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Running Title: Somatosensory detection

Subliminal stimulation and somatosensory signal detection

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Abstract

Only a small fraction of sensory signals is consciously perceived. The brain's perceptual systems may include mechanisms of feedforward inhibition that protect the cortex from subliminal *noise*, thus reserving cortical capacity and conscious awareness for significant stimuli. Here we provide a new view of these mechanisms based on signal detection theory, and gain control. We demonstrated that subliminal somatosensory stimulation decreased sensitivity for the detection of a subsequent somatosensory input, largely due to increased false alarm rates. By delivering the subliminal somatosensory stimulus and the to-be-detected somatosensory stimulus to different digits of the same hand, we show that this effect spreads across the sensory surface. In addition, subliminal somatosensory stimulation tended to produce an increased probability of responding "yes", whether the somatosensory stimulus was present or not. Our results suggest that subliminal stimuli temporarily reduce input gain, avoiding excessive responses to further small inputs. This gain control may be automatic, and may precede discriminative classification of inputs into signals or noise. Crucially, we found that subliminal inputs influenced false alarm rates only on blocks where the to-be-detected stimuli were present, and not on pre-test control blocks where they were absent. Participants appeared to adjust their perceptual criterion according to a statistical distribution of stimuli in the current context, with the presence of supraliminal stimuli having an important role in the criterion-setting process. These findings clarify the cognitive mechanisms that reserve conscious perception for salient and important signals.

Keywords

Highlights

- Subliminal stimuli reduce sensitivity to detect stimuli on the same digit

- Reduced sensitivity spreads to adjacent fingers, suggesting a central mechanism

- Subliminal stimuli may trigger reductions in sensory input gain

- Sensory systems may implement an adaptive coding dynamically and preconsciously

1. Introduction

Subliminal perception is a classic but controversial topic in experimental psychology (Dehaene and Changeux, 2011). Conventional belief that perception of a sensory stimulus is always conscious is challenged by considerable evidence that the construction of perceptual awareness depends on cognitive processes that operate unconsciously. Only a small fraction of sensory signals is consciously perceived. Neurons in the cerebral cortex respond to thalamic inputs, but weak peripheral stimuli can still produce cortical activity that falls short of a complete cortical response, and is insufficient for conscious detection (Libet et al., 1967). On this view, only late levels of processing within the cortical hierarchy are associated with conscious awareness: incoming stimuli are filtered by a "*signal-or-noise?*" process. This process suppresses awareness of stimuli that have insufficient intensity or duration to trigger conscious perception. Thus, a *gatekeeper* function within the cortex selects which inputs will procede to such processing. Importantly, this selection may be adaptive, rather than a fixed threshold. Accordingly, selective attention, expectation, stimulus history, and backward masking all influence whether a given near-threshold stimulus will be detected or not. Understanding the differences between processing of subliminal and supraliminal stimuli is a crucial step in understanding the mechanisms that produce conscious awareness.

As early as in 1885, Pierce and Jastrow suggested that subliminal stimuli might unconsciously influence perception. Here we focus on a recent example in the somatosensory system: subliminal stimulation delivered 30 ms before a near-threshold stimulus, caused a decrease in somatosensory detection relative to a baseline condition (Blankenburg et al., 2003). Subliminal stimulation also caused blood oxygenation level-dependent (BOLD) signal decreases in somatosensory cortical areas, while suprathreshold stimulation normally results in BOLD signal increases (Blankenburg et al., 2003). Thus the subliminal shocks were interpreted as causing transient cortical deactivation, reducing the neuronal response to subsequent near-threshold test stimuli. Recordings from single neurons in animals (Swadlow, 1983) and intracranial and EEG recordings in humans (Curio, 2000) suggest that feed-forward thalamocortical or corticocortical inhibitory circuits underlie these effects.

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The decrease in somatosensory detection caused by subliminal stimuli was interpreted as an automatic and unconscious noise-suppression mechanism, arising at a low level of sensory processing, and acting to reserve cortical capacity and conscious awareness for significant stimuli (Blankenburg et al., 2003). Prior to perceiving an event, a sensory system needs to determine, based on afferent signals, whether any sensory event has occurred at all, or whether afferent input is "just noise". Sequential information is important for this decision: a weak stimulus that is "just noise" may not be followed by further input. In that case, thalamocortical inhibition acts to close the gate to further processing, and raising the threshold for future cortical activation. This prevents unnecessary responding to future noise, but also impairs detection of subsequent signals. This mechanism ensures that only sufficiently strong or sustained afferent inputs reach full cortical processing and achieve awareness (Libet et al., 1967). Crucially, this mechanism imposes an early classification of stimuli as signals or noise, on the basis of intensity. In particular, weak subliminal stimuli are classified as irrelevant noise. The system then raises the detection threshold to exclude such noise stimuli (Blankenburg et al., 2003), although the precise mechanism for doing so remains unclear.

Previous methods delivered continuous trains of subliminal stimulation at 7 Hz (Blankenburg et al., 2003; Taskin et al., 2007) in which the to-be-detected near-threshold shocks were embedded. The regular temporal pattern could assist in identifying a subliminal stimulus as task irrelevant, on the basis of its timing as well as its energy. In contrast, when a *single* low-energy stimulus occurs, the brain faces a challenge in distinguishing whether it is merely noise - in which case neural responsivity could be adaptively decreased -, or whether it is in fact a relevant and important event - in which case responsivity should be increased.

In this study we have addressed these questions directly, seemingly for the first time. We have used signal detection theory to investigate how a single subliminal somatosensory stimulus might influence conscious perception of a near-threshold shock, either on the same digit, or on neighbouring digits.

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2. Materials and Methods

2.1. Experiment 1

2.1.1. Participants

Eight naïve right-handed participants took part in Experiment 1 (3 male, mean age ± SD: 22.8 ± 3.4 years). Participants were recruited by means of the UCL Psychology Subject Pool. The sample size was set in advance of testing based on the average sample size in two previous similar studies (cf. Blankenburg et al., 2003), and was also used as data-collection stopping rule. Exclusion criteria include the presence of neurological and psychiatric disorders, sensitive skin on the hands (e.g., eczema), and analgesic medication (i.e., paracetamol, aspirin, ibuprofen, codeine) or recreational drug consumption in the last 24 hours. Written informed consent was obtained from all participants. The study was conducted in accordance with the principles of the Declaration of Helsinki. All experimental procedures were approved by the local ethics committees.

2.1.2. Stimuli and procedure

Somatosensory stimulation was provided by digital nerve shocks via a pair of ring electrodes (Digitimer, UK) placed over the distal phalanxes of the left index finger with the cathode 1 cm proximal to the anode. Stimulation was a single rectangular current pulse delivered with a neurophysiological stimulator (Stanmore stimulator, Medical Physics Department, UCL, UK), whose current level and pulse duration were controlled by a computer. Within the range used here, shock intensity depends only on the total charge transferred from the electrode, which is the product of current pulse amplitude and pulse duration. Therefore, we obtained estimates of somatosensory perception by holding pulse amplitude at 10 mA and varying pulse duration.

