Filling-in of the Blindspot is Multisensory

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Abstract

The blind spot is an area on the retina that lacks photoreceptors, thus no visual information is encoded. Yet, we can maintain the sense of a seamless visual field owing to perceptual filling-in. Traditionally viewed as a surface interpolation mechanism, filling-in has been studied predominantly under unimodal conditions. However, there are limits to this process; the brain cannot always reconstruct all surfaces. Multisensory processing may bolster the process of perceptual filling-in to occur even with complex and dynamic perceptual stimuli. In this study, we employed the Audiovisual (AV) Rabbit Illusion to investigate how auditory stimuli influence visual filling-in at the blind spot. Our findings confirmed that auditory cues can induce the perception of an illusory flash within the blind spot, indicating that the brain leverages multimodal information to enrich visual scenes. This suggests that perceptual filling-in is not merely unimodal surface interpolation but a cross-modally integrated spatial representation and therefore more similar to other visual field locations than previously hypothesized. Furthermore, for blind spot filling-in to occur, visual stimuli do not need to be spatially contiguous, they simply need to be crossmodally associated (or grouped), which supports a higher-level sensory processing in filling-in than previously understood.

1 Introduction

Perceptual filling-in at the blind spots is a rapid and automatic process that allows us to maintain a seamless visual representation of the world. Every individual has a physiological blind spot in each eye, located at the optic disc where the optic nerves exit the retina. This area lacks photoreceptors, therefore no visual signals are sent from it to the brain for further processing. The blind spot typically measures on average 6° x 7° and is centered approximately 16° from the fovea, positioned about 2° below the horizontal meridian[1]. Despite the blind spot's significant size, people still perceive a complete scene, even when only using one eye. This is achieved by perceptual filling-in, where the visual system uses surrounding information to fill in these gaps[2]. Apart from naturally occurring scotomas (the physiological blind spots discussed above), perceptual filling-in also occurs in artificial scotomas[3,4], and with scotomas caused by visual diseases, such as age-related macular degeneration, though with certain limitations[5,6]. Perceptual filling-in is also the central mechanism behind some classic visual illusions such as the watercolor effect[7], the Craik-O'Brien-Cornsweet illusion[8,9,10], and neon-color spreading[11].

Perceptual filling-in is broadly regarded as an active process of surface interpolation, where the visual system compensates for missing information by drawing upon the surrounding visual cues to create a continuous representation across space. In a seminal macaque neurophysiological study, Matsumoto and Komatsu[12] demonstrated this by presenting bar stimuli of varying lengths, such that one end extended either partially into or fully across the blind spot, while recording from V1 neurons linked to the tested and fellow (non-tested) eyes respectively. Neural activity increased steadily as the bar extended across the receptive field of the V1 neurons associated with the fellow eye, while the neurons associated with the tested eye did not increase activity as the bar spanned across the receptive field, but showed a non-linear rise as soon as the bar crossed the blind spot, corresponding with perceptual completion. Currently, there are two schools of thought that explain the neural mechanisms underlying perceptual filling-in. The isomorphic theory postulates a local, lateral spread of activation across the retinotopic map of the visual cortex. A two-dimensional array of neurons, which encodes point-by-point representations of visual features, receives input from this spread of activity[13,14,15]. An alternative symbolic theory suggests that early visual areas only extract contrast information at the border, and shape and color are derived in subsequent stages. A recent computational study posits that perceptual filling-in follows hierarchical predictive coding of natural images, in which estimates of the visual image in early visual areas are corrected by top-down predictions, which are influenced by learned statistical regularities in natural scenes[16].

