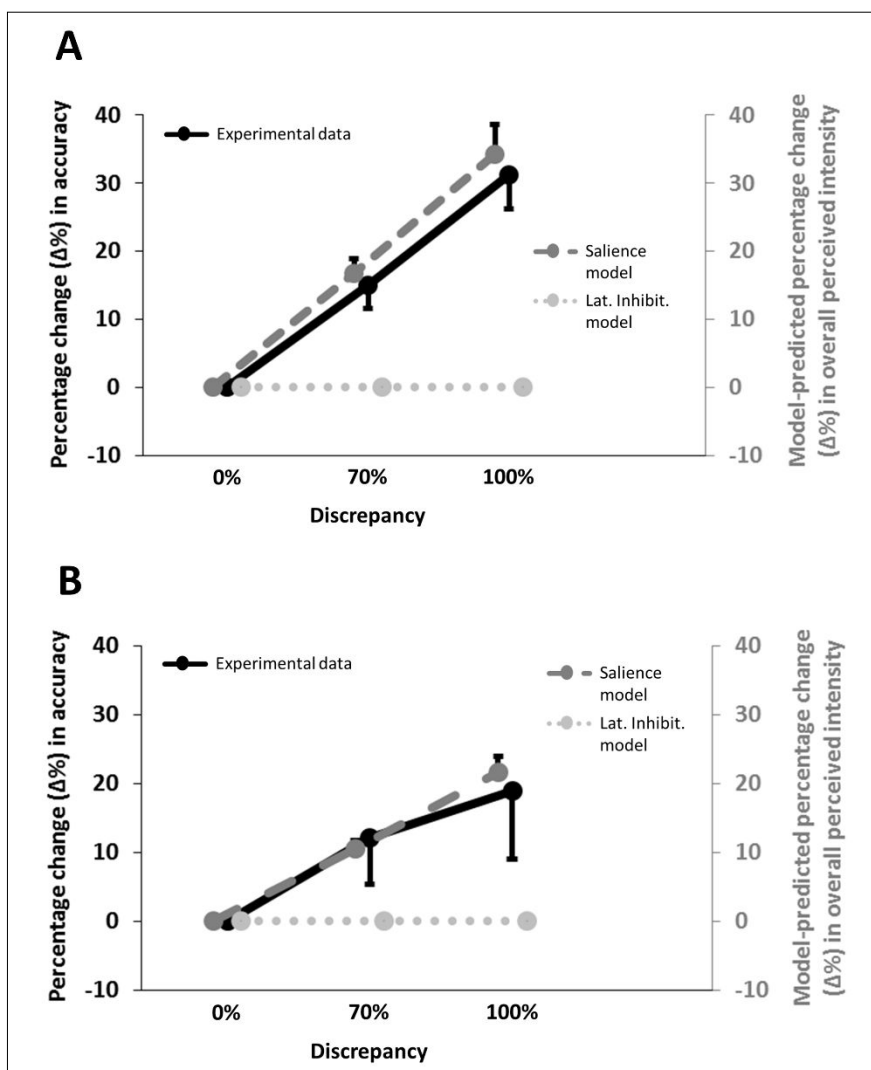


Figure 8. Actual and predicted percentage change between the non-discrepant condition (0%) and the two discrepant conditions in Experiment 2 (70%, 100%) for the small (A) and the large (B) totals. Experimental data (black line) are referred to the left Y axis, and perceived intensities predicted by the models (grey lines) are referred to the right Y axis. The lateral inhibition model (dotted grey line) predicts no change in perception of overall intensity as a function of discrepancy. Error bars show standard error of the mean.

To evaluate the models shown in figure 8, we used Akaike Information Criterion (AIC) (Akaike, 1973, 1978; Bozdogan, 1987), following the procedures of Wagenmakers & Farrell (2004). Briefly, we first calculated the AIC values for each model, using the small-sample correction value AICc (Burnham & Anderson, 2002). We then computed $\Delta(\text{AICc})$, as the difference between the AICc score of each model minus that of the best

model, and the Akaike weights, $w(AICc)$, as the normalised probability of each model being the best model given the data and the set of candidate models (with the sum of all weights of the set being equal to 1). Finally, we calculated an evidence ratio by converting these probabilities to odds.

Table 1 shows the AIC results for the salience model and the lateral inhibition model, for the small and large total intensities. The evidence ratio (defined as the ratio between the Akaike weights of one model over the other) showed that the salience model was 1.66×10^7 times more likely than the lateral inhibition model in fitting the data for the smaller total intensity, and 5.84 times more likely for the large total.

<i>Model</i>	<i>No. Par</i>	<i>AIC</i>	<i>AICc</i>	$\Delta(AICc)$	$w(AICc)$	<i>ER</i>
<i>Small total</i>						
Salience model	1	355.06	355.13	0	> 0.999	1.66×10^7
Lateral inhibition	1	388.31	388.38	33.24	< 0.001	
<i>Large total</i>						
Salience model	1	417.73	417.80	0	0.85	5.84
Lateral inhibition	1	421.26	421.33	3.53	0.15	

Table 1. Results of the model comparison analysis using AIC to quantify the goodness of fit of the salience model vs. the lateral inhibition model for the small (top) and large (bottom) totals tested in Experiment 2.

Model comparison between the salience model and the lateral inhibition model in Experiment 3

In a second comparison analysis, we tested the goodness of fit of the salience model against the lateral inhibition model in fitting the data from Experiment 3. Again, we fed each model with the physical intensities delivered during of single/double, non-discrepant/discrepant stimuli. Then we computed the percentage change between the single weak stimulus condition and all the other conditions in both real and predicted data (see Figure 9). As expected, both models produced the same results for the double non-discrepant condition, where the two inputs have equal salience. However, the models

deeply diverged in the double discrepant condition. While the lateral inhibition model predicted the same total intensity for double discrepant and non-discrepant pairs, the salience model predicted an overestimation of the total intensity of the discrepant pair, due to a higher weighting of the strongest stimulus in the pair. Again, a model comparison analysis using AIC (see Table 2) strongly favoured the salience model showing that it was 104.4 times more likely than the lateral inhibition model.

Thus, a simple model of salience-based weighting was able to describe and explain overestimation of total intensity of double simultaneous stimulations at increasing level of discrepancy.