To identify individual somatosensory thresholds, the method of limits was used to estimate the lowest shock intensity at which a tactile stimulus could be reliably detected. Pulses of increasing width were

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applied until participants reported a sensation. The pulse intensity obtained was tested in a detection block to check that 50% of pulses were reliably detected. This level was considered as working estimate for near-threshold electrical stimulation in each participant (mean and standard deviation for subjective threshold are reported in Table 1). Subliminal stimulation was delivered at below threshold intensity (15% less then threshold intensity, cf. Blankenburg et al., 2003). A sensory pre-test detection block with 10 subliminal pulses and 10 stimulus-absent trials was conducted to check whether subliminal stimuli were detectable.

Participants detected near-threshold shocks on the finger, randomly preceded by a subliminal conditioning pulse 30 ms earlier. The 30 ms delay was chosen because it far exceeds the refractory period of peripheral nerve fibers (Swadlow and Gusev, 2000). Further, somatosensory activation within the primary somatosensory cortex persist for at least 60 ms (Allison et al., 1992; Mauguiere et al., 1997). Thus, the processing of both subliminal conditioning pulse and near-threshold test pulse overlapped within the primary somatosensory cortex (Chung et al., 2002; Martin-Cortecero and Nunez, 2014; Nakagawa et al., 2014). The rationale behind this specific timing comes from the retention times of the somatosensory signal in the primary somatosensory areas, as recently confirmed (Tamè et al., 2015a; Tamè et al., 2015b).

The somatosensory detection task consisted of a 2 (somatosensory near-threshold stimulus present/absent) x 2 (subliminal stimulus present/absent) design, with the following trial types: 40 trials with shock intensity at threshold delivered on the left index finger, 40 trials in which a subliminal shock was delivered 30 ms before the near-threshold test pulse on the left index finger, 40 trials in which only the subliminal shock was presented on the left index finger, without a near-threshold test pulse and 40 trials in which neither subliminal shock nor near-threshold test pulse were present. Trial order was randomised, so that participants could not predict stimulus presence and stimulus intensity. Participants were blindfolded throughout the task. The beginning of each trial was signalled by an auditory cue. The shock, if present, was delivered after a variable interval of time between 800 ms and 850 ms. 800 ms later, a second auditory cue indicated the end of the trial. Participants were required to indicate whether or not they felt the shock, making unspeeded verbal responses. Data for each trial were recorded and analysed later.

		Finger			
		Index	Middle	Ring	Little
Experiment 1	M	50.75			
	SD	19.38			
Experiment 2	M	56.00	55.25		
	SD	14.93	15.59		
Experiment 3	M	47.00	47.71	45.29	41.71
	SD	9.98	6.45	8.60	8.36

Table 1.

Somatosensory threshold in microsecond pulse duration (means and standard deviations) for a 10mA current delivered to each finger in each experiment.

2.1.3. Results

For the pre-test detection block, the percentage of "yes" responses to subliminal stimuli was compared to the percentage of "yes" responses to stimulus absent trials, using a paired t-test. A one-tailed test was used, since any standard account of perception would predict that "yes" responses should be *increased* by the actual presence of a stimulus, rather than decreased. Cohen's *d* for independent samples was calculated to estimate effect size, following Dunlap's (1996) recommendation of using the original standard deviations of the scores in case of paired t-tests. Subliminal stimuli did not evoke significantly more "yes" responses, strongly suggesting lack of conscious detection (mean percentage of "yes" responses to stimulus absent trials = 8.75%, SD= 24.75%; mean percentage of "yes" responses to subliminal stimuli = 11.25%, SD= 21.01%; t_7 = -0.424, p=0.342; Cohen's *d* = -0.11; 95% CI for effect size [-1.08, 0.88]).

Somatosensory detection results were analysed using signal detection analysis (Macmillan and Creelman, 1991). According to our experimental design, we considered two experimental conditions: near-threshold shocks that were preceded by a subliminal conditioning pulse and near-threshold shocks that were not. Subliminal only trials have been considered as signal absent trials for calculating signal detection values in the near-threshold preceded by subliminal pulse condition. Then, we computed the number of hits

(number of stimulus-present trials in which participants said "yes"), false alarms (number of stimulus-absent catch trials in which participants said "yes"), misses (number of stimulus-present trials in which participants said "no") and correct rejections (number of stimulus-absent catch trials in which participants said "no") independently for both experimental conditions (Table 2). Hit rates [P("yes" | stimulus present), proportion of hit trials to which subject responded "yes"] and false alarm rates [P("yes" | stimulus not present), proportion of trials in which there is not actually the stimulus to which subject responded "yes"] were calculated (Macmillan and Creelman, 1991). These were used to obtain the perceptual sensitivity (d') and response bias (C) estimates for near-threshold shocks that were preceded by a subliminal conditioning pulse and near-threshold shocks that were not. The difference between these values represents an index of the strength of putative subliminal inhibition.

Subliminal conditioning pulses significantly reduced sensitivity to the near-threshold shock (near threshold sensitivity: mean= 2.06, SD= 1.79; subliminal + near threshold sensitivity: mean= 1.18, SD= 1.70; t_7 = 2.800, p = 0.027; Cohen's d = 0.50; 95% CI for effect size [-0.52, 1.47]), and produced a trend (near threshold response bias: mean= 1.15, SD= 0.58; subliminal + near threshold sensitivity: mean= 0.73, SD= 0.47; t_7 = 2.060, p = 0.078; Cohen's d = 0.80; 95% CI for effect size [-0.26, 1.77]) towards liberal response bias (i.e., an increased probability of responding that the shock was present, irrespective of actual stimulation) (Figure 1A).

2.1.4. Discussion

Subliminal stimulation impairs detection of a subsequent somatosensory stimulus, delivered 30 ms later. Importantly, we used signal detection theory to clarify the nature of this impairment. We found that a subliminal stimulus decreased sensitivity for somatosensory signals. In addition, we also found a trend for subliminal stimulation to produce a liberal bias, i.e., an increased probability of responding "yes", whether the near-threshold stimulus was present or not. Since both subliminal and near-threshold stimuli were delivered on the same finger, our results could reflect inhibitory mechanisms at any of several levels, including the peripheral receptor, the afferent neuron, the spinal circuitry, brainstem nuclei, thalamus or

