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

Yash R. Wani^{1,2}, Silvia Convento^{1,3}, Jeffrey M. Yau¹

¹Department of Neuroscience, Baylor College of Medicine, Houston, TX

²Department of Chemistry, Rice University, Houston, TX

Corresponding author: Jeffrey M. Yau
One Baylor Plaza
T111
Houston, TX 77030
jeffrey.yau@bcm.edu

³Present affiliation: ChaiOne, Houston, TX

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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 about how vision modulates tactile perception offline. 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 in the absence of visual distractors. 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 changes. Our collective results reveal the obligatory and systematic influences of vision on both online and offline tactile spatial perception. The nervous system appears to automatically leverage multiple sensory modalities to build representations and calibrate decision processes for bimanual tactile spatial perception.

Keywords: multisensory, signal detection, visuo-tactile, attention, learning, modeling

Introduction

We live in chaotic multisensory environments and the nervous system combines information over multiple sensory cues to support perception (Stein and Stanford, 2008; Fetsch et al., 2013; Yau et al., 2015). Interactions between sensory signals can result in more reliable sensory estimates (Ernst and Bulthoff, 2004; Green and 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; Shams et al., 2011; Senna et al., 2014; 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 and Seitz, 2008).

For spatial perception, we rely extensively on vision and touch, and these modalities exhibit robust interactions in the perception of space (Ladavas et al., 1998; Maravita et al., 2000; Farne et al., 2003; Ro et al., 2004), size (Ernst and Banks, 2002), shape (Streri and Molina, 1993; Hadjikhani and Roland, 1998; Bisiach et al., 2004; Helbig et al., 2012), 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; Zhou and Fuster, 2000; Yau et al., 2009, 2016) and shared representations (Amedi et al., 2002; Konkle et al., 2009; Lacey and 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 and Spence, 1998; Spence et al., 2000a) and there is evidence that shared attention processing resources may support both vision and touch as well as their multisensory engagement (Spence and Driver, 1996; Macaluso et al., 2002; Lakatos et al., 2009). Critically, much of the multisensory literature focused on visual influences on touch has concentrated on the perceptual processing of tactile cues experienced in a unimanual context. Far less is understood regarding multisensory influences on bimanual touch (though see, Spence et al., 2004). This is a crucial knowledge gap as many of our routine behaviors involve sensorimotor coordination between the hands (Swinen and Wenderoth, 2004) and tactile cues experienced on one hand can influence tactile perception on the other (Sherrick, 1964; Verrillo et al., 1983; Craig and Qian, 1997; Tamè et al., 2011; Kuroki et al., 2017; Rahman and Yau, 2019). Because the hands can be flexibly positioned and bimanual tactile interactions can vary depending on the

relative positions of the hands in space (Driver et al., 1996; Shore et al., 2002, 2005; D'Amour and Harris, 2016), characterizing the influence of vision on bimanual touch may be especially important for theories of spatial perception and understanding how spatial representations are learned and modified through multisensory experience.

To address some of these gaps, we characterized the effects of brief light flashes (distractors) on the performance of a simple bimanual spatial perception task requiring healthy human subjects to detect and localize faint taps that were delivered to one hand or both hands simultaneously. 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 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). To establish a preliminary understanding for how visual distractors influence bimanual tactile perception, we implemented overly simplistic signal detection models. Through model competition, we tested distinct hypotheses regarding how the online and offline effects of vision on bimanual touch related to changes in either sensitivity or decision criterion.

Materials and Methods

Participants

Sixteen healthy individuals (10 females; 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.

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: 44.1kHz) 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).

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 (Figure 1A). 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 (Figure 1B). Participants maintained their hands in a supinated position with their arms outstretched and separated by 38 cm. This posture created a $\sim 140^\circ$ 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). In half of the participants, the bright LED was fixed to the tactor on the left (right) index finger while the dim LED was fixed to the tactor on the right (left) index finger. 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 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).

Establishing tactile detection thresholds

As we have done previously (Convento et al., 2018), a Bayesian adaptive staircase procedure (QUEST) (Watson and 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,

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

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 and 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) 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 and Yau, 2019).

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 the trials. A change in the color of the fixation cross from blue to red indicated when stimuli were potentially delivered. Subjects were cued to respond when the fixation cross reverted back to blue. 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.