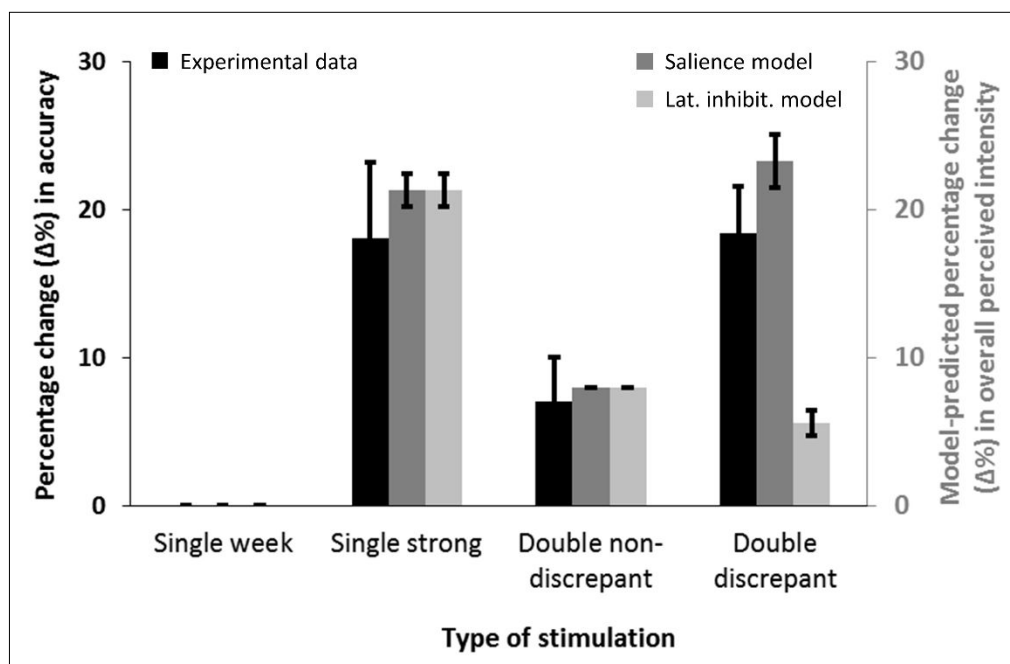


Figure 9. Actual and predicted percentage change between the single weak stimulus condition and the other conditions in Experiment 3 (single strong, double non-discrepant, double discrepant). Experimental data (black bar) are referred to the left Y axis, and predicted intensities (grey bars) are referred to the right Y axis. Both models predicted the same results for the double non-discrepant condition, where the two inputs had equal salience. However, the two models produced very different outcomes for the double discrepant condition, where one stimulus in the pair was more salient (was stronger than the average of the total stimulation). Note that model performance is consistent with the previous simulations of Experiment 2 (see Figure 8), where the lateral inhibition model predicted no change in perception of overall intensity at different levels of discrepancy. Here, the numerical difference between the non-discrepant and discrepant double

stimulations for the lateral inhibition model is due to the fact that the intensity of x_1 and x_2 in Experiment 3 were adjusted to be perceptually, rather than physically identical. Error bars show standard error of the mean.

<i>Model</i>	<i>No. Par</i>	<i>AIC</i>	<i>AICc</i>	$\Delta(AICc)$	$w(AICc)$	<i>ER</i>
Saliency model	1	208.87	208.98	0	0.99	104.4
Lateral inhibition	1	218.17	218.27	9.30	0.01	

Table 2. Results of the model comparison analysis on the conditions of Experiment 3. AICc weights strongly favoured the saliency model over the lateral inhibition model.

Saliency, attention and integration

We have assumed that the more intense stimulus of a pair is also the more salient. In general, physiological responses such as startle confirm that intense stimuli are, ipso facto, highly salient (Koch, 1999; Yeomans, Li, Scott, & Frankland, 2002; Davis, 1984; Landis & Hunt, 1939). In the psychological literature, however, saliency may be used in a different sense, to mean a stimulus that stands out from other, distractor stimuli. In this second sense, a less intense stimulus might potentially be salient within a field of more intense stimuli. Our study follows the first principle, namely that more intense stimuli are more salient than less intense stimuli. Intense stimuli attract attention and trigger orienting reactions, since they represent potential threats. In neuropsychology, saliency has typically been studied in the context of exogenous attention (Corbetta & Shulman, 2002), and is thought to trigger *selective* processing. For example, a sudden flash at a particular spatial location triggers attention, and gaze shifts, to *that* location. Our studies show that saliency also has important effects on non-selective, integrative processing, in this case the aggregation of component stimuli to form a common, overall percept. Interestingly, the effects of saliency on integrative processing are amplificatory, as also

1
2
3 are many effects of salience on selective processing. It remains unclear whether effects
4 of salience on perceptual aggregation represent a failure of selectivity (e.g., a leakage of
5 selection-based modulations of gain to surrounding stimuli), a non-specific effect of
6 salience such as arousal, or a specific mechanism for enhancing processing stimuli that
7 are both intense and spatially extensive (and perhaps therefore particularly threatening).
8
9

10
11
12
13
14 **Given that our overestimation effect was clearly explained by a model involving**
15 **divisive normalisation but not by a model involving lateral inhibition only, neural**
16 **populations with multidigit receptive fields in Brodmann areas 1 and 2 (Krause et al.,**
17 **2001) may underly our saliency-detection mechanism.** In any event, our results suggest
18 that the traditional focus in perceptual psychology on the link between salience and
19 selectivity is only one aspect of saliency.
20
21
22
23
24
25
26
27
28
29
30
31

32 Conclusion

33
34 Our study sheds light on the cognitive processes underlying the integration of multiple
35 simultaneous tactile stimuli to produce an overall percept. Despite the fact that such
36 stimuli constitute the rule – rather than the exception – of our daily interactions with the
37 environment, to our knowledge this is the first attempt to uncover the mechanisms behind
38 the integration of discrepant intensities in a single percept.
39
40
41
42
43
44

45
46 Across three experiments, we demonstrated that: (1) when the individual
47 components of a multi-touch stimulus are discrepant, the perceived total intensity is
48 overestimated; (2) the underlying mechanism appears to be an increased weighting of
49 more salient stimuli in the cognitive process of aggregating the individual components;
50 (3) this salience-based reweighting reflects a change in perceptual sensitivity, rather than
51 a cognitive heuristic or response bias; (4) the reweighting process is not a trivial
52 consequence of merging or ‘funneling’ of the component stimuli, since it is present even
53
54
55
56
57
58
59
60

1
2
3 when participants clearly perceive two distinct stimuli, and can report the intensity of
4
5 either stimulus alone; (5) the reweighting process is pre-attentive and automatic, since
6
7 overestimation can occur even when the discrepancy between individual component
8
9 stimuli cannot be perceived; (6) the data can be explained by a simple model that uses
10
11 divisive normalisation to compute the salience of component stimuli, and then weights
12
13 the contribution of each component to the total percept by its salience.
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Acknowledgements

We thank Miriam Adorno for helping with data collection.

Declaration of Conflicting Interests

The Authors declare that there is no conflict of interest.

Funding

AC was supported by a PhD fellowship from the Italian Ministry of Education, Universities and Research (MIUR) and by a donation by Dr Shamil Chandaria to the Institute of Philosophy, School of Advanced Study, University of London. ERF was supported by The British Academy Award [grant number SG162313]. PH was additionally supported by a European Research Council Advanced Grant HUMVOL [323943], by a Medical Research Council Project Grant [MR/M013901/1], and by a research collaboration grant from NTT Japan.

