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Vision automatically exerts online and offline influences on bimanual tactile spatial perception

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ABSTRACT

Vision and touch interact in spatial perception. How vision exerts online influences on tactile spatial perception is well-appreciated, but far less is known regarding how recent visual experiences modulate tactile perception offline, particularly in a bimanual context. Here, we investigated how visual cues exert both online and offline biases in bimanual tactile spatial perception. In a series of experiments, participants performed a 4-alternative forced-choice tactile detection task in which they reported the perception of peri-threshold taps on the left hand, right hand, both hands, or no touch (LRBN). Participants initially performed the LRBN task in the absence of visual cues. Subsequently, participants performed the LRBN task in blocks comprising non-informative visual cues that were presented on the left and right hands. To explore the effect of distractor salience on the visuo-tactile spatial interactions, we varied the brightness of the visual cues such that visual stimuli associated with one hand were consistently brighter than visual stimuli associated with the other hand. We found that participants performed the tactile detection task in an unbiased manner prior to experiencing visual distractors. Concurrent visual cues biased tactile performance, despite an instruction to ignore vision, and these online effects tended to be larger with brighter distractors. Moreover, tactile performance was biased toward the side of the brighter visual cues even on trials when no visual cues were presented during the visuo-tactile block. Using a modeling framework based on signal detection theory, we compared a number of alternative models to recapitulate the behavioral results and to link the visual influences on touch to sensitivity and criterion reductions. Our collective results imply that recent visual experiences alter the sensitivity of tactile signal detection processes while concurrent visual cues induce more liberal perceptual decisions in the context of bimanual touch.

1. Introduction

We live in chaotic multisensory environments and the nervous system combines information over multiple sensory cues to support perception (Fetsch et al., 2013; Stein & Stanford, 2008; Yau et al., 2015). Interactions between sensory signals can result in more reliable sensory estimates (Ernst & Bulthoff, 2004; Green & Angelaki, 2010), more accurate perceptual decisions (Odegaard et al., 2015), and faster behavioral responses (Hecht et al., 2008; Otto et al., 2013). Commonly, the nervous system combines sensory signals that convey redundant or correlated information. Importantly, interactions between multisensory cues not only modulate immediate behavioral responses, but they can also induce persistent behavioral changes (Ernst, 2007; Navarra et al., 2007; Senna et al., 2014; Shams et al., 2011; Zilber et al., 2014). Accordingly, there has been longstanding interest in characterizing multisensory interactions in different perceptual domains and relating these multisensory effects to behavioral adaptation and learning (Shams & Seitz, 2008).

For spatial perception, we rely extensively on vision and touch, and these modalities exhibit robust interactions in the perception of space (Farne et al., 2003; Ladavas et al., 1998; Maravita et al., 2000; Ro et al., 2004), size (Ernst & Banks, 2002), shape (Bisiach et al., 2004; Hadjikhani & Roland, 1998; Helbig et al., 2012; Streri & Molina, 1993), and motion (Bensmaia et al., 2006; Konkle et al., 2009). With feature-specific processing, visuo-tactile interactions have been related to analogous coding mechanisms (Maunsell et al., 1991; Yau et al., 2016, 2009; Zhou & Fuster, 2000) and shared representations (Amedi et al., 2002; Konkle et al., 2009; Lacey & Sathian, 2011; Mancini et al., 2011; Van Der Groen et al., 2013). Visuo-tactile processing, particularly involving simple sensory cues, has also been linked to spatial attention interactions (Driver & Spence, 1998; Spence et al., 2000a) and there is evidence that shared attention processing resources may support

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both vision and touch as well as their multisensory engagement (Lakatos et al., 2009; Macaluso et al., 2002; Spence & Driver, 1996).

In addition to visual influences on touch experienced on a single hand, there is also extensive evidence that vision modulates tactile perception in bimanual contexts (Heed & Azañón, 2014; Soto-Faraco et al., 2004; Spence, Pavani, Maravita et al., 2004). Understanding bimanual touch is critical as many of our routine behaviors involve sensorimotor coordination between the hands (Swinnen & Wenderoth, 2004) and tactile cues experienced on one hand can influence tactile perception on the other (Craig & Qian, 1997; Kuroki et al., 2017; Rahman & Yau, 2019; Sherrick, 1964; Tamè et al., 2011; Verrillo et al., 1983). Studies exploiting the visuo-tactile crossmodal congruency effect (Shore et al., 2006; Spence, Pavani and Driver, 2004) have shown that ignored visual cues presented near the hands automatically exert strong influences on the performance of a bimanual task requiring subjects to localize peri-threshold tactile cues that differ in elevation. While these perceptual effects reveal the attentional, spatial, and temporal constraints for visuo-tactile interactions in a bimanual context, it is unclear how these interactions can be understood according to signal detection theory. Conceivably, vision could influence bimanual touch by modulating either the sensitivity or decision criterion parameters in the tactile signal detection processes. Indeed, visual distractors have been reported to increase the tactile detection rates on a single hand through criterion reductions rather than sensitivity increases (Lloyd et al., 2008; Mirams et al., 2017). Furthermore, to the extent that visual or multisensory experience results in immediate changes in how tactile cues are subsequently perceived, it would also be important to relate these learning or adaptation effects to changes in sensory processing or decision making.

Here, we sought to understand how online and offline visuo-tactile interactions in a bimanual context can be understood according to signal detection theory. In psychophysical experiments, we characterized the effects of brief light flashes (distractors) on the performance of a simple bimanual spatial task that required healthy human subjects to detect and localize faint taps that were delivered to one hand or both hands simultaneously. By pairing bright distractors with one hand and dim distractors with the other hand, we established the dependence of the visuo-tactile interactions on distractor brightness. Although we explicitly instructed participants to ignore the visual distractors, we hypothesized that the non-informative visual stimuli would nevertheless exert spatially-specific influences on tactile spatial perception. We measured tactile localization behavior prior to exposing participants to multisensory experiences and we compared performance during this baseline block to performance during subsequent visuo-tactile blocks that comprised both visuo-tactile and tactile-only trials. This design allowed us to quantify the influence of visual distractors on the detection and localization of simultaneously experienced taps (online effects) as well as changes in performance that occurred even in the absence of visual distractors (offline effects). Using a modeling framework which assumed separate signal detection processes for the two hands, we evaluated how visual distractor effects related to changes in either sensitivity or decision criterion. By dissociating online and offline effects, we compared how these were separately related to the signal detection parameters and evaluated how they interact.

2. Materials and methods

2.1. Participants

Sixteen healthy individuals (10 females; mean age $\pm$ SD: 23 ± 4.5 age; range: 18–32 years) participated in the experiment. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). All participants reported normal tactile sensitivity and normal or corrected-to-normal vision. No participant reported a neurological or psychiatric history. All testing procedures were conducted in compliance with the policies and procedures of the Baylor College of Medicine Institutional Review Board. All participants gave their written informed consent and were paid for their participation.

2.2. Tactile and visual stimulation

Tactile and visual stimuli were digitally generated in Matlab (2011b, MathWorks) and presented with Psychtoolbox-3 (Kleiner et al., 2007) running on a MacBook Pro (model A1278; OS X 10.9.5, 2.5 GHz Core i5, 4 GB of RAM). Tactile stimuli were generated and delivered using previously described methods (Convento et al., 2018). In brief, analog signals (sample rate: 44.1 kHz) were passed through the auxiliary port to power amplifiers (Krohn-Hite Wideband Power Amplifier, model 7500). The amplified signals were delivered to the subject's left and right index fingers through a pair of electromechanical tactors (type C-2, Engineering Acoustics, Inc). The tactors were fastened to the distal phalanges of the index finger on the right and left hands using self-adherent cohesive wrap bandages. Visual stimuli were presented using two LEDs (Dorado 1-Watt; green emitting color, 527 nm) which were mounted on the left- and right-hand tactors. LEDs were activated by TTL pulses sent via a DAQ device (model USB-1208FS, Measurement Computing Corporation).