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To clarify this issue, we have investigated whether the effect of subliminal stimuli would be found in conditions where subliminal and near-threshold information come from different peripheral locations.
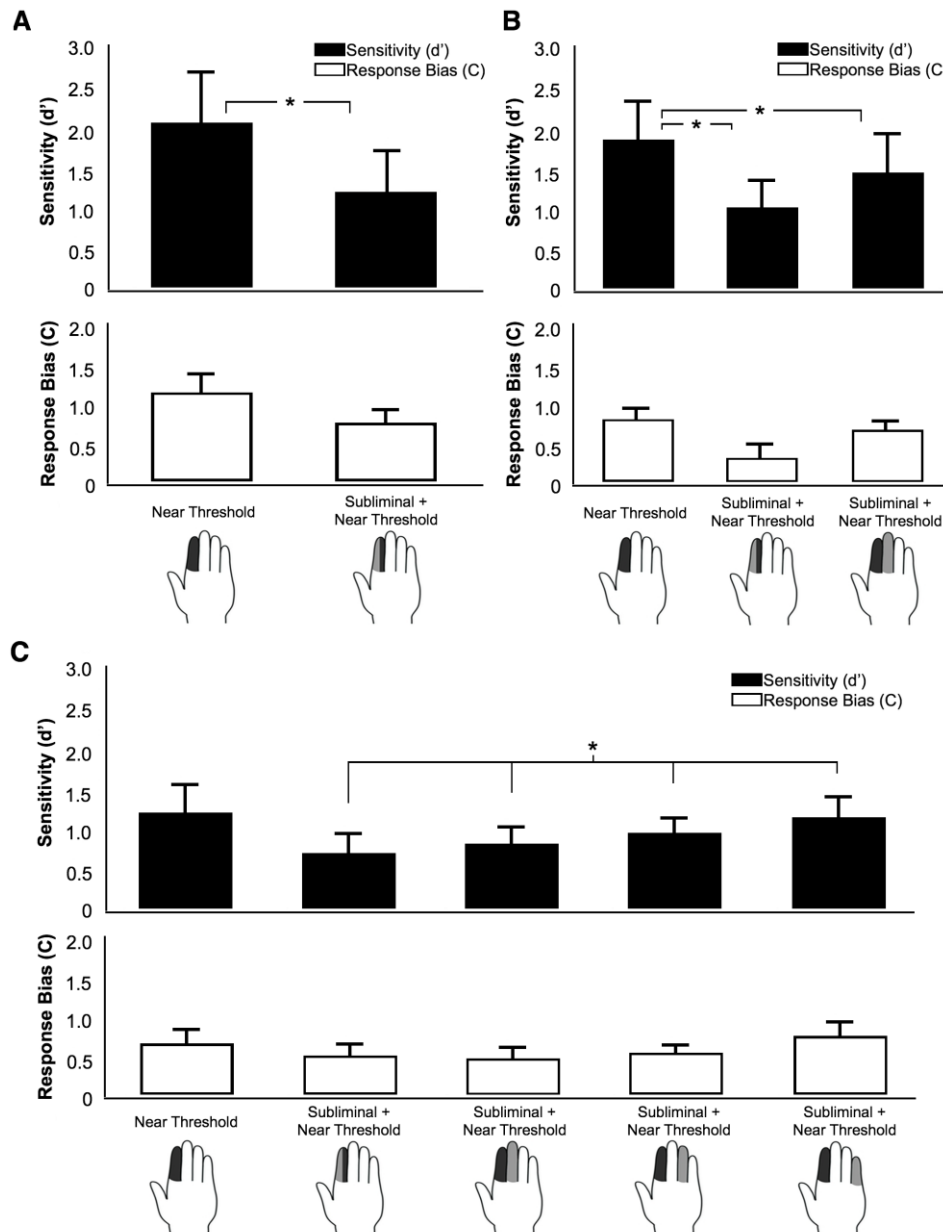

Figure 1. Sensitivity and Response Bias results.

A: Results of Experiment 1. A preceding stimulus reduces sensitivity to a subsequent near-threshold stimulus, and produces a tendency towards liberal bas.

B: Results of Experiment 2. Sensitivity reduction is found when the subliminal stimulus is delivered to the adjacent finger.

C: Results of Experiment 3. The spatial spread of sensitivity modulation shows a clear linear gradient across fingers. There is no linear gradient for bias.

2.2. Experiment 2

2.2.1. Participants

Eight naïve right-handed participants took part in Experiment 2 (3 male, mean age ± SD: 26.9 ± 5.8 years). <mark>Participants were recruited by means of the UCL Psychology Subject Pool. Exclusion criteria include the presence of neurological and psychiatric disorders, sensitive skin on the hands (e.g., eczema), and analgesic medication (i.e., paracetamol, aspirin, ibuprofen, codeine) or recreational drug consumption in the last 24 hours. Written informed consent was obtained from all participants. The study was conducted in accordance with the principles of the Declaration of Helsinki. All experimental procedures were approved by the local ethics committees.</mark>

2.2.2. Stimuli and procedure

Ring electrodes were placed over the distal phalanxes of the left index and middle finger. Somatosensory thresholds were identified for both the index and middle finger <mark>(see Table 1).</mark> The somatosensory detection task consisted of 6 trial types: 30 trials with shock intensity at threshold delivered on the left index finger, 30 trials in which a subliminal shock was delivered 30 ms before the near-threshold test pulse on the left index finger, 30 trials in which a subliminal stimulus was presented on the middle finger 30 ms before the near-threshold delivered on the index finger, 30 trials in which only the subliminal shock was presented on the left index finger, 30 trials in which only the subliminal shock was presented on the middle index finger and 30 trials in which no signal was present. Settings and timings were as in Experiment 1. Participants were instructed to detect whether a near-threshold pulse was delivered on the index finger. <mark>A sensory pre-test detection block with subliminal pulses and stimulus absent trials was conducted to verify whether subliminal stimuli were detectable by participants. Independent blocks were administered for the index finger and middle finger.</mark>

2.2.3. Results

The percentage of "yes" responses to subliminal stimuli was compared to the percentage of "yes" responses to stimulus absent trials, collected in the pre-test detection block. Subliminal stimulus delivered on the index finger did not evoke significantly more "yes" responses, confirming lack of conscious detection (mean percentage of "yes" responses to stimulus absent trials = 5%, SD= 7.56%; mean percentage of "yes" responses to subliminal stimuli = 12.50%, SD= 15.81%; t_7= -1.342, p= 0.111; Cohen's d = -0.61; 95% CI for effect size [-1.57, 0.43], one tail). Similar results were found for the middle finger (mean percentage of "yes" responses to stimulus absent trials = 6.25%, SD= 11.87%; mean percentage of "yes" responses to subliminal stimuli = 10%, SD= 11.95%; t_7= 0.753, p= 0.238; Cohen's d = -0.31; 95% CI for effect size [-1.28, 0.69], one tail).