References

- Akaike, H. (1973). Problems of control and information. In *2nd International Symposium on Information Theory, Budapest: Akademiai Kiado* (pp. 267-281).
- Akaike, H. (1978). On the likelihood of a time series model. *The Statistician*, 27, 217-235.
- Albrecht, D. G., & Geisler, W. S. (1991). Motion selectivity and the contrast-response function of simple cells in the visual cortex. *Visual Neuroscience*, 7(6), 531-546.
- Bensmaia, S. J. (2008). Tactile intensity and population codes. *Behavioural Brain Research*, 190(2), 165-173.
- Besle, J., Sánchez-Panchuelo, R. M., Bowtell, R., Francis, S. T., & Schluppeck, D. (2013). Single-subject fMRI mapping at 7T of the representation of fingertips in S1: a comparison of event-related and phase-encoding designs. *American Journal of Physiology-Heart and Circulatory Physiology*.
- Besle, J., Sánchez-Panchuelo, R. M., Bowtell, R., Francis, S., & Schluppeck, D. (2014). Event-related fMRI at 7T reveals overlapping cortical representations for adjacent fingertips in S1 of individual subjects. *Human brain mapping*, 35(5), 2027-2043.
- Bolanowski Jr, S. J., Gescheider, G. A., Verrillo, R. T., & Checkosky, C. M. (1988). Four channels mediate the mechanical aspects of touch. *The Journal of the Acoustical society of America*, 84(5), 1680-1694.
- Bozdogan, H. (1987). Model selection and Akaike's information criterion (AIC): The general theory and its analytical extensions. *Psychometrika*, 52(3), 345-370.
- Brouwer, G. J., Arnedo, V., Offen, S., Heeger, D. J., & Grant, A. C. (2015). Normalization in human somatosensory cortex. *Journal of Neurophysiology*, 114(5), 2588-2599.
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: understanding AIC and BIC in model selection. *Sociological methods & research*, 33(2), 261-304.
- Cacciamani, L., Ayars, A. A., & Peterson, M. A. (2014). Spatially rearranged object parts can facilitate perception of intact whole objects. *Frontiers in Psychology*, 5.

- 1
2
3 Carandini, M., & Heeger, D. J. (2011). Normalization as a canonical neural computation. *Nature*
4
5 *Reviews Neuroscience*, 13(1), 51.
6
7 Carandini, M., Heeger, D. J., & Movshon, J. A. (1997). Linearity and normalization in simple
8
9 cells of the macaque primary visual cortex. *Journal of Neuroscience*, 17(21), 8621-8644.
10
11 Carmon, Z., & Kahneman, D. (1996). *The experienced utility of queuing: experience profiles and*
12
13 *retrospective evaluations of simulated queues*. Durham, NC: Fuqua School, Duke
14
15 University.
16
17 Carter, O., Konkle, T., Wang, Q., Hayward, V., & Moore, C. (2008). Tactile rivalry demonstrated
18
19 with an ambiguous apparent-motion quartet. *Current Biology*, 18(14), 1050-1054.
20
21 Cataldo, A., Ferrè, E. R., di Pellegrino, G., & Haggard, P. (2016). Thermal referral: evidence for
22
23 a thermoceptive uniformity illusion without touch. *Scientific Reports*, 6, 35826.
24
25 Chang, D., Nesbitt, K. V., & Wilkins, K. (2007). The Gestalt principles of similarity and
26
27 proximity apply to both the haptic and visual grouping of elements. In *Proceedings of the*
28
29 *eight Australasian conference on User interface-Volume 64* (pp. 79-86). Australian
30
31 Computer Society, Inc.
32
33 Chen, L. M., Friedman, R. M., & Roe, A. W. (2003). Optical imaging of a tactile illusion in
34
35 area 3b of the primary somatosensory cortex. *Science*, 302(5646), 881-885.
36
37 Cohen, M. A., Dennett, D. C., & Kanwisher, N. (2016). What is the Bandwidth of Perceptual
38
39 Experience? *Trends in Cognitive Sciences*, 20(5), 324-335.
40
41 Collins, J. J., Imhoff, T. T., & Grigg, P. (1996). Noise-enhanced tactile sensation. *Nature*.
42
43 Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in
44
45 the brain. *Nature Reviews Neuroscience*, 3(3), 201-215.
46
47 Craig, J. C. (1972). Difference threshold for intensity of tactile stimuli. *Perception &*
48
49 *Psychophysics*, 11(2), 150-152.
50
51 Craig, J. C. (1974). Vibrotactile difference thresholds for intensity and the effect of a masking
52
53 stimulus. *Perception & Psychophysics*, 15(1), 123-127.
54
55 Craig, J. C. (1976). Attenuation of vibrotactile spatial summation. *Sensory Processes*, 1, 40-56.
56
57
58
59
60

- 1
2
3 Craig, J. C. (1989). Interference in localizing tactile stimuli. *Perception & Psychophysics*, 45(4),
4
5 343-355.
6
7 David, S. V., Mesgarani, N., Fritz, J. B., & Shamma, S. A. (2009). Rapid synaptic depression
8
9 explains nonlinear modulation of spectro-temporal tuning in primary auditory cortex by
10
11 natural stimuli. *Journal of Neuroscience*, 29(11), 3374-3386.
12
13 Davidoff, J., Fonteneau, E., & Fagot, J. (2008). Local and global processing: Observations from
14
15 a remote culture. *Cognition*, 108(3), 702-709.
16
17 Davis, M. (1984). The mammalian startle response. In *Neural mechanisms of startle behavior*
18
19 (pp. 287-351). Springer US.
20
21 Deutsch, D. (1986). An auditory paradox. *The Journal of the Acoustical Society of America*,
22
23 80(S1), S93-S93.
24
25 DiCarlo, J. J., & Johnson, K. O. (1999). Velocity invariance of receptive field structure in
26
27 somatosensory cortical area 3b of the alert monkey. *Journal of Neuroscience*, 19(1), 401–
28
29 419.
30
31 DiCarlo, J. J., & Johnson, K. O. (2000). Spatial and temporal structure of receptive fields in
32
33 primate somatosensory area 3b: effects of stimulus scanning direction and orientation.
34
35 *Journal of Neuroscience*, 20(1), 495–510.
36
37 DiCarlo, J. J., Johnson, K. O., & Hsiao, S. S. (1998). Structure of receptive fields in area 3b of
38
39 primary somatosensory cortex in the alert monkey. *Journal of Neuroscience*, 18(7), 2626–
40
41 2645.
42
43 Erdfelder, E., Faul, F., & Buchner, A. (1996). GPOWER: A general power analysis program.
44
45 *Behavior research methods, instruments, & computers*, 28(1), 1-11.
46
47 Faul, F., Erdfelder, E., Buchner, A., & Lang, A. G. (2009). Statistical power analyses using G*
48
49 Power 3.1: Tests for correlation and regression analyses. *Behavior research methods*,
50
51 41(4), 1149-1160.
52
53 Farnè, A., Brozzoli, C., Làdavas, E., & Ro, T. (2008). Investigating multisensory spatial cognition
54
55 through the phenomenon of extinction. In Haggard, P., Rossetti, Y., & Kawato, M.,
56
57
58
59
60

1
2
3 *Sensorimotor foundations of higher cognition: Attention and performance XXII*, 183-203.
4
5 Oxford University Press, USA.

7 Foard, C. F., & Kemler, D. G. (1984). Holistic and analytic modes of processing: The multiple
8 determinants of perceptual analysis. *Journal of Experimental Psychology: General*, 113(1),
9 104-119.

13 Forster, B., Cavina-Pratesi, C., Aglioti, S. M., & Berlucchi, G. (2002). Redundant target effect
14 and intersensory facilitation from visual-tactile interactions in simple reaction time.
15 *Experimental brain research*, 143(4), 480-487.