2.3. General procedures

Each participant was tested in a single session. The session comprised (1) an initial stimulus calibration period that included threshold assessments, (2) a baseline tactile test block, and (3) 4 test blocks which involved visual and tactile stimulation (Fig. 1A). The total duration of the experiment was between 75–90 min. Participants sat in front of a monitor with their head supported on a table-mounted chin rest. The monitor displaying a central fixation cross was placed in front of the participant's head at a viewing distance of 33 cm (Fig. 1B). Participants maintained their hands in a supinated position with their arms outstretched and separated by 38 cm. This posture created an $\sim 140^{\circ}$ viewing angle between the hand-fixed LEDs when the participants maintained central fixation. One LED was fastened to the left index finger and the other was fastened to the right index finger. The luminance of the LEDs was manipulated using resistors such that one was perceptually brighter (2212.9 cd/m^2) than the other (6.2 cd/m^2). The hands associated with the bright and dim LEDs was counterbalanced across subjects such that the bright LED was fixed to the tactor on the left index finger while the dim LED was fixed to the tactor on the right index finger in half of the subjects. In the other subjects, the bright LED was associated with the right index finger while the dim LED was associated with the left index finger. This counterbalanced design ensured that performance variations related to LED brightness could not be trivially attributed to the biased performance between left and right hand touch. Accordingly, *each participant's left and right hand performance data were analyzed based on whether the hand was associated with the bright or dim LED (i.e., the bright-associated hand or the dim-associated hand)* even in the baseline block or when no LEDs were illuminated.

Participants underwent a visual test to ensure that they could properly see the LEDs flashing and perceive the luminance difference between the bright and the dim LEDs. As participants maintained visual fixation, each LED was illuminated (5 ms) a total of 5 times in random order and participants verbally reported

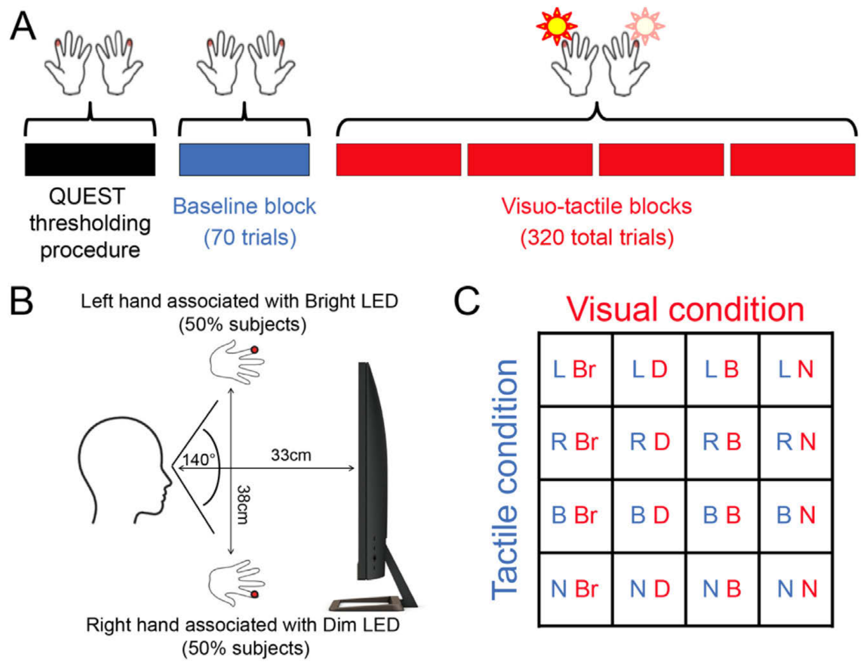

Fig. 1. Experimental design. (A) Each session comprised an initial period for establishing tactile detection thresholds and stimulus calibration, a block of tactile-only trials (Baseline block), and 4 visuo-tactile blocks where tactile stimulation could be paired with the illumination of a bright or dim LED. For each subject, the bright LED was fastened to one hand and the dim LED was fastened to the other hand. Accordingly, the hands are labeled as bright-associated or dim-associated in all analyses. (B) Participants maintained visual fixation on a monitor while performing the tactile localization task. The hand associated with the bright LED was counterbalanced across participants with the left hand being bright-associated in 50% of participants. (C) During each trial of the 4AFC task, subjects experienced touch (conditions indicated in blue) to the left hand only (L), right hand only (R), both hands simultaneously (B), or no touch (N) and subjects reported whether and where they detected the tactile stimulation. During the baseline block, no visual cues were delivered on any trials. During the visuo-tactile blocks, the 4 tactile conditions were parametrically combined with visual conditions (indicated in red) which comprised illumination of the bright LED only (Br), dim LED only (D), both LEDs (B), or no LED illumination (N).

when and on which hand they perceived the flash. All participants detected the bright and dim LED flashes with 100% accuracy. We also asked participants to rate the perceived brightness of each LED using a 10-point scale (1 = very dim, 10 = very bright). On average, participants rated the bright LED as 2.5x brighter than the dim LED (Bright LED: 8.43 ± 0.5; Dim LED: = 3 ± 0.8).

2.4. Establishing tactile detection thresholds

As we have done previously (Convento et al., 2018), a Bayesian adaptive staircase procedure (QUEST) (Watson & Pelli, 1983) was used to establish tactile detection thresholds (TDTs) for each participant's left and right index fingers. The procedure was implemented using the QUEST toolbox in Matlab. The QUEST algorithm provides a threshold estimate that updates over increasing numbers of trials. The procedure assumes that the observer's probability of giving a target response follows a Weibull distribution,

$$W_T(x) = 1 - (1-\gamma)\, exp\left[-10^{(x-\alpha)\beta}\right]$$

where x is the test stimulus value, γ is the probability of the target response at x = $-\infty$, β is the slope of the psychometric function, and α is the threshold. The QUEST algorithm accounted for lapse rates with an additional parameter, δ, which was fixed at 0.01 in all experiments (Watson & Pelli, 1983). A probability density function (PDF), representing the current knowledge of the threshold over all previous trials of the procedure, is updated according to the subject's response on each trial and determines the value of the test stimulus on the subsequent trial. Over trials, the variance of the PDF decreases resulting in a more accurate estimate of the threshold. Prior to the QUEST procedures, participants were familiarized with the task and the tactile stimuli. In a single run, we estimated TDTs for the left and right hands with 2 parallel and independent QUEST procedures, one ascending (40 trials) and one descending (40 trials) for each hand (β: 3.5, γ: 0.5, percent correct at threshold: 90%, total trials: 80). Each subject underwent 2–4 runs of the QUEST depending on threshold consistency across runs. On each trial, a single tactile stimulus (5 ms; 1 contact event) was randomly presented to the left or right index finger and the subject verbally reported whether she detected it on the left or right hand. The average TDT was comparable across hands (group average, right hand = 0.018 ± 0.008 a.u.; left hand = 0.018 ± 0.008 a.u.). For reference, a stimulus presented at an amplitude of 0.45 a.u. using our tactors corresponds to 2.3 V measured from the output of the amplifier and ∼280-µm displacement (measured with no load; Rahman & Yau, 2019).

2.5. Bimanual tactile localization task in the absence of visual distractors

Participants performed a 4-alternative forced choice (4AFC) tactile localization task. On each trial, participants experienced a 5-ms tap on the left hand only, the right hand only, both hands simultaneously, or no stimulus (LRBN task). Subjects verbally reported whether they perceived a tactile stimulus on the left hand only ("Left"), right hand only ("Right"), both hands simultaneously ("Both"), or no stimulation ("None"), as they maintained fixation throughout and between the trials. On each trial, the 5-ms stimulus interval was preceded by a 250-ms interval and followed by a 250-ms interval. This combined interval was cued by a change in the color of the fixation cross from blue to red which indicated to the subject the potential for stimulation. Subjects were cued to respond when the fixation cross reverted back to blue. Subjects had an unlimited amount of time to respond. Following a response, there was a 1-s interval before the start of the next trial. Participants experienced tactile-stimulation trials (left, right, and both; 20 repeats each) and no-stimulation trials (10 repeats) in random order. The amplitude of the tactile stimuli was set at 120% of each subject's TDTs (Convento et al., 2018). Performance during this block served as a baseline against which performance achieved with visual distractors could be compared.