Sensitivity estimates of near-threshold detection again dropped when the subliminal conditioning shock was delivered on the same (index) finger, replicating Experiment 1 (near threshold sensitivity: mean= 1.93, SD= 1.38; index finger subliminal + near threshold sensitivity: mean= 0.94, SD= 0.93; t_7= 3.098, p = 0.017; Cohen's d = 0.84; 95% CI for effect size [-0.22, 1.81]). A similar effect was also found when the subliminal pulse was administered on the adjacent, middle finger (middle finger subliminal + near threshold sensitivity: mean= 1.50, SD= 1.46; t_7= 2.764, p = 0.028; Cohen's d = 0.30; 95% CI for effect size [-0.70, 1.27]). The difference in d' for trials with or without a subliminal conditioning shock was calculated for trials in which the subliminal pulse was on the same finger or on the adjacent finger. A direct comparison confirmed that subliminal stimulation similarly affects the detection of subsequent somatosensory stimuli on the same finger or on the adjacent finger (t_7= -1.847, p = 0.107; Cohen's d = -0.78; 95% CI for effect size [-1.75, 0.27]) (Figure 1B).

Response bias estimates showed a liberal trend following subliminal conditioning shocks on the same, index finger (near threshold response bias: mean= 0.76, SD= 0.43; index finger subliminal + near threshold response bias: mean= 0.23, SD= 0.39; t_7= 2.128, p = 0.071; Cohen's d = 1.29; 95% CI for effect size [0.15, 2.29]). No significant changes in the response bias were found when subliminally stimulating the middle finger (middle finger subliminal + near threshold response bias: mean= 0.60, SD= 0.26; t_7= 1.248, p

= 0.252; Cohen's *d* = 0.45; 95% CI for effect size [-0.57, 1.42]). The difference in response bias for trials with or without a subliminal conditioning shock was no significantly different across fingers (t_7 = -1.782, p = 0.118; Cohen's *d* = -0.65; 95% CI for effect size [-1.62, 0.39]) (Figure 1B).

2.2.4. Discussion

Subliminal stimulation affects the detection of subsequent somatosensory stimuli on the same finger or on the adjacent finger. Indeed, sensitivity estimates for near-threshold detection on the index finger dropped when the subliminal pulse was delivered on the index finger or middle finger. To further quantify the apparent spread of feed-forward inhibition across digits, we delivered the subliminal shock either on the same/index finger or on the middle, ring or little finger of the same hand, at random in a third experiment.

2.3. Experiment 3

2.3.1. Participants

Eight naïve right-handed participants took part in Experiment 3 (3 male, mean age ± SD: 23.7 ± 3.1 years). Participants were recruited by means of the UCL Psychology Subject Pool. Exclusion criteria include the presence of neurological and psychiatric disorders, sensitive skin on the hands (e.g., eczema), and analgesic medication (i.e., paracetamol, aspirin, ibuprofen, codeine) or recreational drug consumption in the last 24 hours. Written informed consent was obtained from all participants. The study was conducted in accordance with the principles of the Declaration of Helsinki. All experimental procedures were approved by the local ethics committees. Data from one participant were lost for technical reasons.

2.3.2. Stimuli and procedure

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Ring electrodes were placed over the distal phalanxes of the left index, middle, ring and little finger. Somatosensory thresholds were estimated for each finger. The somatosensory detection task consisted of 10 trial types: 30 trials with shock intensity at threshold delivered on the left index finger, 30 trials in which a subliminal shock was delivered 30 ms before the near-threshold test pulse on the index finger, 30 trials in which a subliminal shock was presented on the middle finger 30 ms before the near-threshold delivered on the index finger, 30 trials in which a subliminal shock was presented on the ring finger 30 ms before the near-threshold delivered on the index finger, 30 trials in which a subliminal shock was presented on the little finger 30 ms before the near-threshold delivered on the index finger, 30 trials in which only the subliminal shock was presented on the index finger, 30 trials in which only the subliminal shock was presented on the middle finger, 30 trials in which only the subliminal shock was presented on the ring finger, 30 trials in which only the subliminal shock was presented on the little finger and 30 stimulus absent trials in which no signal was present. Trial features and timing were the same as in Experiment 1. Participants were instructed to detect whether a near-threshold pulse was delivered on the index finger. A sensory pre-test detection block with subliminal pulses and stimulus absent trials was conducted to verify whether subliminal stimuli were detectable by participants. Independent blocks were administered for each finger.

2.3.3. Results

The percentage of "yes" responses to subliminal stimuli was compared to the percentage of "yes" responses to stimulus absent trials, collected in the pre-test detection block. Subliminal stimulus delivered on the index finger did not evoke significantly more "yes" responses, suggesting lack of conscious detection (mean percentage of "yes" responses to stimulus absent trials = 22.86%, SD= 29.28%; mean percentage of "yes" responses to subliminal stimuli = 20%, SD= 34.16%; t_6 = -0.420, p=0.345, Cohen's d = 0.09; 95% CI for effect size [-0.96, 1.13], one tail). No differences emerged for the middle finger (mean percentage of "yes" responses to stimulus absent trials = 11.43%, SD= 21.93%; mean percentage of "yes" responses to subliminal stimuli = 15.71%, SD= 15.12%; t_7 = 0.596, p= 0.286; Cohen's d = -0.23; 95% CI for effect size [-1.26, 0.84] one tail), ring finger (mean percentage of "yes" responses to stimulus absent trials = 15.71%,

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SD= 20.70%; mean percentage of "yes" responses to subliminal stimuli = 17.14%, SD= 17.04%; t_7 = 0.213, p= 0.419; Cohen's *d* = -0.07; 95% CI for effect size [-1.12, 0.98] one tail) and little finger (mean percentage of "yes" responses to stimulus absent trials = 12.86%, SD= 18.90%; mean percentage of "yes" responses to subliminal stimuli = 28.57%, SD= 26.09%; t_7 = 1.908, p= 0.060; Cohen's *d* = -0.69; 95% CI for effect size [-1.72, 0.43] one tail).

Sensitivity data showed a decreasing spatial gradient across the fingers (near threshold sensitivity: mean= 1.25, SD= 0.98; index finger subliminal + near threshold sensitivity: mean= 0.74, SD= 0.79; middle finger subliminal + near threshold sensitivity: mean= 0.89, SD= 0.77; ring finger subliminal + near threshold sensitivity: mean= 1.07, SD= 0.64; little finger subliminal + near threshold sensitivity: mean= 1.27, SD= 0.85). The difference in d' for trials with vs without a subliminal conditioning shock was calculated. We first performed an ANOVA on these values with Finger for the subliminal conditioning shock (Index, Middle, Ring, Little) as within-subjects factor. The main effect of Finger for the conditioning shock did not reach the significance level ($F_{(3,1)}$=2.063, p=0.141). However, we had a prior hypothesis regarding a spatial somatotopic gradient of decreasing inhibition across the fingers, corresponding to decreasing difference in d' between trials with vs without a subliminal conditioning shock. This hypothesis is driven by physiological evidence showing that inhibitory mechanisms in the somatosensory system follow a somatotopic organization. For instance, suppressive interactions are stronger when simultaneously stimulating the digital nerves of the index and middle fingers compared with index and little fingers (Ishibashi et al., 2000). We therefore used a planned contrast approach to capture this specific prediction about the *pattern* of differences between fingers. In particular, linear trend analysis was used to determine whether subliminally induced inhibition decayed linearly across fingers. While other patterns (exponential, quadratic) might potentially also be present, we had a prior in favour of the simpler, linear pattern. Further, a linear pattern would be consistent with recent high-field neuroimaging results indicating roughly equi-spaced projections of individual fingers onto the somatosensory cortical sheet (Martuzzi et al., 2014), at least for the index, middle, ring and little fingers. The null hypothesis, of no linear gradient for subliminal inhibition would be reflected by the absence of trend. The linear contrast coefficients -3, -1, 1, 3 were used for index, middle, ring and little fingers respectively. A clear linear trend was found t_6 = 5.337, p < 0.001, one tailed), with reduction in

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sensitivity due to subliminal stimulation decreasing for more remote digits. This result is consistent with the view that feed-forward inhibition from the subliminal stimulus spreads in a linearly-decreasing fashion across a topographic skin map.