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: bright LED only, dim LED only, both LEDs, or no LEDs. We adopted a full parametric design (Figure 1C) 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 conditions. Each condition 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 VT blocks each comprising 80 trials. Participants were allowed to rest 2-3 mins between blocks. Note that the sensory cues on the no-LED trials were identical to the sensory cues in the baseline block so differences in performance between these conditions would reflect offline changes that emerge during the visuo-tactile blocks.

Statistical Analysis

Statistical analyses were performed using Matlab (R2015b, R2019b). 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 (left only, right only, 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 additionally quantified spatial performance biases in the visuo-tactile blocks (i.e., how much detection performance became *biased to the hand* associated with the bright or dim LEDs), by defining a lateralization bias index (LBI) for each VT condition separately (bright LED, dim LED, both LEDs, no LEDs):

$$B_{corr} = (B_{1hand}^{VT} + B_{2hand}^{VT} + B_{none}^{VT}) - (B_{1hand}^{BL} + B_{2hand}^{BL} + B_{none}^{BL})$$

$$D_{corr} = (D_{1hand}^{VT} + D_{2hand}^{VT} + D_{none}^{VT}) - (D_{1hand}^{BL} + D_{2hand}^{BL} + D_{none}^{BL})$$

$$LBI = B_{corr} - D_{corr}$$

where B_{corr} and D_{corr} indicate baseline-corrected detection rates on the hand associated with the bright LED and dim LED, respectively, in a given condition. For the bright-associated hand and the dim-associated hand, baseline-corrected rates were calculated as the difference in the detection rates achieved in visuotactile (VT) blocks and the baseline (BL) blocks. Detection rates on each hand were summed over unimanual (1hand), bimanual (2hand), and no-touch (none) trials. Positive LBI values indicate increased detection 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 one-sample t tests with Bonferroni correction comparing LBI values in each VT condition to 0.

Modeling bimanual tactile localization performance in a signal detection theory framework

To model performance on the 4AFC task, we implemented an overly simplistic model based on signal detection theory (SDT; Green and Swets, 1988) that assumed separate detection processes for the two hands. Beyond accounting for performance in the baseline block, we also sought to test alternative models that assumed different online and offline effects of LED illumination on tactile localization performance using this framework. 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 and 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). We fit models to group-averaged data and individual subjects’ data.

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:

$$X_n = N(0,1)$$

$$X_s = N(d'_0, 1)$$

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:

$$P("Absent"|s_h) = 1 - P("Present"|s_h)$$

$$P("Absent"|a_h) = 1 - P("Present"|a_h)$$

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 bright (B) hand and dim (D) hand, the response probabilities in the 4AFC task (i.e., “Bright hand only”, “Dim hand only”, “Both hands”, “No-touch”) were computed from the product of unimanual likelihoods. For example, $P("Bright\ hand\ only"|s_B, a_D) = P("Present"|s_B) * P("Absent"|a_D)$.

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. 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. In model competition, we tested 4 simple hypotheses: The offline effects could have resulted from brightness-dependent changes in d' (Offline model 1: 2 parameters), brightness-dependent changes in λ (Offline model 2: 2 parameters), brightness-invariant changes in d' (Offline model 3: 1 parameter), or brightness-invariant changes in λ (Offline model 4: 1 parameter). We used Akaike Information Criterion (AIC), a metric that accounts for both model performance and complexity (Burnham and Anderson, 2004), to identify the preferred model.

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), brightness-dependent changes in λ (Online model 2: 2 parameters), brightness-invariant changes in d' (Online model 3: 1 parameter), or brightness-invariant

changes in λ (Online model 4: 1 parameter). We again used AIC to determine the preferred model. Note that Bayesian Information Criterion (BIC), a more conservative metric that imposes a greater penalty for model complexity, identified the same preferred online and offline models as AIC.