2.6. Bimanual tactile localization task in the context of visual distractors

In visuo-tactile (VT) blocks, participants performed the LRBN task in the presence and absence of unilateral or bilateral LED flashes. Light stimuli comprised brief (5 ms) illumination of LEDs which coincided with the tactile cues. Four visual-distractor conditions were tested over trials: illumination of the bright LED only, illumination of the dim LED only, illumination of both LEDs, or no LED illumination. We adopted a full parametric design that combined the 4 visual-distractor conditions with each of the 4 tactile-stimulus conditions (left hand, right hand, both hands, no touch) for a total of 16 visuo-tactile trial types (Fig. 1C). Each trial type was repeated 20 times in a pseudo-randomized order. Participants were instructed explicitly to ignore the LEDs and to maintain visual fixation on the central cross while performing the 4AFC tactile task. Trials were divided into 4 visuo-tactile blocks each comprising 80 trials. Each test block lasted 5–6 min. Participants were allowed to rest 2–3 mins between blocks. Note that the tactile cues on the no-LED trials in the visuo-tactile blocks were identical to the tactile cues in the baseline block (i.e., LRBN task performance without visual distractors) so performance differences between these blocks would reflect offline changes that emerge during the visuo-tactile blocks.

2.7. Statistical analysis

Statistical analyses were performed using Matlab (R2015b, R2019b). Uncorrected p-values are reported in the text. Because the right hand was associated with the bright LED in half of the participants and the dim LED in the other half, we analyzed the performance data over subjects according to the hands' association with the bright and dim LEDs.

To test whether performance differed according to the tactile condition in the baseline (tactile-only) block, we conducted a one-way repeated-measures ANOVA (rmANOVA) with tactile condition (touch on bright-associated hand only, touch on dim-associated hand only, touch on both hands, no touch) as the within-subjects factor. We performed post-hoc paired-sample t tests with Bonferroni correction.

To test whether performance during the VT blocks differed according to the tactile and visual conditions, we conducted a two-way rmANOVA with tactile and visual conditions as the within-subject factors. We conducted post-hoc one-way rmANOVA to test for main effects of tactile conditions under each of the visual conditions. We additionally quantified spatial performance biases in the visuo-tactile blocks (i.e., how much localization performance became *biased to the hand* associated with the bright or dim LEDs), by defining a lateralization bias index:

$$LBI_C = B^C_{corr} - D^C_{corr}$$

where B^C_{corr} and D^C_{corr} indicate baseline-corrected response rates for the hand associated with the bright LED and dim LED, respectively, for each VT condition (C) separately (i.e., illumination of the bright LED only, dim LED only, both LEDs, or no LEDs illuminated). For the bright-associated hand, baseline-corrected rates were calculated as the difference in the response rates achieved on trials involving the bright-associated hand in the visuo-tactile block and the baseline (BL) block:

$$B^C_{corr} = \left(B^C_{1hand} + B^C_{2hand} + B^C_{none}\right) - \left(B^{BL}_{1hand} + B^{BL}_{2hand} + B^{BL}_{none}\right)$$

where B^x_{1hand} is the hit rate when the bright-associated hand was stimulated alone, B^x_{2hand} is the proportion of bimanual stimulation trials when the subjects reported only feeling touch on the bright-associated hand, B^x_{none} is the false alarm rate when subjects reported feeling touch on the bright-associated hand when no tactile stimulation was delivered, and x indicates the visuo-tactile block or the baseline block. Baseline-corrected response rates for the dim-associated hand were similarly computed:

$$D^C_{corr} = \left(D^C_{1hand} + D^C_{2hand} + D^C_{none}\right) - \left(D^{BL}_{1hand} + D^{BL}_{2hand} + D^{BL}_{none}\right)$$

The LBI thus describes the relative response rates for the bright- and dim-associated hands under each VT condition after accounting for potential biases that may be evident in the baseline block. Positive LBI values indicate increased response rates on the hand associated with the bright LED compared to the rates for the hand associated with the dim LED. To test whether LBI values differed according to VT condition, we performed a one-way rmANOVA with visual condition as the within-subject factor. We performed post-hoc paired sample t tests with Bonferroni correction comparing LBI values between VT conditions. We also evaluated whether LBI significantly differed from 0 in each condition using one sample t tests with Bonferroni correction.

2.8. Modeling bimanual tactile localization performance in a signal detection theory framework

To model performance on the 4AFC task, we implemented a model based on signal detection theory (SDT; Green & Swets, 1988) that assumed separate detection processes for the two hands. Given that visual influences on unimanual touch have been attributed to criterion changes rather than sensitivity changes (Lloyd et al., 2008; Mirams et al., 2017), we set out to test whether visual influences on touch in a bimanual context could also be exclusively ascribed to a single signal detection parameter. Accordingly, we tested alternative models that assumed online and offline effects resulted from changes in the sensitivity or decision criterion parameters, relative to baseline values. Because we modeled signal detection processes for the bright-associated and dim-associated hands separately, we did allow for the exclusive signal detection parameter in each model to be identical or differ for the two hands. Initial results revealed that more complex models were clearly prohibitive according to our model selection criterion (see below) so we excluded the possibility for non-exclusive effects on the sensitivity and criterion parameters and distractor effects on the non-associated hand.

Specifically, we established the sensitivity (d') and criterion (λ) parameters that accounted for performance in the baseline block and then tested alternative hypotheses for how exposure to LED flashes could modulate the sensitivity and criterion parameters for each hand depending on their association with the bright or dim LED. We fitted parameters using a Bayesian Adaptive Direct Search (BADS) optimization algorithm in Matlab (Acerbi & Ma, 2017). For a given set of SDT parameters, equal-variance Gaussian noise and signal distributions were determined through simulation (10,000 samples). For each dataset, each model type was refit 100 times with random initial parameters. We adopted a staggered fitting approach in which we first estimated the SDT parameters for the baseline data, followed by the *changes* in the SDT parameters associated with the offline effects (which acted on the parameters established for the baseline model), and finally the *additional changes* in the SDT parameters associated with the online "visual-distractor" effects (which acted on the parameters established for both the baseline and offline models). In supplemental analyses, we estimated baseline, offline, and online model parameters in parallel rather than serially; this approach yielded poorer fits relative to the staggered approach because the baseline parameters were influenced strongly by the data in the VT blocks. We fit cross-validated models by estimating model parameters using 80% of the group-aggregated data and testing the model on the remaining 20%. Specifically, the offline model parameters were estimated using a training dataset comprising 80% of all participants' response probabilities randomly drawn from the no-LED trials in the VT blocks. The offline model was then evaluated by computing the total residual errors with the remaining data that was not used for parameter fitting. An analogous process was used to estimate online model parameters from a random 80% sample of all participants' response probabilities in the bright-only, dim-only, and both-LED trials and testing on the remaining 20%. We repeated this 80–20 cross-validation procedure 100 times for each model and report the average model performance and parameters. In supplemental analyses, we performed the same staggered model fitting approach to estimate model parameters based on group-averaged data and on each individual subjects' data (Supplemental Materials).