No reliable spatial gradient for bias was observed (near threshold response bias: mean= 0.65, SD= 0.53; index finger subliminal + near threshold response bias: mean= 0.50, SD= 0.46; middle finger subliminal + near threshold response bias: mean= 0.45, SD= 0.46; ring finger subliminal + near threshold response bias: mean= 0.48, SD= 0.32; little finger subliminal + near threshold response bias: mean= 0.75, SD= 0.68). A linear trend analysis confirmed the absence of spatial gradient in response bias values ($t_6 = 1.001$, $p = 0.178$, one tailed) (Figure 1C).

2.3.4. Discussion

The somatosensory evoked response elicited by two stimuli applied simultaneously to adjacent skin regions, or to different nerves, is reduced relative to the sum of responses evoked by stimulating each skin region or nerve independently. This result has been explained in terms of lateral inhibition mechanisms (Gandevia et al., 1983; Hsieh et al., 1995; Ishibashi et al., 2000). This suppression follows the somatotopic organization of the receptive fields. That is, suppressive interactions are stronger when simultaneously stimulating the digital nerves of the index and middle fingers compared with index and little fingers (Ishibashi et al., 2000). Accordingly, our data revealed a linear spatial gradient in subliminally-induced inhibition.

2.4. Subliminal detection across the three experiments

In all three experiments the subliminal stimulation was set clearly below the threshold intensity for conscious detection (cf. Blankenburg et al., 2003). This was checked prior to each experiment in a pre-test detection block with subliminal pulses and stimulus absent trials. In these pre-test detection blocks, the

percentage of "yes" responses to subliminal stimuli was compared to the percentage of "yes" responses to stimulus absent trials, using paired t-tests. We found no significant evidence that presence of a subliminal stimulus increased "yes" responses in pre-test detection blocks, consistent with lack of conscious detection. Similarly, combining the subjects of the three experiments showed that "yes" responses were no more likely for subliminal stimuli than for stimulus absent trials (mean percentage of "yes" responses to stimulus absent trials = 11.74%, SD= 22.49%; mean percentage of "yes" responses to subliminal stimuli = 14.35%, SD= 23.51%; one-tailed paired t-test, t_{22} = -0.758; p=0.229; Cohen's d = -0.11; 95% CI for effect size [-0.69, 0.45]). In principle, this null result might just reflect low statistical power. We performed a power calculation to estimate the number of participants required to get a significant difference between the "yes" responses for subliminal trials and for stimulus absent trials. The sample size calculation for one-tailed paired t-test, with alpha = 0.05 and power = 0.95, gave a total sample of 843 subjects.

However, the responses to subliminal stimuli delivered alone differed dramatically between these pre-test detection blocks and the main experimental blocks. In the main experimental blocks, subliminal stimulation delivered alone frequently triggered a false alarm (Table 2), while in the pre-test detection blocks, the identical subliminal stimulation did not. That is, false alarm errors were more frequent in blocks when perceptible near-threshold stimuli were delivered, than in blocks when no perceptible stimuli were ever delivered, such as the pre-test detection block. We hypothesised that the context provided by readily perceptible stimuli could increase the probability of responding 'yes' to a subliminal stimulus. We therefore investigated whether this increase in false alarm rate for subliminal-only stimuli relative to stimulus absent trials was larger in the experimental somatosensory detection blocks than in the pre-test detection block. We therefore computed the difference between false alarm rate for subliminal-only stimuli and false alarm rate for stimulus absent trials for both detection blocks. Since no significant differences emerged comparing these values across experiments (all p>0.05; see Table 2), a paired t-test was performed combining the data across all experiments, with the null hypothesis that [False Alarm (subliminal only, somatosensory detection block) – False Alarm (no stimulus, somatosensory detection block)] = [False Alarm (subliminal only, pre-test detection block) – False Alarm (no stimulus, pre-test detection block)]. A one-tailed test was used to test the directional hypothesis, derived from the above putative contextual influence of supra-threshold stimuli on

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perceptual processing, that false-alarm rate was greater in blocks when perceptible near-threshold stimuli are delivered (i.e. somatosensory detection block), than in blocks when no perceptible stimuli are ever delivered (i.e. pre-test detection block). The hypothesis was supported (t_{22}= -1.823; p=0.041, Cohen's d = 0.51; 95% CI for effect size [-0.08, 1.09]). False alarms to exactly the same subliminal stimuli thus increased when detectable stimuli were presented in the same block, compared to when they were not.

	Somatosensory Signal detection Task			
	Hits (%)	Misses (%)	Correct Rejections (%)	False Alarms (%)
Experiment 1				
Near-Threshold	M: 45.63 SD: 22.94	M: 54.38 SD: 22.94	M: 90.00 SD: 14.39	M: 10.00 SD: 14.39
Subliminal + Near-threshold	M: 45.00 SD: 26.76	M: 55.00 SD: 26.76	M: 82.81 SD: 16.00	M: 17.19 SD: 16.00
Experiment 2				
Near-Threshold	M: 56.67 SD: 16.71	M: 43.33 SD: 16.71	M:90.00 SD: 9.76	M: 10.00 SD: 9.76
Subliminal + Near-threshold	M: 57.08 SD: 22.71	M: 42.92 SD: 22.71	M: 73.33 SD: 15.01	M: 26.67 SD: 15.01
Experiment 3				
Near-Threshold	M: 46.19 SD: 11.29	M: 53.81 SD: 11.29	M: 82.38 SD: 21.75	M: 17.62 SD: 21.75
Subliminal + Near-threshold	M: 45.24 SD: 14.51	M: 54.76 SD: 14.51	M: 76.19 SD: 23.92	M: 23.81 SD: 23.92
Combined				
Near-Threshold	M: 49.64 SD: 17.85	M: 50.36 SD: 17.85	M: 87.68 SD: 15.43	M: 12.32 SD: 15.43
Subliminal + Near-threshold	M: 49.28 SD: 21.99	M: 50.72 SD: 21.99	M: 77.50 SD: 18.06	M: 22.50 SD: 18.06

Table 2.