While generally effective and reliable, perceptual filling-in is unable to reproduce all visual phenomena within the blind spots. One example is illusory contours, in which the brain interprets visual cues like lines, patterns, or shading in part of the shape to complete the perception of a form. Maertens and Pollmann[17] used Kanizsa Squares to induce illusory contours, and asked participants to distinguish curvatures of these contours and found a significant impairment in participants' ability to perceive contours crossing the blind spot. The authors suggested that illusory contour completion relies on lower-level visual areas and that

for completion to occur across the blind spot, the stimulus must extend beyond its borders; even a small gap prevents filling-in. They concluded that the blind spot's representation in V1 disrupts the percept unless neurons at the border regions are activated. In contrast, patients with larger bilateral central retinal lesions were able to accurately perceive illusory contour curvature over their retinal scotomas[18], suggesting that the filling-in mechanisms at the blind spot may differ from those in other retinal regions. Additionally, Maus and Whitney[19] demonstrated that perceptual filling-in at blind spots is motion-dependent; sinusoidal gratings had to drift into the blind spots, rather than out, for filling-in to occur. Taken together, these findings suggest that blind spots represent a unique, restrictive case of filling-in, which only happens when the visual stimulus spans or touches the blind spot's border, underscoring its dependence on local information.

Given the limitations of blind spot filling-in and its dependence on local low-level visual information, we propose an alternative approach: achieving perceptual filling-in by engaging higher-level sensory processing, substituting missing visual information with signals from other sensory modalities through cross-modal interactions. Contrary to earlier beliefs, the visual cortex is not purely unimodal. Structural evidence from human and non-human primate studies shows direct projections from auditory cortex to V1, particularly in peripheral visual regions[20,21,22,23]. Functional evidence also supports that sound activates the visual cortex, leading to visual imagery[24], and facilitates visual discrimination[25]. Audiovisual (AV) interactions have also been widely studied in the context of perceptual illusions, such as the Double Flash Illusion[26], where a sound induces the perception of an additional flash, demonstrating the powerful integration of auditory and visual inputs. Therefore, these vigorous auditory-visual interactions could potentially be leveraged to broaden the conditions that permit filling-in of the blind spot.

In this study, we utilized a cross-modal illusion known as the Illusory Audiovisual (AV) Rabbit Illusion[27]. In this illusion, by introducing or silencing a sound, we could either induce an illusory flash (Illusory AV Rabbit) or suppress a real flash (Invisible AV Rabbit) between two real flashes. We mapped the blind spots of neurotypical participants and carefully positioned the visual stimuli so that the illusory flash and/or the second real flash appeared at the center of the blind spot. Our findings confirmed that the AV Rabbit effect successfully induced perceptual filling-in, with the reported location of the illusory flash occurring well within the blind spot – effectively allowing the rabbit to "jump" into the blind region. This discovery could indicate that higher-level neural mechanisms contribute to perceptual filling-in. Such an outcome would have broader implications, shedding light not only on the mechanisms behind typical blind spot filling-in, but also providing a psychophysical baseline for understanding neural compensation mechanisms in pathological low-vision conditions.

2 Results

Blind spot measurements and eye-tracking performance

The blind spot measurements were conducted to assess the extent and characteristics of the blind spots. A total of 20 neurotypical participants (10 females; mean age = 26.7 years,

range = 19–40 years) were included in the analysis. Blind spots among participants were primarily located in similar positions and exhibited comparable sizes (Fig. 1). The average size of the blind spot was measured at 21.6 $\deg^2$ ($SD = 8.99$). The centers of the blind spots were approximately 15.2° from the fovea ($SD = 0.976$) and positioned about 1.69° below the horizontal meridian ($SD = 0.780$) (Supp. Fig. 1).

To ensure we were presenting our stimuli to the correct experimental locations, participants were monitored with eye-tracking throughout the session and stimulus presentation only commenced after a successful 500 ms fixation at the center. We confirmed that participants demonstrated strong adherence to the central fixation, with the distance of their gaze points from the center measured at 0.0161°($SD = 0.00279$) for the left eye and 0.0166°($SD = 0.00341$) for the right eye during the fixation phase (Supp. Fig. 2). Similarly, during stimulus presentation, the gaze point distances from the center remained consistent at 0.0172°($SD = 0.00390$) for the left eye and 0.0175°($SD = 0.00431$) for the right eye. Although participants deviated from the center during the response phase (e.g., for reading the text prompt, evaluating flash location options, or locating corresponding keys on the keyboard), they maintained fixation at the center during stimulus presentation, allowing us to verify that flashes were accurately presented at the intended locations, such as the borders and center of the blind spots. Individual eye tracking performance can be found in Supplementary Figure 3.