Results

Tactile detection and localization in the absence of visual distractors

Participants performed a 4AFC tactile detection task (LRBN task) in which they reported the perception of peri-threshold taps delivered to the left hand, the right hand, both hands, or no touch in the absence of visual cues (Figure 2A; data labeled according to the hands associated with the bright and dim LEDs). Across all conditions, group-averaged accuracy was nearly 80% (unilateral mean $\pm$ SEM = 0.78 ± 0.01 ; bilateral: 0.68 ± 0.04 ; no-touch = 0.89 ± 0.03). Across the group, performance differed significantly according to the tactile conditions ($F = 10.2$, $p = 3.0e-05$, $\eta_p^2 = 0.41$). Post-hoc tests revealed significant performance differences between no-touch trials and unilateral trials ($t_{(15)} = 3.06$, $p = 0.008$, $d = 1.29$) and between no-touch trials and bilateral trials ($t_{(15)} = 4.26$, $p = 6.8e-04$, $d = 1.61$). Performance did not differ significantly between the two hands (Figure 2B) in comparisons of accuracy in the unilateral stimulus conditions ($t_{(15)} = -0.90$, $p = 0.38$, $d = -0.24$), rate of unimanual responses (and conversely misses) on bilateral stimulation trials ($t_{(15)} = -1.52$, $p = 0.15$, $d = -0.47$), or rate of unimanual false alarms on no-touch trials ($t_{(15)} = -1.14$, $p = 0.27$, $d = -0.30$). Thus, while participants' performance differed depending on the number of hands stimulated during each trial, there was no evidence for biased performance toward either the hand associated with the bright LED or the hand associated with the dim LED when participants performed the LRBN task in the absence of visual distractors or prior to experiencing multisensory trials.

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. 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 (Figure 3A) 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 presence of the bright and dim LEDs which were illuminated in isolation or concurrently.

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 (Figure 3C), which indicated the degree to which performance was biased toward the hand associated with the bright LED (positive values) or dim LED (negative values) relative to performance achieved in the absence of visual distractors. LBI values differed significantly according to visual condition ($F = 8.2$, $p = 1.8e-04$, $\eta_p^2 = 0.35$). On trials when a single LED was illuminated, tactile performance was generally biased toward the hand associated with the illuminated LED. Indeed, group-averaged LBI values in the bright-only condition (0.43 ± 0.12) was significantly greater than 0 ($t_{(15)} = 3.49$, $p = 0.003$, $d = 0.87$), indicating a robust bias toward the hand associated with the bright LED. Grouped-averaged LBI values in the dim-only condition were substantially lower and negative on average (-0.13 ± 0.12), but not significantly different from 0 ($t_{(15)} = -0.99$, $p = 0.34$, $d = -0.25$), indicating a tendency for biased performance toward the hand associated with the dim LED. 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 ($t_{(15)} = 0.7$, $p = 0.49$, $d = 0.28$). On trials in which both LEDs were illuminated, LBI values were significantly greater than 0 (0.28 ± 0.09 ; $t_{(15)} = 3.05$, $p = 0.008$, $d = 0.76$), indicating robust performance 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 which were nominally larger with the bright LED.

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 (Figure 3B). 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 (Figure 3C). These data reveal a robust, but non-significant ($t_{(15)} = 2.17$, $p = 0.046$, $d = 0.54$), bias in task performance toward the hand associated with the bright LED even when no visual distractors were presented during the VT LRBN blocks. Importantly, this offline bias likely affected performance on all of the VT-block conditions thereby modulating the apparent strength of the online effects of the bright and dim LEDs.

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 each hand. 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-dependent or brightness-invariant (Figure 4A). Note that these models assumed that offline effects acted upon the baseline model parameters. For the group-averaged data, the model assuming brightness-invariant d' changes (AIC = 8.83) was preferred over the other models according to AIC (brightness-invariant λ : 9.03; brightness-dependent d' : 10.81; brightness-dependent λ : 10.99). The AIC values associated with the 4 offline models fitted to individual subject data were significantly different across models ($F = 3.57$, $p = 0.02$, $\eta_p^2 = 0.19$). Again, the AIC-preferred offline model was that which assumed brightness-invariant d' changes (brightness-invariant d' : 8.73 ± 0.44 ; brightness-invariant λ : 10.39 ± 1.18 ; brightness-dependent d' : 10.45 ± 0.42 ; brightness-dependent λ : 11.14 ± 0.66). For models fitted to the group-averaged data as well as to individual subjects, the offline effects were most consistent with sensitivity

reductions (group-averaged model: $d'_{off} = -0.42$; individual subject models: $d'_{off} = -0.54 \pm 0.11$).