For the baseline model, we assumed that stimulus detection on each hand is mediated by 2 hand-specific processes each with sensory evidence on no-touch "noise" trials (X_n) and touch "signal" trials (X_s) drawn from normal probability density functions:

$$X_n = N(0, 1)$$
$$X_s = N\left(d'_0, 1\right)$$

where the mean of the noise distribution is 0, the mean of the signal distribution is d'_0, and both distributions have variance equal to 1. For each hand (h), the likelihood of reporting touch as "Present" conditioned on the stimulus being delivered (s) or absent (a) is determined by calculating the area under the density functions exceeding a decision criterion (λ_0):

$$P(\text{"Present"}|s_h) = P(X_s > \lambda_0) = \int_{\lambda_0}^{\infty} f_s(x)\, dx$$
$$P(\text{"Present"}|a_h) = P(X_n > \lambda_0) = \int_{\lambda_0}^{\infty} f_n(x)\, dx$$

Accordingly, the likelihood of reporting "Absent" conditioned on the stimulus being delivered or not was determined as:

$$P(\text{"Absent"}|s_h) = 1 - P(\text{"Present"}|s_h)$$
$$P(\text{"Absent"}|a_h) = 1 - P(\text{"Present"}|a_h)$$

Because detection performance in the baseline block was balanced between the hands associated with bright and dim LEDs (see Results), we used the same baseline sensitivity and criterion parameters for the two hands yielding a 2-parameter model to account for baseline block performance. With the decision processes implemented for the bright (Br) hand and the dim (D) hand, the response probabilities in the 4AFC task (i.e., "bright-associated hand only", "dim-associated hand only", "both hands", "no touch") were computed from the product of unimanual likelihoods. For example, $P(\text{"Bright hand only"}|s_B, a_D) = P(\text{"Present"}|s_B) * P(\text{"Absent"}|a_D)$.

To account for performance differences between the no-LED trials in the VT blocks and the baseline block, we assumed that the sensitivity *or* criterion parameters could be changed as a consequence of exposure to LED illumination in the VT blocks. Accordingly, we either fit d'_{off} or λ_{off} parameters that represented the changes in sensitivity or criterion relative to d'_0 and λ_0, respectively. Given that detection on the bright-associated hand and dim-associated hand were modeled with independent signal detection processes, we tested the possibility that the offline effects on sensitivity or criterion could be identical for the two hands (brightness-invariant) or differ for the two hands (brightness-dependent). Thus, in model competition, we tested 4 simple hypotheses: The offline effects could have resulted from brightness-dependent changes in sensitivity (Offline model 1, 2 parameters: d'^{Br}_{off} and d'^{Dim}_{off}), brightness-dependent changes in criterion (Offline model 2, 2 parameters: λ^{Br}_{off} and λ^{Dim}_{off}), brightness-invariant changes in sensitivity (Offline model 3, 1 parameter: d'_{off}), or brightness-invariant changes in criterion (Offline model 4, 1 parameter: λ_{off}). We used residual summed squared (RSS) errors to identify the preferred model. We also performed model comparisons using Akaike Information Criterion (AIC), a metric that accounts for both model performance and complexity (Burnham & Anderson, 2004).

To account for the online effects of visual distraction – experienced during the bright LED, dim LED, and both LED trials – in the VT blocks, we again assumed that only the sensitivity parameter or only the criterion parameter could be changed. Accordingly, we either fit d'_{on} or λ_{on} parameters that represented the changes in sensitivity or criterion relative to the sensitivity and criterion parameters of the preferred offline model (which already incorporated the baseline SDT parameters), respectively. Through model competition, we tested 4 simple hypotheses: The online effects could have resulted from brightness-dependent changes in d′ (Online model 1, 2 parameters: d'^{Br}_{on} and d'^{Dim}_{on}), brightness-dependent changes in λ (Online model 2, 2 parameters: λ^{Br}_{on} and λ^{Dim}_{on}), brightness-invariant changes in d′ (Online model 3, 1 parameter: : d'_{on}), or brightness-invariant changes in λ (Online model 4, 1 parameter: : λ_{on}). We again used model residuals to determine the preferred model, but we evaluated the models according to AIC as well.

3. Results

3.1. Tactile detection and localization in the absence of visual distractors

Participants performed a 4AFC tactile detection task (LBRN task) in which they reported the perception of peri-threshold taps delivered to the hand associated with the bright LED, the hand associated with the dim LED, both hands, or no touch in the absence of visual cues (Fig. 2A). Across all conditions, group-averaged accuracy was nearly 80% (mean ± SEM; touch on the hand associated with the bright LED: 0.77 ± 0.02; touch on the hand associated with the dim LED: 0.79 ± 0.02; touch on both hands: 0.68 ± 0.04; no touch: 0.89 ± 0.03). Across the group, performance (Fig. 2B) differed significantly according to the tactile conditions (F = 10.2, p = 3.0e−05, $\eta_p{}^2$ = 0.41). Post-hoc tests showed that performance on trials when the bright-associated hand was stimulated alone did not differ significantly compared to trials with unimanual stimulation of the dim-associated hand only ($t_{(15)}$ = −0.90, p = 0.38) or when both hands were stimulated ($t_{(15)}$ = 2.18, p = 0.05). Performance when the bright-associated hand was stimulated alone was significantly lower compared to performance on trials when no tactile cues were delivered ($t_{(15)}$ = −3.06, p = 0.0079). Performance when the dim-associated hand was stimulated alone did not differ from performance on the bimanual stimulation trials ($t_{(15)}$ = 2.78, p = 0.014), but it was significantly lower compared to performance on trials when no tactile cues were

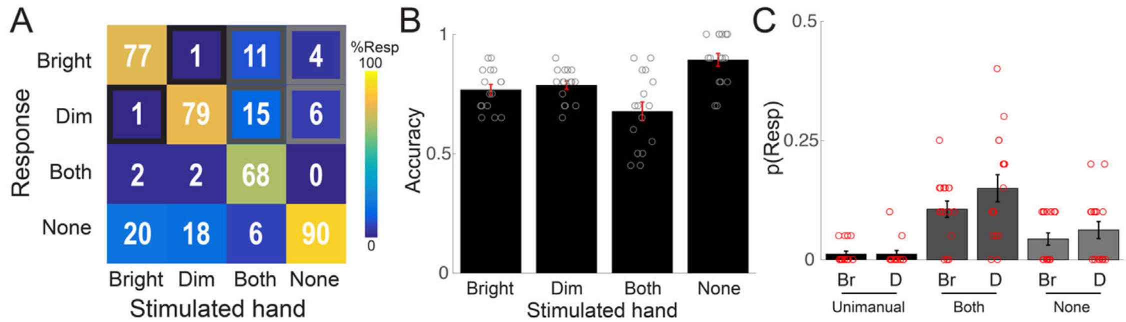

Fig. 2. Baseline block performance. (A) Confusion matrix shows group-averaged (n = 16) response probabilities on trials comprising tactile stimulation to the hand associated with the bright LED, the hand associated with the dim LED, both hands simultaneously, or no tactile stimulation. On each trial, participants reported whether they perceived touch on the bright-associated hand, the dim-associated hand, both hands, or no touch. Outlined cells (dark gray, light gray, and white squares) indicate comparisons depicted in *C*. (B) Bars indicate group-averaged performance accuracy on trials when touch was delivered to the bright-associated hand, the dim-associated hand, both hands, or when there was no touch. Errorbars indicate s.e.m. Circles indicate individual subjects. (C) Bars indicate group-averaged response probabilities for incorrect unimanual responses on unimanual stimulation trials ("Bright hand" (Br) responses when the dim-associated hand was stimulated or "Dim hand" (D) responses when the bright-associated hand was stimulated), "Bright hand" or "Dim hand" responses on bimanual trials, and "Bright hand" or "Dim hand" responses on no-touch trials. Errorbars indicate s.e.m. Circles indicate individual subjects. Response probabilities were statistically balanced between the bright-associated and dim-associated hands in all paired comparisons.

delivered ($t_{(15)} = -2.98$, p = 0.0093). Performance on the bimanual stimulation trials was significantly lower than performance on the no-touch trials ($t_{(15)} = -4.26$, p = 6.79e−04). In sum, performance was higher on the no-touch trials compared to the other stimulation conditions. No other significant performance differences were observed in the baseline block, but accuracy on bimanual stimulation trials was nominally lower compared to unimanual stimulation trials.