19 Friedman, R. M., Chen, L. M., & Roe, A. W. (2008). Responses of areas 3b and 1 in anesthetized
20 squirrel monkeys to single-and dual-site stimulation of the digits. *Journal of*
21 *Neurophysiology*, 100(6), 3185-3196.

26 Gallace, A., Tan, H. Z., & Spence, C. (2006a). Numerosity judgments for tactile stimuli
27 distributed over the body surface. *Perception*, 35(2), 247-266.

30 Gallace, A., Tan, H. Z., & Spence, C. (2006b). The failure to detect tactile change: A tactile
31 analogue of visual change blindness. *Psychonomic Bulletin & Review*, 13(2), 300-303.

34 Gallace, A., Tan, H. Z., & Spence, C. (2008). Can tactile stimuli be subitized? An unresolved
35 controversy within the literature on numerosity judgments. *Perception*, 37, 782-800.

38 Gallace, A., & Spence, C. (2011). To what extent do Gestalt grouping principles influence tactile
39 perception? *Psychological Bulletin*, 137(4), 538.

42 Gallace, A., & Spence, C. (2014). *In touch with the future: The sense of touch from cognitive*
43 *neuroscience to virtual reality*. OUP Oxford.

46 Gardner, E. P., & Spencer, W. A. (1972). Sensory funneling. I. Psychophysical observations of
47 human subjects and responses of cutaneous mechanoreceptive afferents in the cat to
48 patterned skin stimuli. *Journal of Neurophysiology*, 35(6), 925-953.

51 Gescheider, G. A., Bolanowski, S. J., & Verrillo, R. T. (2004). Some characteristics of tactile
52 channels. *Behavioural brain research*, 148(1-2), 35-40.

55 Gibson, R. H., & Tomko, D. L. (1972). The relation between category and magnitude scale of
56 tactile intensity. *Perception and Psychophysics*, 12, 135-8.

- 1
2
3 Green, B. G. (1977). Localization of thermal sensation: An illusion and synthetic heat. *Perception*
4 & *Psychophysics*, 22(4), 331-337.
5
6
7 Green, B. G. (1982). The perception of distance and location for dual tactile pressures. *Perception*
8 & *Psychophysics*, 31(4), 315-323.
9
10
11 Green, D.M., Swets J.A. (1966) *Signal Detection Theory and Psychophysics*. New York: Wiley.
12
13 Halgren, E., Marinkovic, K., & Chauvel, P. (1998). Generators of the late cognitive potentials in
14 auditory and visual oddball tasks. *Electroencephalography and clinical neurophysiology*,
15 106(2), 156-164.
16
17
18 Harris, J. A., Miniussi, C., Harris, I. M., & Diamond, M. E. (2002). Transient storage of a tactile
19 memory trace in primary somatosensory cortex. *Journal of Neuroscience*, 22(19), 8720–
20 8725.
21
22
23 Harris, J. A., Thein, T., & Clifford, C. W. (2004). Dissociating detection from localization of
24 tactile stimuli. *Journal of Neuroscience*, 24(14), 3683-3693.
25
26
27 Heeger, D. J. (1991). Nonlinear model of neural responses in cat visual cortex. *Computational*
28 *models of visual processing*, 119-133.
29
30
31 Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex. *Visual Neuroscience*,
32 9(2), 181-197.
33
34
35 Ho, H. N., Watanabe, J., Ando, H., & Kashino, M. (2011). Mechanisms underlying referral of
36 thermal sensations to sites of tactile stimulation. *Journal of Neuroscience*, 31(1), 208-213.
37
38
39 Hsieh, C. L., Shima, F., Tobimatsu, S., Sun, S. J., & Kato, M. (1995). The interaction of the
40 somatosensory evoked potentials to simultaneous finger stimuli in the human central
41 nervous system. A study using direct recordings. *Electroencephalography and Clinical*
42 *Neurophysiology/Evoked Potentials Section*, 96(2), 135-142.
43
44
45 Johansson, R. S., Vallbo, Å. B., & Westling, G. (1980). Thresholds of mechanosensitive afferents
46 in the human hand as measured with von Frey hairs. *Brain Research*, 184(2), 343-351.
47
48
49 Johnson, K. O., & Phillips, J. R. (1981). Tactile spatial resolution. I. Two-point discrimination,
50 gap detection, grating resolution, and letter recognition. *Journal of neurophysiology*, 46(6),
51 1177-1192.
52
53
54
55
56
57
58
59
60

- 1
2
3 Kahneman, D., Fredrickson, B. L., Schreiber, C. A., & Redelmeier, D. A. (1993). When more
4 pain is preferred to less: Adding a better end. *Psychological Science*, 4(6), 401-405.
5
6
7 Kemp, S., Burt, C. D., & Furneaux, L. (2008). A test of the peak-end rule with extended
8 autobiographical events. *Memory & Cognition*, 36(1), 132-138.
9
10
11 Kimchi, R. (1992). Primacy of wholistic processing and global/local paradigm: a critical review.
12 *Psychological Bulletin*, 112(1), 24.
13
14
15 Kimchi, R. (2014). The perception of hierarchical structure. In Wagemans, J. (2015). *The Oxford*
16 *handbook of perceptual organization*. Oxford Library of Psychology.
17
18
19 Kitagawa, N., Igarashi, Y., & Kashino, M. (2009). The tactile continuity illusion. *Journal of*
20 *Experimental Psychology: Human Perception and Performance*, 35, 1784–1790.
21
22
23
24 Koch, M. (1999). The neurobiology of startle. *Progress in Neurobiology*, 59(2), 107-128.
25
26
27 Krause, T., Kurth, R., Ruben, J., Schwiemann, J., Villringer, K., Deuchert, M., ... & Villringer,
28 A. (2001). Representational overlap of adjacent fingers in multiple areas of human primary
29 somatosensory cortex depends on electrical stimulus intensity: an fMRI study. *Brain*
30 *research*, 899(1-2), 36-46.
31
32
33
34 LaMotte, R. H., & Whitehouse, J. (1986). Tactile detection of a dot on a smooth surface:
35 peripheral neural events. *Journal of Neurophysiology*, 56(4), 1109-1128.
36
37
38
39 Landis, C., & Hunt, W. (1939). *The startle pattern*. Oxford, England: Farrar & Rinehart.
40
41
42 Levitt, H. C. C. H. (1971). Transformed up-down methods in psychoacoustics. *The Journal of the*
43 *Acoustical society of America*, 49(2B), 467-477.
44
45
46
47 Louie, K., Grattan, L. E., & Glimcher, P. W. (2011). Reward value-based gain control: divisive
48 normalization in parietal cortex. *Journal of Neuroscience*, 31(29), 10627-10639.
49
50
51
52
53
54
55
56
57
58
59
60 Louie, K., Khaw, M. W., & Glimcher, P. W. (2013). Normalization is a general neural mechanism
for context-dependent decision making. *Proceedings of the National Academy of Sciences*,
110(15), 6139-6144.
- MacKay, D. M. (1967). Ways of looking at perception. In W. Wathen-Dunn (Ed.), *Models for
the perception of speech and visual form* (pp. 25–43). Cambridge, MA: MIT Press.