Hits, misses, correct rejections and false alarms rates (means and standard deviations) averaged across the three experiments as a function of the experimental condition.

Subliminal stimulation decreased sensitivity for somatosensory signal detection. We present here all and only the studies that we have conducted on this topic. Importantly, the main finding was replicated in three different experiments, involving three different groups of participants. Across three experiments and 23 subjects, we consistently found that a single subliminal stimulus decreased sensitivity for somatosensory signal detection. Pooling the relevant conditions across experiments revealed a reliable subliminally-induced

reduction of sensitivity (t_{22} = 4.847, p < 0.001, Cohen's d = 0.62; 95% CI for effect size [0.019, 1.201]). We also used meta-analysis to investigate the effect size across our three experiments, using random effects models (Borenstein et al., 2011). This approach allowed us to investigate two questions. First, whether the subliminally-induced decrease in somatosensory sensitivity is reliable across experiments. Second, whether there is heterogeneity among experiments. We found a significant overall effect of subliminal stimulation across the three experiments (p = 0.033; 95% CI = [0.06 1.395]). Measures of heterogeneity were used to estimate whether the observed variability in effect size might just be explained by chance, or whether other factors might be involved. Results indicated negligible heterogeneity among studies, Q (2) = 0.439, p = 0.803.

In addition, we also found a trend for subliminal stimulation to produce a liberal bias, i.e., an increased probability of responding "yes", whether the near-threshold stimulus was present or not. Although this effect on bias reached only trend levels in any single experiment, pooling the relevant conditions across experiments revealed a reliable bias effect (t_{22} = 3.207, p = 0.004, Cohen's d = 0.73; 95% CI for effect size [0.12, 1.32]).

Inspection of the detection results (Table 2) suggested that both sensitivity and response bias changes arose because preceding subliminal stimulation increased the false alarm rate. These false alarms following subliminal stimulation occurred despite the fact that the subliminal stimuli alone were imperceptible. Because our results show a strong spatial gradient of subliminal shock efficacy, the false alarm rates presumably reflect a central rather than a peripheral effect. Importantly, we always delivered subliminal shocks and near-threshold stimuli as single pulses, in separate, independent and randomised trials. This arrangement had three advantages: first, it meant that subliminal stimulation did not predict near-threshold stimulation; second, it minimised the possibility that the effect depends on the temporal pattern of subliminal stimuli, as opposed to their energy; and finally it allowed us to apply signal detection theory methods.

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3. General Discussion

Awareness in human perception has been widely debated by philosophers, psychologists, and neuroscientists (Chalmers, 2000; Dennett, 2001; Singer, 1998). Only a subset of sensory signals enters awareness. However, even stimuli that do not enter into consciousness can nevertheless be processed by our brain (Libet, 1967). Our results clearly show that subliminal stimuli do not simply generate weak, subthreshold responses, but rather alter subsequent perception of later stimuli. In particular, we demonstrated that subliminal stimulation decreased sensitivity for detecting a subsequent somatosensory input. This effect was largely due to increased false alarm rates.

Importantly, we found that the reduction in sensitivity decreased when the subliminal and near-threshold shocks were giving to different fingers. This decrease had a linear pattern across the somatotopic space of the digits, although we did not systematically investigate whether other component patterns, such as quadratic trends, might also be present. Subliminal inhibition from remote fingers rules out accounts based on peripheral receptor mechanisms, such as receptor adaptation. Similarly, filtering mechanisms at spinal level also seem unlikely, since the effect was also present when subliminal and near-threshold shocks were delivered to digits that project to different spinal segments (dermatomes). Previous work comparing conscious and unconscious processing emphasised that subliminal stimuli have only local effects. For example, subliminal stimuli do not activate large-scale inter-areal cortical networks (Dehaene et al., 2006). Our data suggest that subliminal stimuli can produce activation beyond the immediate projection site, at least within a single somatotopic cortical area. Neuroimaging studies estimate the distance between somatosensory cortical representations of digits 2 and 5 at around 13 mm (Duncan, 2007), suggesting substantial spread of our subliminal activations across the cortical map. Lateral projection of inhibitory interneurons is an important mechanism of inhibitory interaction in the somatosensory cortex. However, because of interneurons' limited axon length, this interaction spreads only around 350 μm, at least in rodent barrel cortex, and never crosses barrel boundaries (Swadlow, 2002; Harris and Woolsey, 1983). Inhibitory interaction might therefore take place in primary somatosensory cortices, where receptive fields are digit-

Blankenburg and colleagues (2003) suggested that subliminal stimuli down-regulate areas involved in stimulus processing. On this view, subliminal inhibition could enhance cortical selection of significant stimuli, by raising thresholds (Figure 2A), and thus suppression of input noise in the somatosensory system (Blankenburg et al. 2003; Taskin et al. 2008). Our use of signal detection theory identifies specific subliminal effects on sensitivity and bias, and suggests a different view. We found that subliminal stimuli *impair* cortical perceptual processing. In particular, our data show that subliminal stimuli strongly increase false alarm rates, leading to both reduced sensitivity and liberal bias. In contrast, raising the noise threshold should *reduce* false alarms, without affecting sensitivity to signals above that threshold (Figure 2A).

We have investigated how simple cognitive models of sensory signal detection could reproduce subliminally-triggered changes in sensitivity and in false alarm rate. According to one account, subliminal stimulation might reduce the overall input gain of the sensory input pathway (Figure 2B). This would limit the output of a putative sensory detector unit without affecting central noise. Therefore, sensitivity to near-threshold shocks would be reduced because the range of outputs for a given range of inputs would be compressed, leading to greater overlap between the distributions of responses evoked by near-threshold signals and by internal noise alone. If observers would additionally adjust their criterion in line with the altered gain, to maintain a consistent correct detection rate for near-threshold stimuli on interleaved trials with and without subliminal stimulation (Figure 2B, bottom row), then this mechanism would also lead to the increase in the false alarm rate that we observed. Thus, a combination of gain reduction and a liberal shift in response criterion could explain our results.

According to an alternative account, the subliminal prime might transiently increase the level of central noise (Figure 2C). This would reduce sensitivity directly by increasing the overlap between the distributions of neural activity evoked by the near-threshold stimulus, and by noise alone. In our experiments the average correct detection rate for near-threshold stimuli was close to 50%, placing the typical decision criterion near the centre of the signal and noise distribution. Thus, any factor, such as

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increased central noise, that broadened the distributions would leave the hit and miss rates unchanged, while increasing the false alarm rate, as our data show. However, this model cannot readily explain why subliminal stimuli presented alone lead to false alarm rates *only* in experimental blocks where near-threshold stimuli were also presented, and not in catch trials of pre-test blocks where near-threshold stimuli were not presented. If the subliminal prime were simply to increase central noise, one should experience more false alarms in *both* types of block, independent of context. By contrast, our initial model of reduced input gain might increase the false alarm rate only if observers also adjusted their response criterion to match the experienced distribution of near-threshold activity.