To test whether responses were biased to the bright-associated hand or the dim-associated hand in the baseline block, we evaluated a number of specific trial types (Fig. 2C). Note that subjects had not yet experienced the bright and dim LED flashes concurrently with tactile stimulation in the baseline block so we predicted that performance should be balanced between the hands. First, we evaluated responses on the unimanual trials and compared the probability that participants reported feeling touch on the bright-associated hand when touch was delivered to the dim-associated hand (0.013 ± 0.006) to the probability that participants reported feeling touch on the dim-associated hand when touch was delivered to the bright-associated hand (0.013 ± 0.007). These "misattributed touch" response probabilities were not statistically different ($t_{(15)} = 0$, p = 1). Second, we compared the probability that participants reported bimanual touch as only felt on the bright-associated hand (0.11 ± 0.02) versus the dim-associated hand (0.15 ± 0.03). Probabilities for unimanual reports on bimanual trials also did not differ significantly between hands ($t_{(15)} = -1.52$, p = 0.15). Lastly, we evaluated the no-touch trials and compared the false alarm rates to the bright-associated hand (0.04 ± 0.01) and the dim-associated hand (0.06 ± 0.02), which also did not differ significantly ($t_{(15)} = -1.14$, p = 0.27). Thus, in all paired comparisons, we found no evidence for biased responding toward the bright-associated hand or the dim-associated hand when participants performed the LRBN task in the absence of visual distractors or prior to experiencing multisensory trials.

3.2. Tactile detection and localization in the context of visual distractors

After performing the LRBN task without visual distractors, participants performed the LRBN task during blocks in which the tactile cues could be paired with visual distractors (Fig. 3). Importantly, because the visual cues – a bright LED attached to one hand and a dim LED attached to the other – were presented with the tactile conditions in a full factorial design (Materials and Methods), the visual cues were not informative of the tactile condition over trials in the VT blocks. As with the trials performed in the baseline block, task performance during the VT blocks differed significantly according to tactile condition (touch main effect: F = 21.9, p = 6.9e−09, $\eta_p^2 = 0.59$). Although the main effect of visual cues failed to achieve significance (F = 0.47, p = 0.70, $\eta_p^2 = 0.03$), we observed a significant touch x visual cues interaction (F = 5.32, p = 3.3e−06, $\eta_p^2 = 0.26$). This result indicates that the response patterns associated with the different tactile conditions varied depending on LED conditions (i.e., illuminated individually, illuminated concurrently, or not illuminated). Post-hoc tests revealed that performance varied according to the stimulated hand in each LED condition (bright-only: F = 16.47, p = 2.31e−07, $\eta_p^2 = 0.40$; dim-only: F = 18.07, p = 7.7e−08, $\eta_p^2 = 0.41$; both-LED: F = 5.9, p = 0.0017, $\eta_p^2 = 0.20$; no-LED: F = 24.34, p = 1.64e−09, $\eta_p^2 = 0.46$). From visual inspection of the performance data (Fig. 3), the most obvious performance difference pattern over the LED conditions was in the accuracy levels associated with unimanual tactile stimulation of the bright-associated hand or the dim-associated hand. When only the bright LED was illuminated, response accuracy was significantly higher for touch on the bright-associated hand (0.76 ± 0.04) compared to touch on the dim-associated hand (0.61 ± 0.05) ($t_{(15)} = 3.39$, p = 0.004). When only the dim LED was illuminated, response accuracy was instead nominally higher for touch on the dim-associated hand (0.78 ± 0.04) compared to touch on the bright-associated hand (0.66 ± 0.05), but this difference failed to achieve statistical significance ($t_{(15)} = 1.93$, p = 0.073). Response accuracy was again higher for touch on the bright-associated hand compared to touch on the dim-associated hand when both LEDs were illuminated (bright-associated: 0.72 ± 0.04; dim-associated: 0.62 ± 0.05) or when neither LED was illuminated (bright-associated: 0.70 ± 0.05; dim-associated: 0.64 ± 0.03); however, neither of these differences were significant (both-LED: $t_{(15)} = 2.06$, p = 0.057; no-LED: $t_{(15)} = 0.97$, p = 0.35). These results reveal that performance on the bright-associated and dim-associated hands can become imbalanced systematically in the VT blocks, in contrast to the balanced performance in the baseline block. Moreover, performance rates were typically lower in the VT blocks (Fig. 3) compared to the baseline block (Fig. 2) with lower hit rates and higher false alarm rates.

To better quantify the influence of the visual cues on task performance, we calculated a lateralization bias index (LBI) for each visual condition for each participant (Fig. 4), which indicated the degree to which responses were biased toward the

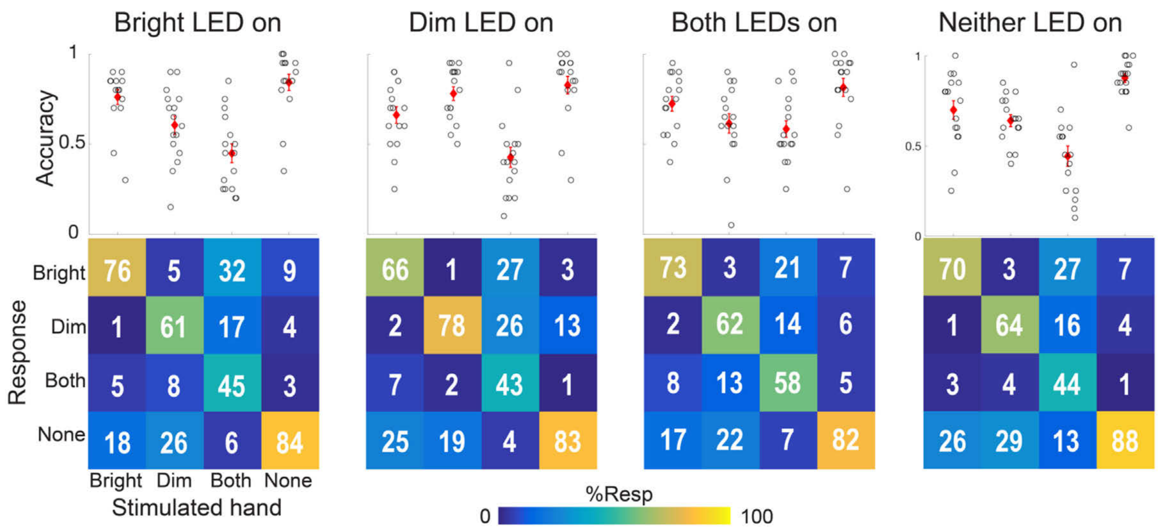

Fig. 3. Visuo-tactile block performance. Confusion matrices show group-averaged (n = 16) response probabilities on trials comprising tactile stimulation to the hand associated with the bright LED, the hand associated with the dim LED, both hands simultaneously, or no tactile stimulation during the visuo-tactile blocks. On each trial, participants reported whether they perceived touch on the bright-associated hand, the dim-associated hand, both hands, or no touch. Separate confusion matrices are shown for the trials comprising illumination of the bright LED only, the dim LED only, both LEDs simultaneously, or no LED illumination. Plots above confusion matrices indicate performance accuracy on trials comprising tactile stimulation on the bright-associated hand, the dim-associated hand, both hands, or no tactile stimulation. The red marker indicates the group average. Errorbars indicate s.e.m. Circles indicate individual subjects.