Both illusions were robust among blind and control spots

To first evaluate the effectiveness of the Illusory AV Rabbit Illusion, we confirmed that participants perceived an illusory flash in response to the presence of an extra beep (Fig. 2A, left, where two real flashes were presented). Stimuli were presented randomly on either the blind spot or control spot; if the left eye was being tested, the control spot was the blind spot of the right eye (i.e., non-testing eye). For a detailed description of stimulus location, refer to Fig. 5B. A factorial ANOVA was conducted to examine the effects of stimulus location (blind spot vs. control spot) and beep condition (0-beep, 2-beep, 3-beep – each paired with 2-flash), as well as their interaction. Since no statistically significant differences were found between the eyes, data from both eyes were combined for simplicity in subsequent analyses.

The main effect of stimulus location (blind spot vs. control spot) was not significant, $F(1, 114) = 3.32, p = 0.071$, indicating no difference in performance between locations. However, the main effect of beep condition was highly significant, $F(2, 114) = 24.4, p < 0.001$, showing that the number of beeps significantly influenced the perception of flashes and demonstrated the presence of an illusory flash. There were no significant interaction effects between stimulus location and beep condition, $F(2, 114) = 0.085, p = 0.919$.

To further investigate the specific effects of beep conditions within and between each stimulus location (blind spot and control spot), we performed post-hoc pairwise comparisons. Conditions were named using the FXBY conven- tion - X: number of flashes, Y: number of beeps. For accurate stimulus timing for each condition, refer to Fig. 5A. Tukey's Honest Significant Difference (HSD) method was applied to control for multiple comparisons, ensuring adjusted p-values that maintain the family-wise error rate. Adjusted p-values are

reported throughout. Post-hoc comparisons revealed significant differences between the 3-beep (F2B3) and 0-beep conditions (F2B0) (blind spot: $p = 0.009$; control spot: $p = 0.041$) and between the 3-beep (F2B3) and 2-beep (F2B2) conditions (blind spot: $p < 0.001$; control spot: $p < 0.001$). There were no significant differences in number of flashes perceived between 2-beep (F2B2) and 0-beep (F2B0) conditions. These results demonstrate that the Illusory AV Rabbit (3-beep, 2-flash) stimulus led participants to perceive significantly more flashes, independent of stimulus location within each beep condition.

Next, we assessed the strength of the Invisible AV Rabbit Illusion. If the illusion is robust, one of the flashes would be suppressed from participants' conscious perception (Fig. 2A, right, where three real flashes were presented). A factorial ANOVA was used again to examine the effects of stimulus location and beep condition, as well as any interaction effects. Significant main effects were observed for both stimulus location, $F(1, 114) = 18.9, p < 0.001$, and beep condition, $F(2, 114) = 26.5, p < 0.001$, suggesting that both factors influenced the perceived number of flashes. No interaction effects were found.

As before, we conducted post-hoc pairwise comparisons to investigate how sound affects visual perception. When no sound was presented (0-beep, F3B0 condition), participants perceived significantly fewer flashes when stimuli were presented on the blind spot compared to those presented on the control spot, $p < 0.001$ This finding suggests that one of the flashes was undetected when stimuli traversed the blind spot, confirming effective stimulus placement.

For conditions with sound, significant differences were observed between the 2-beep (F3B2) and 3-beep conditions (F3B3) (blind spot: $p < 0.001$; control spot: $p = 0.012$), as well as between the 2-beep (F3B2) and 0-beep (F3B0) conditions, though only when stimuli were presented at the control spot, $p < 0.001$. The significant reduction in the perceived number of flashes for F3B0 vs. F3B2 and F3B3 vs. F3B2 at the control spot demonstrates the Invisible AV Rabbit effect, in which sound led to the suppression of one flash.