- 1
2
3 Marks, L. E. (1979). Sensory and cognitive factors in judgments of loudness. *Journal of*
4
5 *Experimental Psychology: Human Perception and Performance*, 5(3), 426.
6
7 Martin, M. (1992). Sight and touch. In *The Contents of Experience*. Cambridge University Press.
8
9 Mathis, K. M., & Kahan, T. A. (2014). Holistic processing improves change detection but impairs
10
11 change identification. *Psychonomic Bulletin & Review*, 21(5), 1250-1254.
12
13 Miron-Shatz, T. (2009). Evaluating multiepisode events: Boundary conditions for the peak-end
14
15 rule. *Emotion*, 9(2), 206.
16
17 Morewedge, C. K., Gilbert, D. T., & Wilson, T. D. (2005). The least likely of times how
18
19 remembering the past biases forecasts of the future. *Psychological Science*, 16(8), 626-630.
20
21 Navon, D. (1977). Forest before trees: The precedence of global features in visual perception.
22
23 *Cognitive Psychology*, 9(3), 353-383.
24
25 Nelson, D. G. (1993). Processing integral dimensions: the whole view. *Journal of Experimental*
26
27 *Psychology: Human Perception and Performance*, 19(5), 1105-1113.
28
29 Olsen, S. R., Bhandawat, V., & Wilson, R. I. (2010). Divisive normalization in olfactory
30
31 population codes. *Neuron*, 66(2), 287-299.
32
33 Ohshiro, T., Angelaki, D. E., & DeAngelis, G. C. (2011). A normalization model of multisensory
34
35 integration. *Nature Neuroscience*, 14(6), 775-782.
36
37 Plaisier, M. A., Bergmann Tiest, W. M., & Kappers, A. M. L. (2009). One, two, three, many
38
39 – Subitizing in active touch. *Acta Psychologica*, 131(2), 163–170.
40
41 Poljac, E., de-Wit, L., & Wagemans, J. (2012). Perceptual wholes can reduce the conscious
42
43 accessibility of their parts. *Cognition*, 123(2), 308-312.
44
45 Porro, C. A., Martinig, M., Facchin, P., Maieron, M., Jones, A. K., & Fadiga, L. (2007). Parietal
46
47 cortex involvement in the localization of tactile and noxious mechanical stimuli: a
48
49 transcranial magnetic stimulation study. *Behavioural Brain Research*, 178(2), 183-189.
50
51 Rabinowitz, N. C., Willmore, B. D., Schnupp, J. W., & King, A. J. (2011). Contrast gain control
52
53 in auditory cortex. *Neuron*, 70(6), 1178-1191.
54
55
56
57
58
59
60

- 1
2
3 Redelmeier, D. A., & Kahneman, D. (1996). Patients' memories of painful medical treatments:
4
5 Real-time and retrospective evaluations of two minimally invasive procedures. *Pain*, 66(1),
6
7 3-8.
8
9 Reynolds, J. H., & Heeger, D. J. (2009). The normalization model of attention. *Neuron*, 61(2),
10
11 168-185.
12
13 Riggs, K. J., Ferrand, L. , Lancelin, D. , Fryziel, L. , Dumur, G. , & Simpson, A. (2006).
14
15 Subitizing in tactile perception. *Psychological Science*, 17, 271–275.
16
17 Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for
18
19 accepting and rejecting the null hypothesis. *Psychonomic bulletin & review*, 16(2), 225-
20
21 237.
22
23 Ruben, J., Krause, T., Taskin, B., Blankenburg, F., Moosmann, M., & Villringer, A. (2005).
24
25 Subarea-specific suppressive interaction in the BOLD responses to simultaneous finger
26
27 stimulation in human primary somatosensory cortex: Evidence for increasing rostral-to-
28
29 caudal convergence. *Cerebral Cortex*, 16(6), 819-826.
30
31 Schneider, P., & Wengenroth, M. (2009). The neural basis of individual holistic and spectral
32
33 sound perception. *Contemporary Music Review*, 28(3), 315-328.
34
35 Serino, A., Giovagnoli, G., de Vignemont, F., & Haggard, P. (2008). Spatial organisation in
36
37 passive tactile perception: Is there a tactile field? *Acta psychologica*, 128(2), 355-360.
38
39 Shepard, R. N. (1964). Circularity in judgments of relative pitch. *The Journal of the Acoustical*
40
41 *Society of America*, 36(12), 2346-2353.
42
43 Sherrick, C. E. (1964). Effects of double simultaneous stimulation of the skin. *The American*
44
45 *Journal of Psychology*, 77(1), 42-53.
46
47 Sherrick, C. E., Cholewiak, R. W., & Collins, A. A. (1990). The localization of low-and
48
49 high-frequency vibrotactile stimuli. *The Journal of the Acoustical Society of America*,
50
51 88(1), 169-179.
52
53 Sinz, F. H., & Bethge, M. (2013). What is the limit of redundancy reduction with divisive
54
55 normalization? *Neural Computation*, 25(11), 2809-2814.
56
57
58
59
60

- 1
2
3 Spence, C., Pavani, F., Maravita, A., & Holmes, N. (2004). Multisensory contributions to the 3-
4 D representation of visuotactile peripersonal space in humans: evidence from the
5 crossmodal congruency task. *Journal of Physiology Paris*, 98(1-3), 171-189.
6
7
8
9 Squires, N. K., Squires, K. C., & Hillyard, S. A. (1975). Two varieties of long-latency positive
10 waves evoked by unpredictable auditory stimuli in man. *Electroencephalography and*
11 *clinical neurophysiology*, 38(4), 387-401.
12
13
14
15 Stevens, J. C., & Patterson, M. Q. (1995). Dimensions of spatial acuity in the touch sense: changes
16 over the life span. *Somatosensory & motor research*, 12(1), 29-47.
17
18
19
20 Tamè, L., Farnè, A., & Pavani, F. (2011). Spatial coding of touch at the fingers: insights from
21 double simultaneous stimulation within and between hands. *Neuroscience Letters*, 487(1),
22 78-82.
23
24
25
26 Tamè, L., Moles, A., & Holmes, N. P. (2014). Within, but not between hands interactions in
27 vibrotactile detection thresholds reflect somatosensory receptive field organization.
28 *Frontiers in psychology*, 5, 174.
29
30
31
32 Tame, L., Pavani, F., Papadelis, C., Farne, A., & Braun, C. (2015). Early integration of bilateral
33 touch in the primary somatosensory cortex. *Human brain mapping*, 36(4), 1506-1523.
34
35
36
37 Turner, R. S. (1977). The Ohm-Seebeck dispute, Hermann von Helmholtz, and the origins of
38 physiological acoustics. *The British Journal for the History of Science*, 10(01), 1-24.
39
40
41 Verrillo, R. T., & Gescheider, G. A. (1975). Enhancement and summation in the perception of
42 two successive vibrotactile stimuli. *Perception & Psychophysics*, 18(2), 128-136.
43
44
45 von Békésy G *Experiments in Hearing*. New York: McGraw-Hill, 1960.
46
47 von Békésy G *Sensory Inhibition*. Princeton, NJ: Princeton Univ. Press, 1967.
48
49 Wagenmakers, E. J., & Farrell, S. (2004). AIC model selection using Akaike weights.
50 *Psychonomic Bulletin & Review*, 11(1), 192-196.
51
52
53 Walsh, L., Critchlow, J., Beck, B., Cataldo, A., de Boer, L., & Haggard, P. (2016). Salience-
54 driven overestimation of total somatosensory stimulation. *Cognition*, 154, 118-129.
55
56
57 Wetzels, R., Grasman, R. P., & Wagenmakers, E. J. (2012). A default Bayesian hypothesis test
58 for ANOVA designs. *The American Statistician*, 66(2), 104-111.
59
60

1
2
3 Wile, D., & Balaban, E. (2007). An auditory neural correlate suggests a mechanism underlying
4 holistic pitch perception. *PloS one*, 2(4), e369.