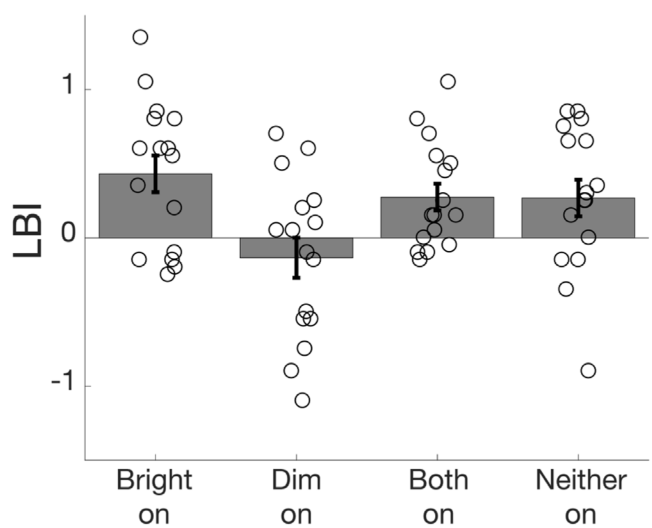

Fig. 4. Lateralization bias index (LBI). LBI values indicate baseline-corrected response bias to the hand associated with the bright LED (positive values) or the hand associated with the dim LED (negative values). Bars indicate mean LBI values under each LED condition in the visuo-tactile blocks. Errorbars indicate s.e.m. Circles indicate individual subjects.

hand associated with the bright LED (positive values) or dim LED (negative values) after accounting for subject-specific baseline performance biases. Across all LED conditions, the mean LBI value (0.21 ± 0.06) was significantly greater than 0 ($t_{(63)} = 3.29$, $p = 0.002$), indicating a general bias for reporting tactile stimulation on the hand associated with the bright LED during the visuo-tactile blocks. LBI values differed significantly according to visual condition ($F = 5.01$, $p = 1.25e{-}05$, $\eta_p^2 = 0.52$). The mean LBI value in the bright-only condition was significantly greater than the mean LBI value in the dim-only condition ($t_{(15)} = 3.65$, $p = 0.0024$), but did not differ compared to the both-LED ($t_{(15)} = 1.76$, $p = 0.10$) or no-LED ($t_{(15)} = 1.33$, $p = 0.20$) conditions. The mean LBI value in the dim-only condition was also lower than that of the both-LED and no-LED conditions, but the differences were only significant with the latter after correcting for multiple comparisons (dim vs. both: $t_{(15)} = -2.81$, $p = 0.01$; dim vs. none: $t_{(15)} = -4.52$, $p = 4.09e{-}04$). Mean LBI values did not differ between the both-LED and no-LED conditions ($t_{(15)} = 0.064$, $p = 0.95$).

To infer how LED illumination biased localization responses, we evaluated the signs of the LBI values when one or both LEDs were illuminated and whether the mean LBI value in these conditions differed significantly from 0 (Fig. 4). When a single LED was illuminated, tactile performance was generally biased toward the hand associated with the illuminated LED. Indeed, the group-averaged LBI value in the bright-only condition (0.43 ± 0.12) was significantly greater than 0 ($t_{(15)} = 3.49$, $p = 0.003$). Conversely, the group-averaged LBI value in the dim-only condition was negative (−0.13 ± 0.12), but this value was not significantly different from 0 ($t_{(15)} = -0.99$, $p = 0.34$). Although bias magnitude appeared to scale with the brightness of the visual cues, a direct comparison of the absolute magnitude of LBI values calculated for the bright-only trials compared to the dim-only trials revealed no significant differences ($t_{(15)} = 0.7$, $p = 0.49$). On trials in which both LEDs were illuminated, LBI values were significantly greater than 0 (0.28 ± 0.09; $t_{(15)} = 3.05$, $p = 0.008$), indicating clear biases toward the hand associated with the bright LED. LBI values for the both-LED condition were positive and of an intermediate absolute magnitude relative to LBI values for the bright and dim conditions. This pattern is consistent with the notion that the spatial bias observed with the illumination of both LEDs reflects some combination of the spatial biases observed with the unilateral LEDs.

Because trials with no visual distractors were randomly interleaved with the trials comprising LED illuminations during the VT LRBN blocks, performance on these trials provided an opportunity to characterize behavioral biases that potentially emerged as a consequence of repeated exposure to the bright and dim LEDs. Indeed, LBI values for the no-LED condition (0.27 ± 0.12) tended to be positive and of a comparable magnitude as those seen in the both-LED condition (Fig. 4), suggesting that responses were biased toward the hand associated with the bright LED even when no LEDs were illuminated. Although the mean LBI value in the no-LED condition did not differ significantly from 0 after accounting for the number of visual conditions ($t_{(15)} = 2.17$, $p = 0.046$),

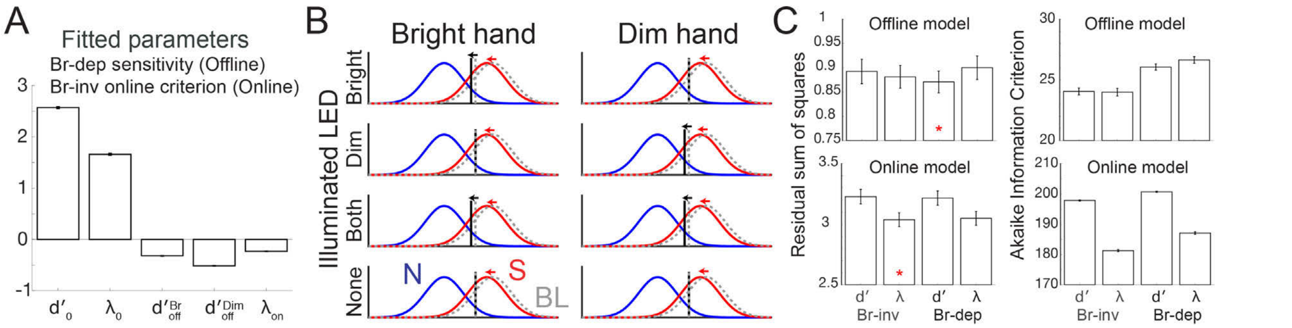

Fig. 5. Signal detection models for bimanual localization and visual influences. Baseline performance is explained by combined outputs from separate signal detection processes for the bright-associated and dim-associated hands. (A). Baseline, offline, and online sensitivity and criterion parameters for the full RSS-preferred model. Offline effects are captured by sensitivity changes that differ for the bright-associated and dim-associated hands (d'^{Br}_{off} and d'^{Dim}_{off}). Online effects are captured by brightness-invariant criterion changes (λ_{on}) that apply equally to the two hands. Bars indicate mean parameter estimates over 100 repeats of the 80–20 cross-validation procedure (Materials and Methods). Errorbars indicate s.e.m. (B) Depiction of signal detection processes for bright-associated hand (left column) and dim-associated hand (right column) according to RSS-preferred model parameters in *A*, under each LED condition. Online and offline effects are depicted with the noise (blue) and signal (red) density functions along with the decision criterion values (vertical black line). Dashed gray curve and vertical line indicate baseline signal distribution and criterion, respectively. Arrows denote conditions in which sensitivity (red) or criterion (black) are changed with respect to baseline parameters. The RSS-preferred model explained an average of 0.813 ± 0.0028 of response variance in the test datasets. (C) Left panel shows residual sum of square (RSS) errors used in model competitions to evaluate hypotheses regarding how offline effects (*top*) and online effects (*bottom*) relate to changes in sensitivity (d′) or criterion (λ) relative to the baseline model. Bars indicate the average RSS calculated from 100 repeats of a 80–20 cross-validation procedure. The red asterisks indicate the RSS-preferred offline and online models which yielded the lowest residual errors on average. The online models assume the same baseline and RSS-preferred offline model parameters. Right panel shows the average Akaike information criterion values for the offline models (*top*) and online models (*bottom*). Errorbars indicate s.e.m. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

a Bayesian analysis (Bayes factor = 1.6) indicated inconclusive evidence for the alternative hypothesis rather than strong evidence for the null hypothesis. Notably, the number of individual participants whose non-zero LBI values were positive (11) was significantly greater than expected by chance (binomial test, $p = 0.01$). Importantly, to the extent that participant responses were biased toward the bright-associated hand even in the absence of LED illumination, this offline bias likely affected performance on all of the VT-block conditions conceivably augmenting the online effects of the bright LED and counteracting the online effects of the dim LED.

3.3. Modeling LRBN task performance in a signal detection theory framework

In order to better understand the online and offline effects of visual distractors on LRBN task performance, we used a signal detection theory (SDT) framework to capture visual influences on touch through sensitivity (d′) and criterion (λ) changes. We assumed that responses on each LRBN task trial were determined from the combined outcomes of separate signal detection processes that operated for the bright-associated and dim-associated hands. We employed a staggered modeling approach to separate baseline response characteristics, offline visual effects, and online visual effects.