However, for stimuli presented at the blind spot, it is perhaps more fitting to describe the perceptual phenomenon as the Illusory AV Rabbit, as presenting 3 beeps enabled participants to perceive an additional flash that was previously undetected due to the lack of photoreceptors within the blind spot. In summary, the critical condition for the Invisible AV Rabbit (3-flash, 2-beep) stimulus led participants to report perceiving significantly fewer flashes. When stimuli were presented at the blind spot, one flash remained undetected by participants, effectively causing them to experience the Illusory AV Rabbit (2-flash, 3-beep) stimulus.

Lastly, we evaluated whether participants equated the number of beeps with the number of flashes, which could confound the perception of the AV Rabbit Illusion. In the second block of the experiment, participants were asked to report the number of beeps they perceived (Fig. 2B). Factorial ANOVA analyses showed a significant main effect of beep condition on beep perception (2 real flashes: $F(2, 114) = 15.7, p < 0.001$; 3 real flashes: $F(2, 114) = 13.1, p < 0.001$), but no significant effects for stimulus location or interaction

effects. Post-hoc comparisons indicated significant differences in the number of beeps perceived across all beep conditions ($p < 0.001$), with no differences between stimulus locations. For simplicity, these comparisons were combined in the figure. These findings rule out the possibility that participants were simply matching the number of beeps to flashes, confirming that the auditory stimulus genuinely altered visual perception.

Accurate selections on flash locations

After each stimulus presentation, participants were asked to report where they perceived the flash(es) by choosing from five equidistant locations (1-5; see Fig. 5D). Locations 2 and 4 were positioned on the cardinal borders of the blind spot, while location 3 was located centrally. Notably, locations 2 and 4 corresponded to the true flash positions, with location 3 also being a true flash position in the F3 condition (three real flashes). To determine which locations were selected significantly above chance across conditions, we performed a series of one-sample t-tests with a conservative Bonferroni correction for multiple comparisons, adjusting the significance threshold to $p = 0.01$. This analysis combined data from both eyes, with a sample size of 20 participants (20 participants x 2 eyes; $df = 39$). The results showed that locations 2, 3, and 4 were selected significantly above chance (Table 1; Fig. 3), particularly when participants reported perceiving two or three flashes. Interestingly, while it was expected that two locations would be chosen significantly more often when participants reported seeing two flashes, we found significant selection for three locations instead. To investigate this unexpected finding, we conducted chi-square tests to identify which specific pairs of locations were chosen more frequently. These tests were performed on the 10 possible location pairs when participants reported seeing two flashes, with a Bonferroni-adjusted significance level of $p = 0.005$. Notably, the pair [2, 4] was the most frequently selected across all conditions (Table 2). To be more specific, when participants reported seeing two flashes, they tended to accurately perceive the flashes at the intended locations (2 and 4). Furthermore, when participants perceived three flashes, the stimuli were correctly perceived at locations 2, 3, and 4 in the F3 condition (three real flashes), while in the F2 condition (two real flashes), the illusory third flash was perceived between the two real flashes, with location 3 being the only available option.

Illusory flash locations confirm consistent representation across blind and control spots

In addition to flash location reports via selecting from five pre-defined locations, a subset of the participants (N = 10) completed flash localization trials using mouse clicks for fine-grained localization (see Methods: Experimental Design – Additional flash localization task). A Wilcoxon signed-rank test indicated that the reported locations of the illusory flash significantly deviate from the center of the control spot towards the first flash ($M = -0.06, Mdn = -0.101, SD = 0.252), W = 495, p = 0.033$, but not for stimuli presented on the blind spot ($M = -0.054, Mdn = -0.126, SD = 0.282), W = 659, p = 0.088$. For location reports on the last flash, all reports significantly deviate from the locations of the veridical flash towards the first flash: blind spot ($M = -0.185, Mdn = -0.230, SD = 0.359), W = 680, p < 0.001$, control spot ($M = -0.119, Mdn = -0.134, SD = 0.279), W = 831, p < 0.001$ (Fig. 4). These results confirm that illusory flashes were perceived similarly in both the blind spot

and control spot, suggesting that the brain integrates auditory and visual cues to create a unified percept, even when part of the visual field lacks direct input, such as in the blind spot.