7 Witt, J. K., Taylor, J. E. T., Sugovic, M., & Wixted, J. T. (2015). Signal detection measures cannot
8 distinguish perceptual biases from response biases. *Perception*, 44(3), 289-300.

11 Yeomans, J. S., Li, L., Scott, B. W., & Frankland, P. W. (2002). Tactile, acoustic and vestibular
12 systems sum to elicit the startle reflex. *Neuroscience & Biobehavioral Reviews*, 26(1), 1-
13 11.

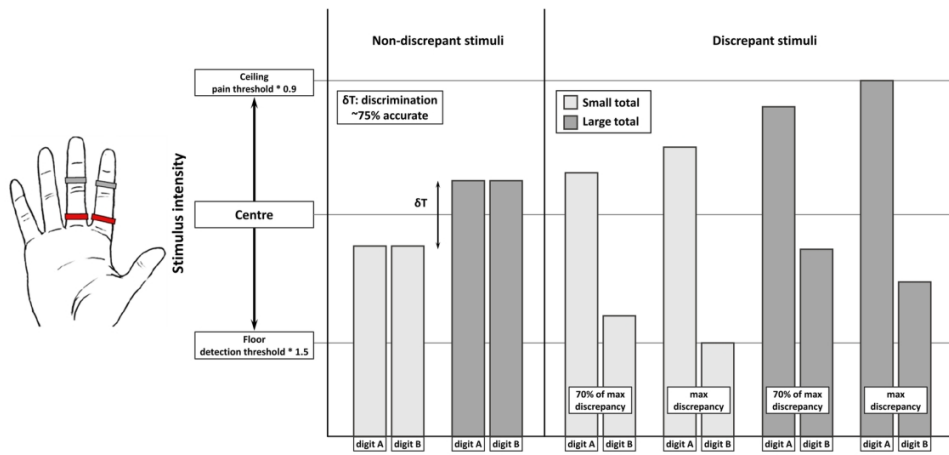


Figure 1. Stimulation levels for Experiment 1 (non-discrepant stimuli and 70% discrepant stimuli) and Experiment 2 (all the stimuli). In both experiments, electrodes were placed on participants' right index and middle fingers. The intensity of the electro-tactile stimulation in each condition was established on the basis of individual detection and pain thresholds. For non-discrepant stimulus pairs, intensities were chosen so that participants discriminated small from large stimuli at approximately 75% correct. In Experiment 1 stimulus pairs were based on 70% of this maximal discrepancy. In Experiment 2, aside the 70% discrepant stimuli, maximally discrepant stimuli spanned the range from detection to pain thresholds, and were total-matched to non-discrepant stimuli.

169x95mm (300 x 300 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

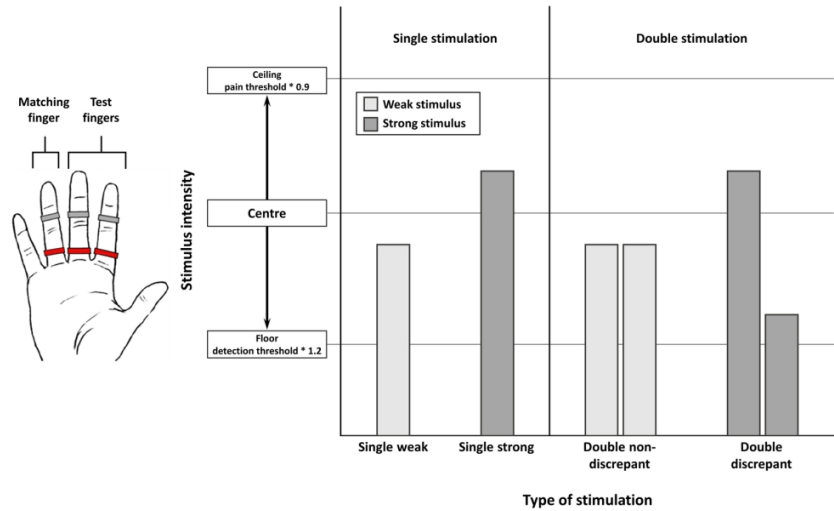


Figure 2. Stimulation of index and middle fingers in Experiment 3, was discrepant or non-discrepant as in Experiment 1. Additional trials delivered weak or strong stimuli either to index or middle fingers alone, matching the intensity of component stimuli in stimulus pairs. Participants adjusted shocks to ring finger to have the same perceived intensity of the stimuli delivered to index and middle fingers.

169x95mm (300 x 300 DPI)

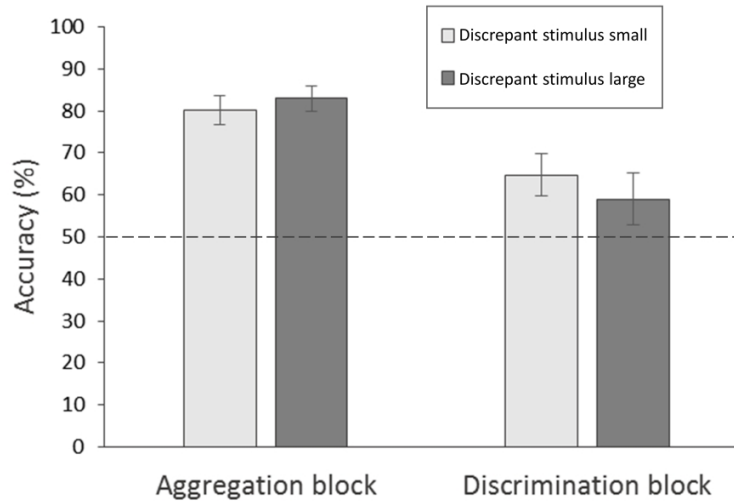


Figure 3. Accuracy in the Aggregation/Discrimination blocks in Experiment 1. Participants' performance was significantly higher in the Aggregation block compared to the Discrimination block. Accurate judgement of total intensity was possible even if discrimination of the overall discrepancy between the stimuli was just slightly above chance level. The dashed line represents the chance level (50%). Error bars show standard error of the mean.