Because baseline block performance on the Bright- and Dim-associated hands did not differ, we fit a baseline signal detection model that assumed common sensitivity and criterion parameters for the two hands to the baseline data. The baseline model parameters fitted to the group-averaged data (d'_0: 2.57; λ_0: 1.66) were generally consistent with the SDT parameters estimated for individual subjects (d'_0: 2.91 ± 0.16; λ_0: 1.97 ± 0.19).

To account for the offline influences of the visual distractors on LRBN performance, which were marked by biased performance toward the hand associated with the brighter LED on the no-LED trials, we compared 4 models that assumed either changes in sensitivity or criterion that were either brightness-invariant or brightness-dependent (Fig. 5). Note that these models assumed that offline effects – change parameters that act on the baseline model parameters – emerged as a consequence of exposure to LED illumination in the VT blocks. The brightness-invariant models capture changes in sensitivity (or criterion) that are identical for the bright-associated and dim-associated hands. In contrast, the brightness-dependent models capture sensitivity (or criterion) changes that differ in magnitude for the bright-associated and dim-associated hands. The same models were considered to account for online effects of LED illumination. In model competition, we identified the combination of offline and online model parameters that yielded the lowest average residual errors in the cross-validation procedure (Fig. 5A). The full RSS-preferred model accounted for 81% ± 0.3% of the response variance in the held out dataset on average. The RSS-preferred offline model comprised brightness-dependent reductions in sensitivity, with smaller sensitivity reductions on the bright-associated hand compared to the dim-associated hand. These d′ changes account for the general reduction in hit rates in the VT blocks compared to the baseline condition (Fig. 5B). The brightness-dependent sensitivity changes can also explain the general bias toward the bright-associated hand in the VT blocks. The RSS-preferred online model comprised brightness-invariant reductions in the decision criterion (Fig. 5A). This λ change accounts for the slight hit rate increase when a LED was illuminated (i.e., correct reporting of touch on the bright-associated hand when the bright LED was on) compared to the no-LED trials. The criterion shift (Fig. 5B), which corresponds to more liberal reporting, also accounts for the relative increase in false alarms in the VT blocks compared to the baseline block while counteracting the offline sensitivity reductions.

Fig. 5C depicts the average residual errors over the 100 repeats of the cross-validation procedure (Materials and Methods) for the offline and online models. The offline model assuming brightness-dependent d′ changes produced the lowest model errors on average (RSS = 0.87 ± 0.02) compared to the other offline models (brightness-dependent λ RSS = 0.90 ± 0.02; brightness-invariant d′ RSS = 0.89 ± 0.03; brightness-invariant λ RSS = 0.88 ± 0.02). The online model assuming brightness-invariant λ changes produced the lowest model errors on average (RSS = 3.04 ± 0.06) compared to the other online models (brightness-invariant d′ RSS = 3.23 ± 0.06; brightness-dependent d′ RSS = 3.22 ± 0.06; brightness-dependent λ RSS = 3.05 ± 0.06). In addition to comparing the models based on residuals from the cross-validation procedure, we also compared the models using AIC (Fig. 5C).

This metric, which penalizes model complexity, recommended brightness-invariant models to explain both offline and online effects. These models would capture some of the performance differences seen in the VT blocks compared to the baseline block (e.g., the increased false alarm rates and general hit rate reductions), but they fail to account for the net bias for reporting touch on the bright-associated hand in the VT blocks. Notably, AIC-preferred models identified for group-averaged data and individual subjects' data also comprise only brightness-invariant terms (Supplemental Materials). Thus, although the inclusion of brightness-dependent d′ changes adequately accounts for the significantly biased reporting toward the bright-associated hand in the VT blocks (Fig. 4), this improved model performance through an additional model parameter is insufficient to overcome AIC's model complexity penalty.

4. Discussion

We set out to characterize the influence of non-informative visual cues on the detection of peri-threshold taps on the two hands. We found that detection performance on the left and right hands was unbiased during the baseline block, prior to exposure to visual distractors and multisensory trials. During the visuo-tactile blocks, tactile performance could be strongly influenced by the visual distractors. On trials comprising unilateral LED illumination, responses were significantly elevated on the hand associated with the visual cue with significant bias toward the bright LED and a nominal bias toward the dim LED. On trials comprising bilateral LED illumination, responses were significantly biased to the hand associated with the bright LED. A non-significant bias toward the hand associated with the bright LED was observed even when unimanual and bimanual taps were delivered in the absence of visual distractors. We tested hypotheses that related the online and offline visual distractor effects to either changes in the sensitivity or decision criterion parameters of signal detection processes implemented for each hand. The modeling results suggest that the modulating effects of visual distractors experienced concurrently with the tactile stimuli can be understood as brightness-invariant reductions in the decision criterion parameters, which result in more liberal responses. In contrast, the modeling results – based on residual errors, but not AIC – suggest that offline effects characterized by nominally biased performance toward the bright-associated hand can be understood as brightness-dependent reductions in the sensitivity parameters. These results imply that uninformative visual cues automatically induce online and offline spatial biases in bimanual tactile behavior that are based on different processes.

Even in the absence of visual distraction, bimanual somatosensory processing is known to involve robust and systematic interactions between the hands. In the baseline block, detection accuracy for peri-threshold taps was nominally lower for bimanual touch compared to unimanual touch, consistent with patterns described in earlier reports (Farne et al., 2007). This pattern is likely related to the fact that detection thresholds increase on a given finger as a consequence of simultaneous stimulation of the homologous digit on the other hand (Sherrick, 1964; Tamè et al., 2011, 2014). Using the LRBN task, we have also previously shown that bimanual processing may be more vulnerable to central perturbations compared to unimanual processing (Convento et al., 2018). These bimanual perceptual interactions, like other bimanual effects that operate in specific feature domains and with other task demands (Braun et al., 2005; Craig & Qian, 1997; Kuroki et al., 2017), are often understood as masking effects that may be explained by divisive normalization computations in the somatosensory system (Brouwer et al., 2015; Rahman & Yau, 2019). Interestingly, while our baseline signal detection model did not comprise across-hand interactions explicitly, the estimation of a single sensitivity parameter and a single criterion parameter (that were shared for the decision processes for the hands) was sufficient to capture the pattern of a slight performance loss in the bimanual conditions implicitly (single-subject baseline model predictions, bright-hand: 0.80 ± 0.02; dim-hand: 0.81 ± 0.02; bimanual: 0.72 ± 0.04). Ongoing efforts are aimed at developing a more mechanistic model that may bridge the behavioral patterns with the signal detection model.

The pairing of touch with illumination of the distractor LEDs induced substantial changes in tactile localization performance. We quantified the biased performance under each of the VT block conditions using a lateralized bias index (Fig. 4), which revealed significantly biased performance toward the bright-associated hand with unilateral bright illumination and bilateral illumination. Similarly, performance with unilateral dim illumination was generally biased toward the hand associated with the dim LED; however, this effect failed to achieve statistical significance. These perceptual effects are consistent with a number of studies that have reported enhanced detection of tactile stimulation by spatially congruent visual cues (Lloyd et al., 2008; Maravita et al., 2002; Mirams et al., 2017; Wesslein et al., 2014). It is worth considering why the biasing effect toward the dim-associated hand failed to achieve significance. A likely reason for this statistical result was that online dim-LED effects tended to be more variable across subjects, with LBI values in some subjects showing biased behavior toward the hand associated with the bright LED. Critically, this variability is unlikely to have resulted from participants not perceiving the dim LED as often as its bright counterpart because the total illuminations of each LED were matched over the experiment – they occurred with equal probability on all trials in the VT blocks – and both LEDs were detected on 100% of exposures during the calibration period at the start of each experiment. The weaker effects of the dim LED may also be attributed to counteracting effects of the offline bias that promoted responses toward the bright-associated hand. Indeed, this offline bias may have driven, in part, the significant bias toward the bright-associated hand when both LEDs were illuminated, in addition to luminance differences. Notably, with the cross-validated online models (Fig. 5C), both residual errors as well as AIC supported a model assuming reductions in response criterion that were identical for the bright-associated and dim-associated hands. AIC-based competition on models fit without cross-validation to group-averaged data and to individual subjects' data also supported the notion that offline effects were better explained by brightness-invariant reductions in response criterion (Supplemental Material). Critically, our inference that online visual influences on bimanual touch result from changes in decision criterion rather than sensitivity is consistent with results from visuo-tactile interactions on unimanual detection (Lloyd et al., 2008; Mirams et al., 2017).