Interestingly, participants demonstrated a systematic bias in location reports for both illusory and last flashes, with responses shifted toward the first flash. A two-sample Kolmogorov-Smirnov test revealed no significant difference in the distributions of normalized distances between the reported and true locations for stimuli presented on the blind spot and the control spot($D = 0.148, p = 0.508$ for illusory flashes; $D = 0.122, p = 0.556$ for last flashes). The observed location bias, while intriguing, reflects a general characteristic of the AV Rabbit Illusion and does not differentiate the blind spot from other regions. This result demonstrates consistent cross-modal integration across the visual field, regardless of visual input.

3 Discussion

We present here the first successful demonstration that the visual system can integrate multisensory information to fill in perceptual gaps within the blind spot. Most previous studies have focused on unimodal (vision-only) filling-in, often explained through predictive coding, where the brain uses surrounding visual context to predict and complete missing information[16,28,29,30,31]. While effective in many cases, predictive coding fails in scenarios like illusory contours, where there is no local visual information to guide completion[17]. Our study shows that by using a multisensory stimulus, we successfully induced perceptual filling-in even when immediate local visual information was not provided. In both the Illusory and Invisible AV Rabbit conditions, auditory cues successfully altered visual perception within the blind spot, and performance was comparable to control spots (Fig. 2). These findings suggest that the brain integrates multisensory inputs across time, relying on both predictive and postdictive processes to maintain perceptual continuity. Our results contribute to the growing body of evidence on the multisensory and postdictive nature of perception, particularly in cross-modal illusions such as the Double Flash Illusion[26], where auditory cues modify visual perception. By successfully inducing a cross-modal illusion within the blind spot, we reveal how the brain compensates for sensory gaps using both temporal and multisensory information.

A key distinction between our study and other perceptual filling-in studies is that (1) there is no local contextual visual information available for the blind spot, meaning the filling-in is not simply a result of surface interpolation, (2) the filled-in percept occupies a retinal area smaller than the physiological blind spot, (3) temporal dynamics are involved as part of multisensory processing. These claims are supported by subjective reports of flash locations (Table 1 and Fig. 3). When participants perceived three flashes (two real and one illusory), they accurately identified the locations of the real flashes and the illusory flash within the blind spot. In cases where no illusion was perceived (i.e., only two real flashes were seen), participants correctly selected the flash locations at the borders of the blind spot (Table 2). Our findings provide insights into the neural mechanisms underlying filling-in at the blind spot, particularly the role of top-down processing in the absence of direct visual input.

The conventional view might suggest that unimodal (visual) processing occurs earlier in the sensory pathway, while multisensory processing is relegated to later or higher cortical areas. However, our refined location data and the specific positioning of the illusory flash – occupying a smaller retinal area within the blind spot – suggest that perceptual filling-in in this case may involve smaller spatial scales or receptive fields than previously assumed. Furthermore, the critical involvement of a latter multisensory stimulus, which influences the perception of a previously presented stimulus[32,33], emphasizes that temporal dynamics are essential, indicating that earlier projections, possibly at V1, are likely involved in filling-in when influenced by cross-modal inputs.

Traditional theories of filling-in, based on predictive coding, propose that bottom-up feedforward signals convey "prediction error", while top-down feedback signals deliver "contextual estimates"[16,28,34,35]. However, in out study, the bottom-up visual signals were identical across conditions (i.e., F2B0, F2B2, F2B3: two real flashes at fixed locations). The only variable we manipulated was the number of beeps, which significantly altered participants' perception, leading them to perceive three flashes instead of two. According to traditional blind spot filling-in models, perception should remain stable since the feedforward-feedback loop was driven by the same visual inputs.