To account for the online influences of the visual distractors on LRBN performance, which were marked by a general pattern for biased performance toward the illuminated hand, we compared 4 models that assumed either changes in sensitivity or criterion that were either brightness-dependent or brightness-invariant (Figure 4A). Note that these models assumed that online effects acted upon the baseline and offline model parameters. For the group-averaged data, the model assuming brightness-invariant λ changes (AIC = 23.32) was preferred over the other models according to AIC (brightness-invariant d' : 23.91; brightness-dependent λ : 25.24; brightness-dependent d' : 25.91). The AIC values associated with the 4 online models fitted to individual subject data were significantly different across models ($F = 11.94$, $p = 1.15e-05$, $\eta_p^2 = 0.43$). Again, the preferred model according to AIC was a simpler one involving a brightness-invariant parameter change. Specifically, the AIC-preferred online model was that which assumed brightness-invariant λ changes (brightness-invariant λ : 22.71 ± 1.37 ; brightness-invariant d' : 23.27 ± 1.68 ; brightness-dependent λ : 24.60 ± 1.40 ; brightness-dependent d' : 24.93 ± 1.70). For models fitted to the group-averaged data as well as to individual subjects, the online effects were most consistent with reductions in criterion on the hand associated with LED illumination (group-averaged model: $\lambda_{on} = -0.28$; individual subject models: $\lambda_{on} = -0.31 \pm 0.09$). The full AIC-preferred model comprised 4 parameters (Figure 4B,C; d'_0 , λ_0 , d'_{off} , λ_{on}) to explain a substantial amount of response variance (Figure 4D) over all conditions for the group-averaged data ($r^2 = 0.95$) and individual subjects data ($r^2 = 0.81 \pm 0.03$).

Discussion

We set out to characterize the influence of non-informative visual cues on bimanual spatial perception. We found that tactile localization performance for peri-threshold taps delivered to 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 localization behavior 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 trend for bias toward the dim LED. On trials comprising bilateral LED illumination, responses were significantly biased to the hand associated with the bright LED. A substantial but 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 simple 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. In contrast, the offline effects characterized by nominally biased performance for the hand associated with the bright LED can be understood as brightness-invariant reductions in the sensitivity parameters. These results imply that uninformative visual cues automatically induce online and offline spatial biases in bimanual tactile behavior.

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 lower for bimanual touch compared to unimanual touch, consistent with 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 (Craig and Qian, 1997; Braun et al., 2005; 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 and 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 (Figure 3) which revealed significant biased

performance toward the hand associated with the bright LED 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 (Maravita et al., 2002; Lloyd et al., 2008; Wesslein et al., 2014; Mirams et al., 2017). 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 many 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. Additionally, although the direct comparison between the absolute magnitude of LBI values in the bright-only and dim-only conditions failed to reveal a significant difference, the fact that LBI values in the bilateral LED condition were significantly biased toward the bright side suggests an additive, counteracting effect of the bright and dim LEDs. Notably, the competition between online models also indicated a lack of brightness-dependent effects, as the AIC-preferred model comprised only brightness-invariant reductions in response criterion. A close inspection of the modeling results, though, revealed that the online model which assumed brightness-dependent criterion changes more accurately reproduced the observed performance data ($RSS = 0.71 \pm 0.14$) compared to the AIC-preferred model ($RSS = 0.77 \pm 0.13$), as indicated by a significant difference in model performance ($t_{(15)} = 2.65$, $p = 0.02$, $d = 0.11$). Thus, from both the behavioral and modeling results, there is some evidence for brightness-dependent online effects. Importantly, irrespective of their dependence on brightness, the online influences of visual distractors on LRBN task performance appear to be related to criterion changes rather than sensitivity changes, consistent with results from visuotactile 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 magnitude of the LBI values in this condition were comparable to those

observed in the both-LED condition. In fact, 11 of 16 participants had positive LBI values in this condition. 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 implicates 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 showed that the offline effects were most consistent with changes in the sensitivity of the tactile signal detection processes. Notably, the AIC-preferred offline model did not comprise brightness-dependent sensitivity change parameters, without which it would be impossible to recapitulate the pattern for nominally biased performance toward the hand associated with the bright LED. However, greater scrutiny of the models revealed that the model assuming brightness-dependence (of the sensitivity parameter) yielded significantly ($t_{(15)} = 3.01$, $p = 0.009$, $d = 0.77$) better offline behavior predictions compared to the model assuming brightness-invariance (dependent model RSS vs invariant model RSS: 0.10 ± 0.02 vs 0.19 ± 0.04). Thus, as with the online results, there is some evidence for brightness-dependent offline effects from both the behavioral and modeling results. Regardless of their dependence on brightness, the offline influences of visual distractors on LRBN task performance appear to be related to sensitivity changes rather than criterion changes.