Blankenburg et al. (2003) presented their subliminal stimuli in continuous trains. In principle, the brain might extract the regular temporal pattern of subliminal stimuli. If subliminal stimuli could be classified as non-targets on the basis of their timing alone, then thresholds for conscious detection (Figure 2A) could be raised accordingly. Thus, those stimulus parameters and analysis methods may have favoured discriminative mechanisms that selectively suppress weak stimuli. Importantly, this mechanism does not involve any general adjustment of sensory processing *within* the sensory pathway, it merely prevents weak stimuli from entering the pathway. In contrast, we delivered single subliminal stimuli, with or without a to-be-detected near-threshold shock, and we analysed the results using signal detection theory. Therefore, threshold adjustments based on stimulus timing cannot account for our data. Rather, an automatic and preconscious process appears to identify a single weak stimulus, and trigger appropriate adjustments to cortical perceptual machinery, even though the subliminal stimulus itself remains imperceptible. Any sensate organism must balance the need to respond to unexpected, faint, but potentially-relevant stimuli, with the need to focus processing capacity on those stimuli that are currently most important or most salient. Our results suggest that gain modulation of sensory pathways is one key mechanism for achieving this balance.

Subliminal somatosensory inhibition is often attributed to inhibitory thalamocortical (feed-forward) and intracortical interneuronal (feedback) connections (Blankenburg et al., 2003), though other circuits may also contribute. Our data provide new and important findings about such mechanisms. First, this mechanism operates by changing the gain of the somatosensory pathway. Second, gain regulation operates

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automatically under bottom-up influence, since it is caused by subliminal stimuli that are not consciously perceived. Third, our results raise the intriguing possibility that gain regulation is intensity-dependent. Reducing the gain in response to a near-threshold stimulus occurring alone would scarcely be a functional process in a detection task, yet reducing gains in response to a subliminal stimulus may protect against excessive responsivity to minimal stimuli. We suggest that afferent signals trigger an initial, pre-perceptual classification of stimuli based on their energy level. The output of this classifier could then be immediately used to regulate gains within the somatosensory pathway. The subliminal shock itself must trigger a specific set of neural processes which alters signal detection, for example by gain reduction. This triggering process must be bottom-up, rapid, automatic, but also context-sensitive.

Most importantly, we show that processing of subliminal somatosensory signals depends on context and stimulus distribution. We found that subliminal shocks increased false alarm rates in experimental blocks where near-threshold shocks were also present. However, the same subliminal shocks did not increase false alarm rates in pre-test detection blocks containing only subliminal shocks and catch trials, and in which no readily perceptible stimuli were present. The presence of some detectable stimuli appeared to be necessary for subliminal shocks to influence somatosensory signal processing. We proposed above that subliminal shocks might automatically trigger a reduction of the input gain in the somatosensory pathway. This reduction in gain would only translate into increased false alarms, and thus altered sensitivity and bias, when observers lowered their detection criteria to match the reduced gain. However, lowering the detection criterion would not be a functional strategy in our pre-test blocks, where no clearly detectable stimulus ever occurred, and accordingly, we found no increase in false alarms to subliminal stimuli in pre-test blocks. Thus, we suggest that subliminal somatosensory inhibition involves at least two quite distinct effects. The subliminal stimulus leads to an automatic reduction in input gain. When some detectable stimuli were present, participants also appear to strategically lower their response criterion, perhaps reflecting a belief that detection rates should be roughly constant. The mechanisms underlying these responses are different. Signal detection theory has the advantage of clearly separating them.

A **Increased Threshold Model**

G_i G_c C

Signal → X → + → X → Conscious Perception

Signal or Noise? Filter N_c

B **Overall Gain Reduction Model**

G_i G_c C

Signal → X → + → X → Conscious Perception

N_c

C **Increased Central Noise Model**

G_i G_c C

Signal → X → + → X → Conscious Perception

N_c

Near Threshold

C Near Threshold

Noise   Signal+Noise

Hits

False Alarms

'*No*' Region   '*Yes*' Region

Sensory Continuum

Subliminal + Near Threshold

C Subliminal + Near Threshold

Noise   Signal+Noise

Hits

False Alarms

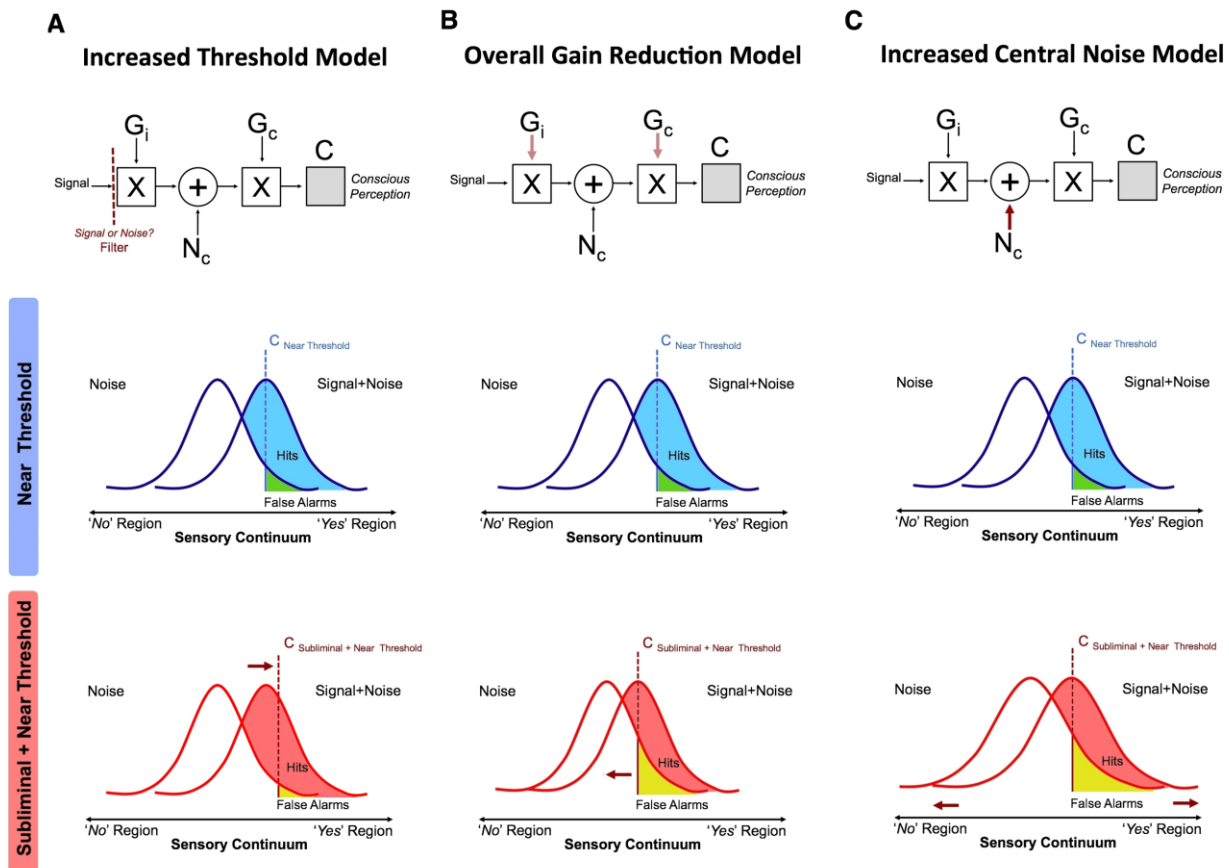'*No*' Region   '*Yes*' Region

Sensory Continuum

Figure 2. Functional Models.