We propose that multisensory stimuli activated alternate sensory pathways, allowing sound to exert a direct influence on primary visual cortex (V1), as documented in multisensory illusion literature[36,37,38]. Structural evidence from human and non-human primate studies supports this, showing direct projections from the auditory cortex to V1, especially within peripheral visual areas[20,21,22,23]. Our use of a multisensory postdictive stimulus likely bypassed traditional predictive coding mechanisms, enabling sound to directly activate V1 and achieve perceptual filling-in at the blind spot. Thus, these findings highlight the importance of cross-modal interaction and combined predictive and postdictive processing in perceptual filling-in when visual information alone is insufficient.

One of the most significant findings of our study is that the illusory flash consistently appeared between the locations of the two real flashes, regardless of means of location reports. Location 3 was selected consistently as where the illusory, sound-induced flash was perceived, between locations 2 and 4 (where the real flashes were; Fig. 3). When asked to click on the location of the illusory flash, it falls within the blind spot i.e., between the locations of the two real flashes (Fig. 4). This midpoint bias in the location of the illusory flash highlights the brain's tendency to integrate multisensory information across spatial and temporal gaps, especially in the absence of direct sensory input, as is the case in the blind spot. This consistent spatial bias also reflects a broader, hierarchical pattern in multisensory perception, where spatial location is inferred based on temporal and spatial cues from the surrounding stimuli. Participants' reports further showed a systematic shift in flash location responses, both for flashes in the blind spot and in the control region (Fig. 4). While this bias might stem from various factors, one possibility is that peripheral presentation of stimuli – known for lower spatial acuity[39,40] – left participants with less precise spatial information to begin with, making accurate reproduction challenging. Another perspective comes from Sperling[41] partial report paradigm. When participants reproduced flash locations from a full-screen set

of options (3840 x 2160; monitor resolution), the vast number of choices likely increased cognitive load, reducing their spatial accuracy. However, selecting from just five predefined locations lowered cognitive demand and allowed for improved sensory memory retention during the response phase. Finally, the presentation of flashes in succession along the same axis may have functioned as a moving stimulus, with visual flashes providing spatial information and auditory beeps providing temporal cues. This integration of sensory signals could mean that participants perceived flashes as closer together in time and space than they actually were. Although further exploration of stimulus timing and spatial reproduction bias is beyond the scope of this paper, these findings provide an intriguing insight into the integration of spatial and temporal cues in perceptual filling-in.

The blind spot may not be so "blind" after all. Since we were able to induce a flash percept within the blind spot using sound, this finding suggests that we may need to rethink the operational definition of blindness. With the expanding body of multisensory research, it is increasingly clear that sensory processes are not strictly unimodal, but involve an intricate balance and interaction across sensory domains. This raises important questions about how we define blindness and whether it is limited to the visual domain alone. It may not simply refer to the absence of visual input, but could extend to cases where other sensory modalities compensate for a lack of vision, such as in the case of auditory-induced percepts within the blind spot. This line of thought opens up fascinating possibilities for sensory substitution technologies, which aim to replace or enhance a lost sensory modality with input from another. For example, sensory substitution devices that convert visual information into auditory or tactile stimuli have shown promise in helping individuals with visual impairments navigate their environments[42,43,44,45]. Our findings support the idea that the brain is highly adaptable and capable of using alternative sensory inputs to "fill in" for missing information, suggesting a broader, more fluid understanding of sensory processing. The success of such multisensory integration challenges the traditional view of blindness as a rigid, unimodal phenomenon and encourages us to explore how the brain can leverage other sensory modalities to overcome deficits in one, ultimately enhancing sensory substitution applications.