338x190mm (300 x 300 DPI)

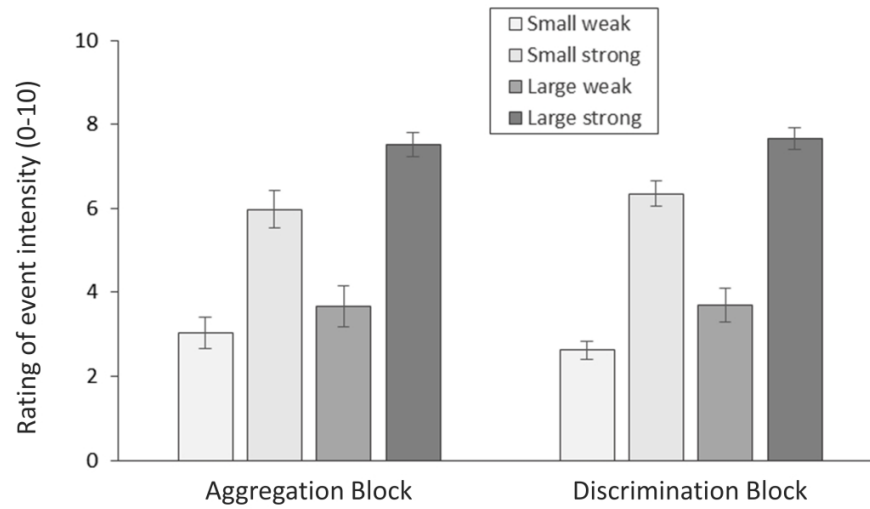


Figure 4. Magnitude estimate of single events in the rating trials presented in Experiment 1. Participants showed accurate perception of the intensity of each stimulus (weak/strong event, small/large total) in both the Aggregation and the Discrimination block. Error bars show standard error of the mean.

338x190mm (300 x 300 DPI)

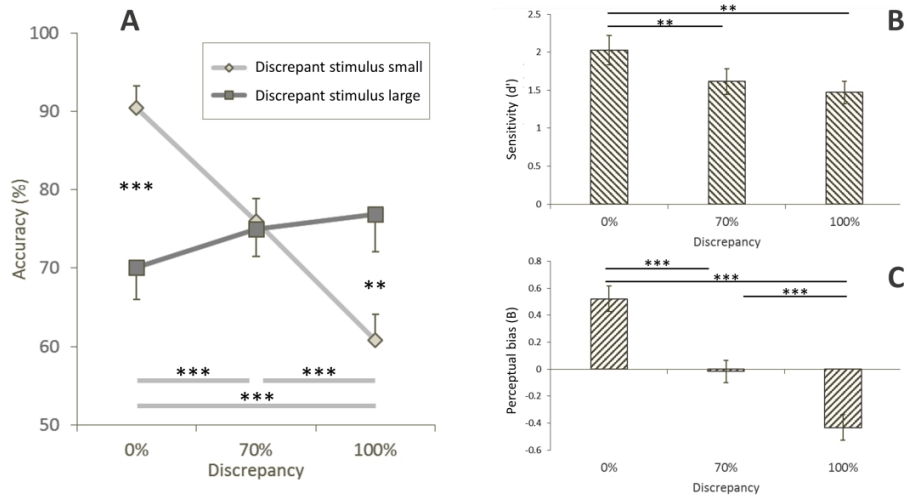


Figure 5. Accuracy, sensitivity, and perceptual bias along discrepancy in Experiment 2. Participants' accuracy (A) decreased along with discrepancy when the discrepant pair had a small total intensity, but not when the discrepant stimulus had a large total intensity. Both sensitivity (B) and perceptual bias (C) were significantly modulated by the discrepancy between the two simultaneous stimuli in the pair. Error bars show standard error of the mean.

338x190mm (300 x 300 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

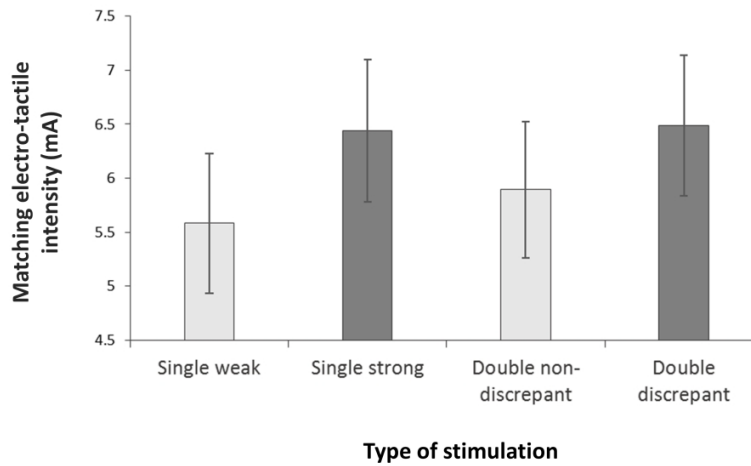


Figure 6. Matching electro-tactile intensity of single/double weak/strong stimuli in Experiment 3. Participants perceived a larger total intensity when a strong stimulus was present in the stimulation, compared to when the single or double stimulation was composed by the small stimulus/i, suggesting that the perception of double discrepant stimulation is strongly biased towards the more salient stimulus in the pair.

338x190mm (300 x 300 DPI)

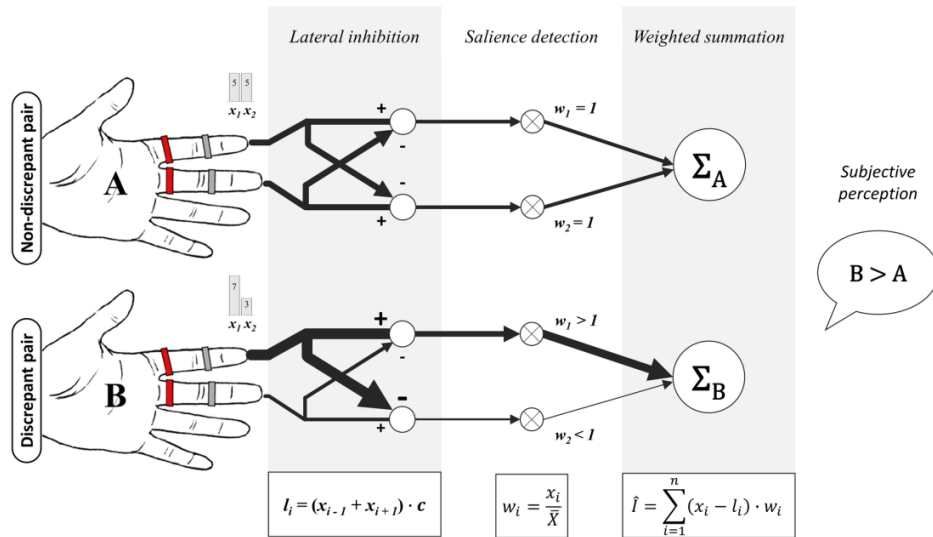


Figure 7. Putative model of somatosensory integration of multiple discrepant and non-discrepant stimuli. A. When non-discrepant multiple simultaneous somatosensory stimuli are aggregated in a total percept, the physical intensity delivered to each finger (i) is first reduced by lateral inhibition (l_i) (top left of the scheme). Experiment 1 shows that at this stage, the intensity of each input after lateral inhibition is retrievable. Next, in non-discrepant pairs, the saliency value is the same for both stimuli. Therefore, the weight assigned to each stimulus (w_i) is 1 (top centre of the scheme), and the weighted summation of the events only reflects the sub-additive effect of lateral inhibition (top right of the scheme). B. Multiple discrepant stimuli are also subject to lateral inhibition from the adjacent fingers. However, the amount of lateral inhibition is different among the stimuli, with the weak stimuli producing less inhibition of the strong stimuli (bottom left of the scheme). Single stimulus intensity of discrepant patterns after lateral inhibition is also accessible. Next, as the strong stimulus is larger than the average intensity of the multiple stimulation, the weight assigned to it is > 1 , while the weight of the weak stimulus is < 1 (bottom centre of the scheme). Finally, the weighted summation of the discrepant pair is biased towards the strong stimulus in the pattern (bottom right of the scheme). As a result, the comparison between equally-intense non-discrepant and discrepant pairs produces an overestimation of the discrepant pattern, driven by the saliency of the strongest stimulus (far right of the scheme).