Upper row: simplified flow-diagram of conscious perception and stimulus-response functions of a hypothetical sensory channel. G_i=Input Gain; N_c=Central Noise; G_c=Central Gain; C=Criterion. Lower row: effects of a preceding subliminal shock on the signal detection scenario.

Increased Threshold Model (A): on this model, subliminal stimuli increase thresholds for detecting subsequent stimuli. The signal detection scenario shows that the two distributions shift toward the left but the criterion (i.e. the threshold) is stable, causing decreasing in hit rate and in false alarm rate, and thus increased sensitivity.

Overall Gain Reduction (B): on this model, subliminal stimuli cause an overall gain decrease, while leaving central noise unaffected. The overlap between signal-induced responses and low-amplitude noise is thus greater, implying increased false alarm rate and decreased sensitivity. The criterion may shift leftward (more liberal), to maintain a consistent response rate to near-threshold stimuli.

Increased Central Noise (C): on this model, subliminal stimuli trigger an increase in the central noise. The response to low-amplitude noise stimuli is increased, and the distribution is substantially broader because of the central noise. This produces greater overlap, implying a higher false alarm rate and decreased sensitivity.

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4. Conclusions

Our data suggest that subliminal stimuli can have two important, dynamic effects on sensory processing. On the one hand, they can automatically trigger a reduced somatosensory gain. On the other hand, they trigger a criterion adjustment that appears to be contextual and strategic, based on the range of signals present in a given context. Taken together, these mechanisms suggest that subliminal stimuli could trigger complex processes for dynamic range adaptation. Automatic processes that are nevertheless context- and distribution-sensitive have been identified before. In particular, studies of implicit sensory learning (Garrido et al., 2013) suggest that automatic predictive learning depends on the distribution of stimulation. Such learning can occur even in the absence of conscious awareness of the pattern, although it is generally studied with suprathreshold stimuli, which are readily perceived. We believe ours may be the first study to show that the neural processing of subliminal stimuli also depends on the statistics of stimulus distribution.

Acknowledgements

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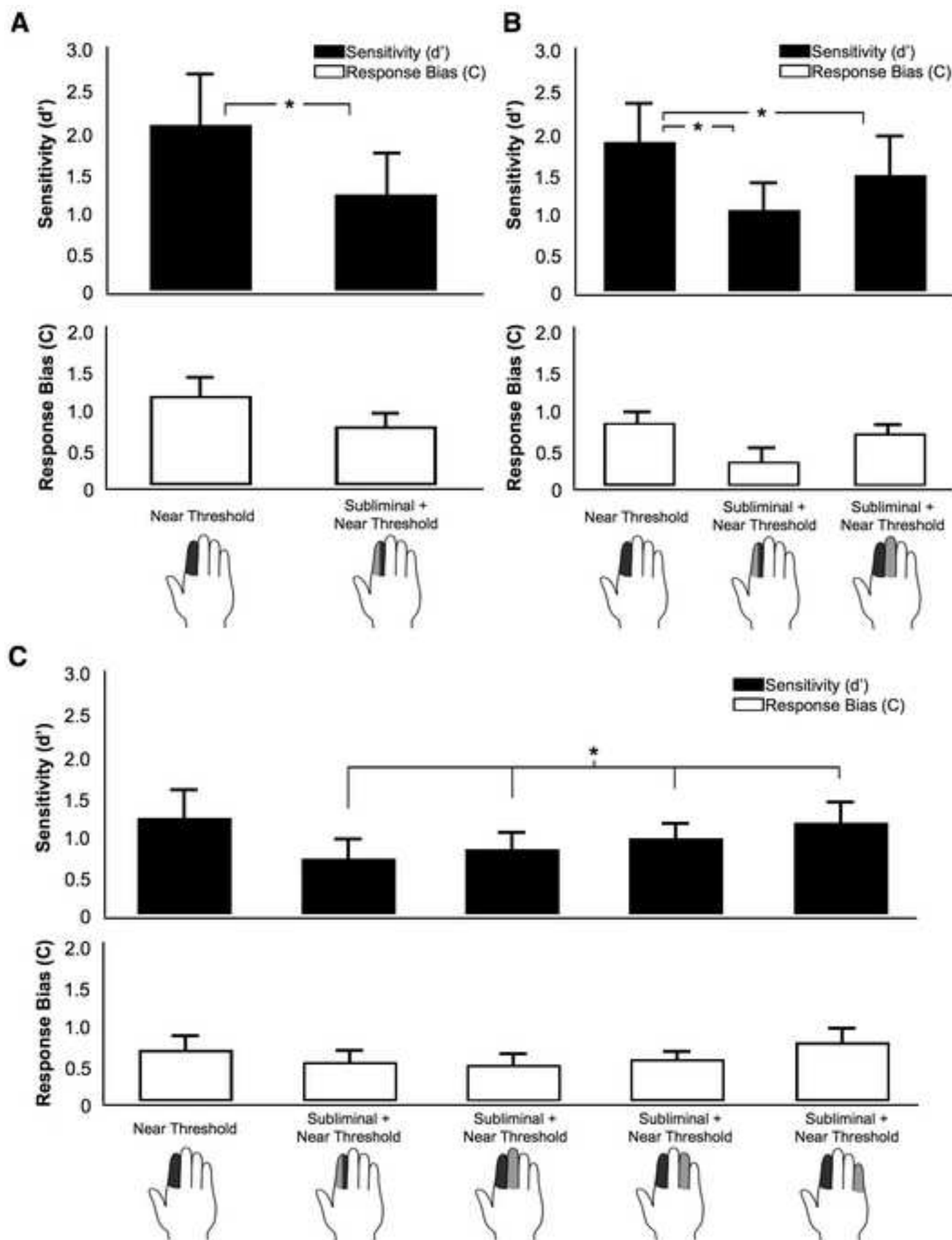**Figure 1**
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Figure 2
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Figure 2

A Increased Threshold Model **B** Overall Gain Reduction Model **C** Increased Central Noise Model