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 overly-simplistic 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 (Maravita et al., 2002; Lloyd et al., 2008; Pasalar et al., 2010; Wesslein et al., 2014; Mirams et al., 2017) and we extend this work to include interactions within a bimanual behavioral context. 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 and Spence, 1998; Spence et al., 2000b; Macaluso and Driver, 2005). There is a clear need to establish how spatial attention relates to the signal detection processes we modeled. Another open question pertains to the spatial reference frame in which visuo-tactile interactions in bimanual processing operate (Azañón and Soto-Faraco, 2008; Azanon et al., 2010; Heed and Azañón, 2014; Badde et al., 2015; Heed et al., 2015). The influence of touch on visual processing often depends on the particular location of the tactile cue in space (Macaluso et al., 2000; Bolognini and Maravita, 2007; 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 (Ro et al., 2004; Azanon et al., 2010; Pasalar et al., 2010; Konen and Haggard, 2014; Heed et al., 2015). However, the existence of multisensory neural populations whose visual and somatosensory receptive fields are anchored to body rather than fixed in

space (Mountcastle et al., 1975; Graziano and Gross, 1993; Iriki et al., 1996; Duhamel et al., 1998; Maravita and Iriki, 2004; Hihara et al., 2015) 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.

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Figure 1. Experimental design. (A) Each session comprised an initial period for establishing tactile detection thresholds and stimulus calibration, a block of tactile-only trials, 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 is fastened to one hand and the dim LED is fastened to the other hand. The hand associated with the bright LED was counterbalanced across participants. (B) Participants maintained visual fixation on a monitor while performing the tactile detection and localization task. (C) During each trial of the 4AFC task, subjects experienced touch to the left hand only, right hand only, both hands simultaneously, or no touch and subjects reported whether and where they detected the touch. During the baseline block, no visual cues were delivered on any trials. During the visuo-tactile blocks, each of the 4 tactile conditions is paired with illumination of the bright LED only, dim LED only, both LEDs, or no visual cues.

Figure 2. Baseline block performance (A) Confusion matrix shows group-averaged ($n = 16$) response probabilities in participants detecting taps delivered to the index finger on the left hand, right hand, both hands, or no touch during the baseline block. Data is sorted according to each hand's association with the bright or dim LED. Outlined cells (dark gray, light gray, and white squares) indicate comparisons depicted in B. (B) Group-averaged probabilities for responding "Bright hand" (BR) or "Dim hand" (D) on unimanual trials, bimanual trials, and no-touch trials. Circles indicate individual subjects. Errorbars indicate s.e.m. Response probabilities were statistically balanced between the hands in all 3 trial types.

Figure 3. Visuo-tactile block performance (A) Confusion matrix shows group-averaged ($n = 16$) response probabilities in participants detecting taps delivered to the index finger on the left hand, right hand, both hands, or no touch during the visuo-tactile blocks. Data is sorted according to each hand's association with the bright or dim LED. Separate confusion matrices are shown for the trials comprising illumination of the bright LED, the dim LED, or both LEDs. These data indicate the online effects of visual distractors. (B) Response probabilities for trials performed in the absence of LED illumination during the visuo-tactile blocks. These data indicate the offline effects of visual distractors. (C). Lateralization bias index (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. Circles indicate individual subjects. Errorbars indicate s.e.m.

Figure 4. Signal detection models for bimanual localization and visual influences.

Baseline performance is explained by combined responses from separate signal detection processes for each hand. **(A)** Akaike information criterion (AIC) values are used in model competitions to test hypotheses regarding how offline effects (*top*) and online effects (*bottom*) relate to brightness-invariant or brightness-dependent changes in sensitivity (d') or criterion (λ). Bars indicate AIC values for models fitted to performance data averaged over subjects. Blue lines indicate the average AIC values for models fitted to individual subjects. Errorbars indicate s.e.m. The red asterisks denote AIC-preferred models. **(B)**. Baseline, offline, and online parameters for the full AIC-preferred model. Conventions as in A. **(C)** Depiction of signal detection processes for the hand associated with the bright LED and the hand associated with the dim LED according to parameters shown in B. Online and offline effects are captured by the noise (blue) and signal (red) density functions under each LED condition along with the decision criterion values (vertical black line). Dashed gray curve and vertical line indicate baseline signal distribution and criterion, respectively. **(D)** Scatterplot shows observed and predicted response probabilities (for data averaged over participants) for baseline block performance and performance achieved under each LED condition in the visuo-tactile blocks. Inset plot indicates goodness-of-fit for AIC-preferred model fitted to individual subjects.