4 Methods

Participants. After giving written informed consent, 20 neurotypical volunteers participated in the study (10 females; mean age 26.7 years, range 19 – 40 years). All participants had normal or corrected-to-normal vision (20/20) and audition. The study was approved by the institutional review board at the California Institute of Technology (IR19-0926).

Stimuli and conditions. Audiovisual stimuli consisted of visual flash(es) and auditory beep(s). The visual flash was a white bar (0.28 visual degrees in width, 1.2 visual degrees in length) presented on a black background (i.e., 100% contrast) briefly for one frame (i.e., 16.7 ms, as defined by the monitor refresh rate of 60 Hz). The auditory beep was a pure tone (800 Hz) of 7 ms duration. Six conditions were tested using the naming convention FXBY, where X is the number of flashes and Y is the number of beeps – two unimodal, flash

only conditions: F2B0, F3B0; two bimodal congruent conditions: F2B2, F3B3; two bimodal incongruent conditions: F2B3 (Illusory Audiovisual Rabbit), F3B2 (Invisible Audiovisual Rabbit). For accurate stimulus timing, refer to Figur 5A. Possible stimulus locations were 0.5 visual degrees outside the borders (left, right, top, bottom) and at the center of the blind and control spots (Figure 5B). On any given trial, flash presentation follows either the horizontal or vertical trajectory. For example, a F3B0 trial can have flashes presented sequentially along the horizontal axis (i.e., left – center – right); a F2B0 trial, on the other hand, only shows flashes on the borders (i.e., left – right).

The participant's blind spots were mapped using a flickering target on a black background. The target was a small circular disc (covering 0.5 degrees of the visual field), flickering between black (0% contrast) and white (100% contrast) at a frequency of 7 Hz. As a control, spots corresponding to the blind spot of the fellow (non-tested) eye were also evaluated (referred to as "control spots"; see below) (Note: the blind spots are within the binocular visual field). The fellow eye was covered with an eye patch.

By using the fellow eye's blind spot as a control but testing it on the normal visual field of the tested eye, the experiment allows for a direct comparison of perceptual performance for stimuli falling on the same locations within the visual field. This comparison contrasts situations where stimuli are fully visible (within normal visual field) and partially visible (one flash landing on the blind spot). For example, if the left eye is being tested, the control spot would be the location corresponding to the right eye's blind spot, but tested in the left eye's normal visual field.

Experimental design. *Blind spot mapping protocol.* There were three trials in the blind spot mapping task. The stimulus used was a flickering target on a black background (circular disc subtending 0.5 visual degrees, flickering between black (0% contrast) and white (100% contrast) at 7 Hz). Participants wore an eye patch over the non-tested eye. They were eye tracked at all times to ensure they stayed fixated at the center. In each trial, participants were asked to move the flickering target across the screen and report the borders of their blind spots, i.e., when the target disappeared and reappeared. This procedure was repeated at least three times in each trial. In trial 1, participants reported left and right borders; in trial 2, participants reported top and bottom borders; in trial 3, participants reported left and right borders. Before we concluded the run and moved on to the other eye, we displayed the estimated cardinal border points and the area formed by them on screen. We asked participants to verify if the shape's edges were blurry (successful mapping, move on to next eye), or well defined (unsuccessful mapping, redo all trials).

Audiovisual Rabbit Task. In this task, participants were presented with a sequence of (i) two or three flashes and (ii) zero, two, or three beeps (Fig 5A). Participants wore an eye patch over the non-tested eye. On each trial, stimulus presentation began after a successful fixation at the center for 500 ms (verified by an eye tracker). Participants were shown the response prompt 500 ms post stimulus presentation. In block one, participants were asked to select flash location(s) from the five options (Figure 5C). All options were equidistant from each other. For example, in a F3B0 trial, the correct response is locations 2, 3, and 4. Location 2

corresponds to the left border, location 3 at the center of the blind or control spot, location 4 at the right border. In block two, participants were asked to report the number of beeps presented.