169x95mm (300 x 300 DPI)

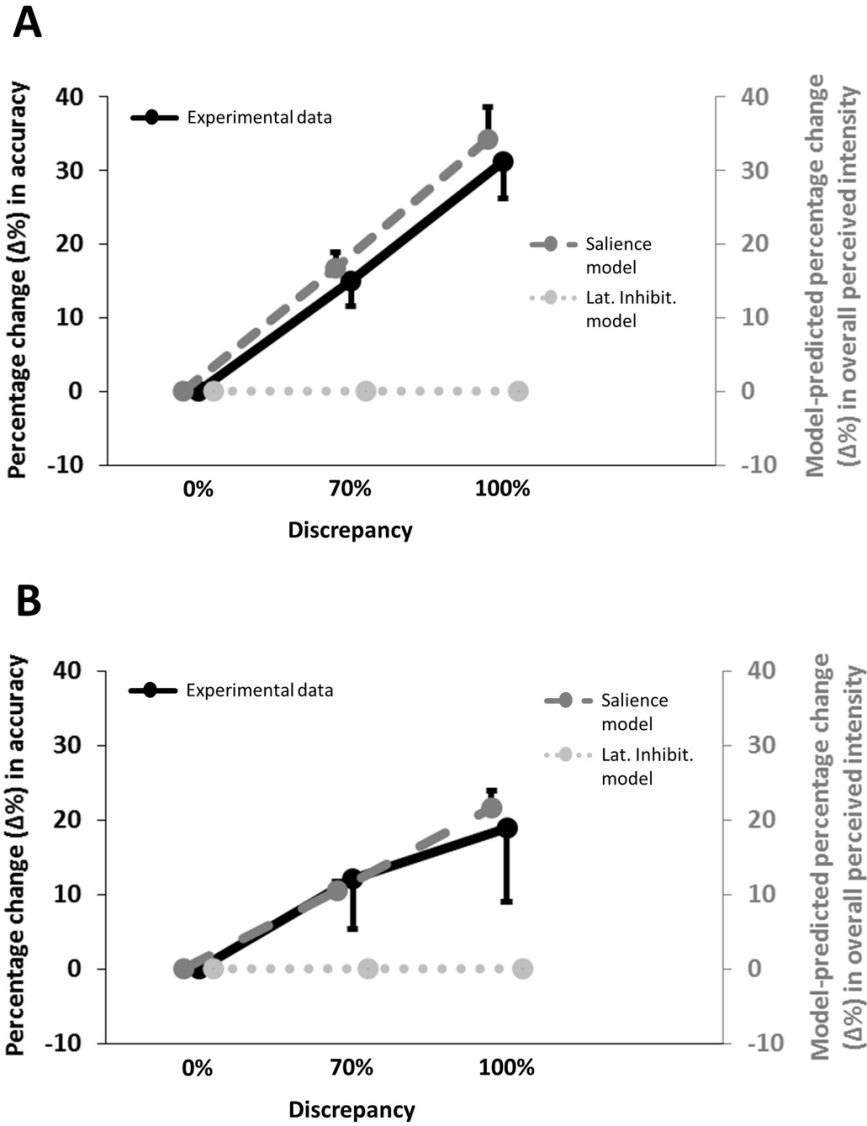


Figure 8. Actual and predicted percentage change between the non-discrepant condition (0%) and the two discrepant conditions in Experiment 2 (70%, 100%) for the small (A) and the large (B) totals. Experimental data (black line) are referred to the left Y axis, and perceived intensities predicted by the models (grey lines) are referred to the right Y axis. The lateral inhibition model (dotted grey line) predicts no change in perception of overall intensity as a function of discrepancy. Error bars show standard error of the mean.

94x117mm (300 x 300 DPI)

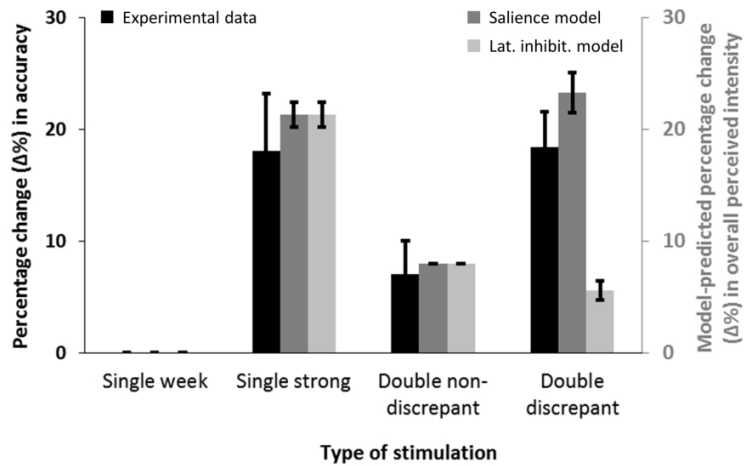


Figure 9. Actual and predicted percentage change between the single weak stimulus condition and the other conditions in Experiment 3 (single strong, double non-discrepant, double discrepant). Experimental data (black bar) are referred to the left Y axis, and predicted intensities (grey bars) are referred to the right Y axis. Both models predicted the same results for the double non-discrepant condition, where the two inputs had equal salience. However, the two models produced very different outcomes for the double discrepant condition, where one stimulus in the pair was more salient (was stronger than the average of the total stimulation). Note that model performance is consistent with the previous simulations of Experiment 2 (see Figure 8), where the lateral inhibition model predicted no change in perception of overall intensity at different levels of discrepancy. Here, the numerical difference between the non-discrepant and discrepant double stimulations for the lateral inhibition model is due to the fact that the intensity of x_1 and x_{-2} in Experiment 3 were adjusted to be perceptually, rather than physically identical. Error bars show standard error of the mean.

169x95mm (300 x 300 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

<i>Model</i>	<i>No. Par</i>	<i>AIC</i>	<i>AICc</i>	<i>Δ(AICc)</i>	<i>w(AICc)</i>	<i>ER</i>
<i>Small total</i>						
Saliency model	1	355.06	355.13	0	> 0.999	1.66 x 10 ⁷
Lateral inhibition	1	388.31	388.38	33.24	< 0.001	
<i>Large total</i>						
Saliency model	1	417.73	417.80	0	0.85	5.84
Lateral inhibition	1	421.26	421.33	3.53	0.15	

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

<i>Model</i>	<i>No. Par</i>	<i>AIC</i>	<i>AICc</i>	$\Delta(AICc)$	$w(AICc)$	<i>ER</i>
Saliency model	1	208.87	208.98	0	0.99	104.4
Lateral inhibition	1	218.17	218.27	9.30	0.01	