On no-LED trials during the VT blocks, subjects also exhibited a tendency for increased responding toward the hand associated with the bright LED. Although the LBI values in the no-LED condition were not statistically different from 0 after correcting for multiple comparisons, the group-averaged LBI in this condition was comparable to that observed in the both-LED condition and the number of subjects exhibiting response bias toward the bright-associated hand was significant. Because LBI values are computed relative to baseline performance achieved prior to LED exposure and experience with the multisensory trials, the observation of positive LBI values, which were substantial in some subjects, suggests some form of adaptation or learning. One possibility is that the salience learned from the multisensory events – the correlated events pairing bright flashes to touch on one hand and dimmer flashes to touch on the other hand – induced a perceptual learning effect that transferred to unisensory tactile representations. In other paradigms, multisensory experiences can lead to subsequent changes in unisensory processing. In line with this, our modeling results based on comparisons of model residual errors showed that the offline effects were most consistent with brightness-dependent changes in the sensitivity parameter in the tactile signal detection processes. Importantly, model selection based on AIC instead supported an offline model that assumes identical sensitivity changes for the two hands. Comparison of models that were fitted to group-averaged data and individual subjects' data (Supplemental Material) also find that offline models assuming brightness-dependent sensitivity changes yield better predictions (i.e., lower residual errors) even as AIC recommended the simpler brightness-invariant model. Crucially, a full model comprising only brightness-invariant parameters would fail to explain the significant general bias toward the bright-associated hand in the VT blocks, so a model selection criterion like AIC may simply be too conservative given our data. Regardless, all of our analyses suggest that offline effects are attributable to sensitivity changes rather than criterion changes. This would imply that the reduction in hit rates was the dominant difference when comparing performance in the VT blocks to the baseline block.

Collectively, our full RSS-preferred model accounts for a number of features in our behavioral results. First, brightness-dependent sensitivity reductions account for the lower hit rates in the VT blocks (Fig. 3) compared to the baseline block (Fig. 2), which are particularly evident on trials involving stimulation of both hands. Second, the sensitivity reductions also explain the general bias toward the bright-associated hand in the VT blocks. It remains unclear whether these d′ reductions emerge merely from exposure to the bright and dim LEDs or if they require the multisensory pairing of LED illuminations with touch. Third, brightness-invariant criterion reductions result in more liberal decisions which account for boosts in hit rates and false alarms when LEDs are illuminated compared to no-LED trials in the VT block. Importantly, these results imply that online influence of visual distractors serves to offset the offline effect of reduced sensitivity in the signal detection processes for each hand. Although previous studies, using unimanual detection paradigms, have related visuo-tactile interactions to criterion reductions (Lloyd et al., 2008; Mirams et al., 2017), these studies did not report immediate or persistent sensitivity changes. An intriguing possibility is that the uncorrelated pairing of visual distractors with the tactile cues in different spatial locations drove the sensitivity reductions. This could reflect the recalibration of multisensory neural circuits by spatially incongruent signals like that observed in the superior colliculus (Wallace & Stein, 2007; Xu et al., 2012; Yu et al., 2009).

There are a number of study limitations to note with respect to the experimental design. First, although we systematically established each participant's tactile thresholds, we did not tailor the visual stimuli to each subject. Thus, despite our effort to ensure that the bright and dim LEDs were equally detectable, there is no guarantee that participants perceived their relative brightness similarly. This may have contributed to the extensive across-subject variance in our data. Second, while our design equated the stimulation rate on the left and right hands and ensured that the same number of bright and dim LED flashes occurred, the instantiation of the online effect (i.e., the significant bias toward the bright side) necessitated an increase in the probability that subjects would respond as feeling touch on the hand associated with the bright LED. Conceivably, a change in response probability alone could have induced the offline biasing effect, although presumably this would have involved a criterion shift rather than a sensitivity change. A control experiment that explicitly manipulates the response probability, even in the absence of visual distractors, would address this issue. There are also a number of limitations to concede regarding our modeling approach. First, we compared a very limited set of models that focused on a small number of alternative hypotheses. We assumed that baseline signal detection processes involved zero-centered noise and uniform variance for the noise and signal density functions. For the online and offline models, we tested models that assumed exclusive effects on either the sensitivity or criterion and ignored nested models that included changes to both parameters. Moreover, we assumed that the visual distractor effects were restricted to only the ipsilateral tactile detection process while ignoring potential effects on the contralateral hand, though the distance between the hands (and LEDs) may have been at the limits of visuotactile spatial effects (Gepshtein et al., 2005; Mirams et al., 2017). Although there are countless model variations that we could have fitted and compared using various model selection metrics, most of these alternative models likely would comprise more free parameters and our limited modeling exercise already demonstrated that the significant improvements in model performance attained with an additional parameter for the online or offline effects did not outweigh the complexity penalty. Future efforts likely will require more data or alternative model selection criteria.

In conclusion, our results are consistent with previous reports of visual cues, perceived near the body or signaling locations on the body, modulating the perception of touch (Lloyd et al., 2008; Maravita et al., 2002; Mirams et al., 2017; Pasalar et al., 2010; Wesslein et al., 2014) and we extend this work to include interactions within a bimanual behavioral context that can be related to signal detection processes. The intimate spatial relationship between vision and touch has led to the notion that the two sensory modalities are supported in part by shared or interactive spatial attention mechanisms (Driver & Spence, 1998; Macaluso & Driver, 2005; Spence et al., 2000b). It may be possible to consider the online effects of the visual distractors, the reduction in decision criterion resulting in more liberal reporting, as a consequence of exogenous attention. It may also be possible to consider the offline effects as a rapid change in spatial attention fields that arise from LED exposure. There is a clear need to establish how spatial attention relates to the signal detection processes we modeled and planned experiments are designed to address this relationship. Another open question pertains to the spatial reference frame in which visuo-tactile interactions in bimanual processing operate (Azañón & Soto-Faraco, 2008; Azanon et al., 2010; Badde et al., 2015; Heed & Azañón, 2014; Heed et al., 2015). The influence of touch on visual processing often depends on the particular location of the tactile cue in space (Bolognini & Maravita, 2007; Macaluso et al., 2000; Ramos-Estebanez et al., 2007) and this remapping of touch from body-based space to external coordinates may be performed by neural circuits in the posterior parietal cortex (Azanon et al., 2010; Heed et al., 2015; Konen & Haggard, 2014; Pasalar et al., 2010; Ro et al., 2004). However, the existence of multisensory neural populations whose visual and somatosensory receptive fields are anchored to body rather than fixed in space (Duhamel et al., 1998; Graziano & Gross, 1993; Hihara et al., 2015; Iriki et al., 1996; Maravita & Iriki, 2004; Mountcastle et al., 1975) would also allow for visuo-tactile interactions to occur in body-based coordinates. Ongoing efforts are aimed at establishing the spatial constraints to the visuo-tactile interactions. Finally, it is also imperative to characterize the dynamics of visual influences on bimanual touch by determining how quickly the spatial relationships between the LED flashes and touches are learned and how long these relationships are maintained. A more complete understanding of these spatiotemporal characteristics will enable the development of mechanistic models that link biological networks to the automatic online and offline influences of vision on bimanual touch.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.jmp.2020.102480.

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