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Salience-driven overestimation of total somatosensory stimulation

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ABSTRACT

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

1. Introduction

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

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

Salient information from an unselected channel can sometimes enter consciousness, as in the cocktail party effect (Cherry, 1953). In the case of touch, Tinazzi, Ferrari, Zampini, and Aglioti (2000) described a patient with left tactile extinction. When simultaneously given a salient stroking stimulus on the left hand and a subtler touch stimulus on the right hand, the patient perceived a stroking stimulus on the right hand. Information from both left and right stimuli was clearly processed at some level, but a pathologically-limited bandwidth (Driver & Vuilleumier, 2001) led to the quality of the left-hand stimulus being incorrectly linked to the location of the right-hand stimulus. In healthy participants, a tactile distractor stimulus interferes with perception of a target stimulus in the same modality, both within and between hands (Tamè, Farnè, & Pavani, 2011). Thus, even when bandwidth limitations or selective attention prevent full processing, some features

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of an unselected stimulus may be perceived. Salience—whether defined by stimulus intensity, quality or affect—may play a key role in determining which elements of stimulation enter into conscious awareness. Moreover, the most salient stimulus may have a disproportionately large influence on the perceptual scene as a whole, similar to the 'peak' bias (Fredrickson & Kahneman, 1993) found in the literature on human affective judgements. In general, judgements of the overall affective intensity of a temporally extended event are biased towards the moments of strongest affect within the event period, rather than the average. Low-level perceptual judgements of intensity may be similarly biased towards 'peaks' of intense stimulation, but evidence in support of this claim is lacking.

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

Previous studies have used perceptual illusions to investigate the mechanisms that integrate multiple, simultaneous tactile or thermal stimuli. In the *funneling illusion*, two closely-spaced tactile stimuli are perceived as a single, more intense stimulus at the centroid of the actual stimulation points (Gardner & Spencer, 1972). Activation in primary somatosensory cortex also reflects the illusory location of stimulation, rather than the true locations of the individual stimuli (Chen, Friedman, & Roe, 2003). In the *tactile continuity illusion*, Kitagawa, Igarashi, and Kashino (2009) showed that brief vibrotactile stimuli interspersed with low amplitude noise are perceived as continuous stimulation. Gaps in tactile perception are filled in with illusory sensations sharing the same attributes (e.g., intensity level) as the surrounding physical stimuli. In *thermal referral illusions*, warm or cold thermal stimulators are applied to the ring and index fingers of one hand, and a neutral-temperature stimulator to the middle finger. In this configuration, all three fingers feel warm or cold (Green, 1977, 1978; Ho, Watanabe, Ando, & Kashino, 2010, 2011). Participants accurately perceive total thermal intensity, but distribute the perceived temperature evenly across the fingers, rather than experiencing an exact copy of the intensity on the individual outer fingers referred to the neutral middle finger (Ho et al., 2011). Taken together, these illusions demonstrate an integrative quality in somatosensory processing, which acts to produce a coherent overall percept from multiple stimulations distributed in space and time. This integration might take place at multiple levels in the somatosensory pathway, from peripheral mechanisms (e.g., energy summation in skin receptors) to central mechanisms (e.g., Gestalt perceptual grouping principles).

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

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

2. Methods

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

2.1. Experiment 1

2.1.1. Experimental setup

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

The participant rested their hand palm down on a table, with the thenar and hypothenar eminences, the distal finger pads of digits 2–5 and the lateral side of the thumb pad touching the table surface. Vision of the right hand and wrist was blocked with a screen. Detection and pain thresholds for electrical stimulation of