Across experimental runs, we instructed participants to pay attention to the number and location(s) of flash(es) presented (block one), and number of beeps presented (block two). We never explicitly explained or stated the relationship between number of flashes and beeps. Hence, the 2 x 3 x 4 x 2 factorial design manipulated (i) the number of flashes (i.e., two or three), (ii) the number of beeps (i.e., zero, two or three), (iii) stimulus movement direction (i.e., left to right, right to left, top to bottom, bottom to top), (iv) stimulus location (i.e., blind spot or control spot) yielding 48 conditions in total. In each block, all conditions were presented 5 times, yielding 240 trials in total. All trials within blocks were randomized.

Additional flash localization task. Among the 20 participants, 10 agreed to come back and complete additional flash localization trials. There were 8 F2B3 trials for each eye, 4 on each location (blind spot and control spot). Participants were instructed to stay fixated at the center, monitored by the eye tracker, and move the cursor (full-screen crosshair) to click onto the flash locations. Location of the first flash was already provided on screen.

Experimental setup. Psychtoolbox 3.0.19 (www.psychtoolbox.org) running under MATLAB 2024a (MathWorks) presented visual and audiovisual stimuli. Auditory stimuli were presented at $\approx$ 62 dBSPL via two loudspeakers (Bose Companion 2 Series III) positioned on each side of the monitor). Visual stimuli were presented on a 27 inch LCD screen with a 60 Hz refresh rate (Dell UltraSharp U2720Q). A desktop mounted eye-tracker (EyeLink 1000; SR-Research Ltd., Mississauga, Ontario, Canada) was used to make monocular recordings of the participants' tested eye. The EyeLink system used a remote mode, i.e., with the remote camera option, with a 500-Hz sampling rate. Button presses were recorded using a standard keyboard. Participants were seated in front of the monitor and loudspeakers at a distance of 50 cm, head fixated on a chin rest, eye patch worn over the non-tested eye, in a dark room. The scripts used to run the experiment are openly available on GitHub (https://github.com/chanyca/blindspot-multisensory) under the CC-BY license[46].

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Author Contributions

Conceptualization: A.C., Task design: A.C., N.S., and S. S., Data analysis: A.C., N.S., and C.L., Writing: A.C., N.S., C.L., S.S., Funding Acquisition: N.S., A.T., S.S., Supervision: N.S., C.L., A.T., and S.S.

Competing Interests Statement

The authors declare no competing interests.

Data and code availability statement

The figures in this article, as well as the data and plotting scripts necessary to reproduce them, are available openly under the CC-BY license[46]. Additionally, custom scripts developed for the experiments are included in this release.

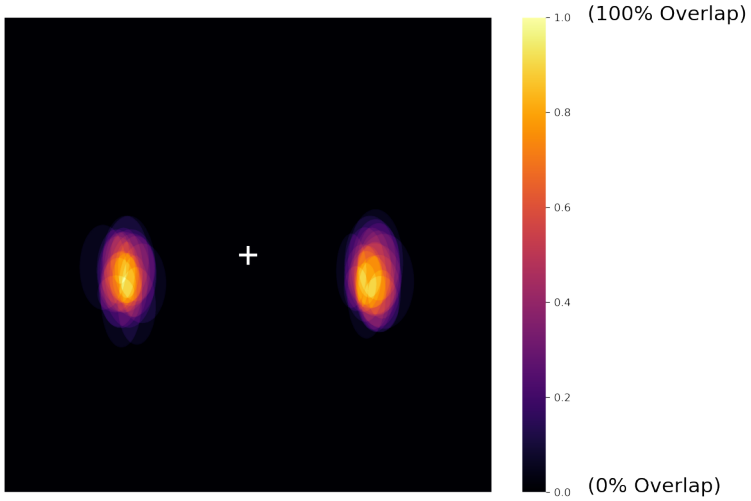

Figure 1: **Heatmap showing locations of left and right eyes' blind spots in participants (N = 20).** The white cross indicates the center of the visual field (monitor), and also acted as a fixation point for participants during the trial.

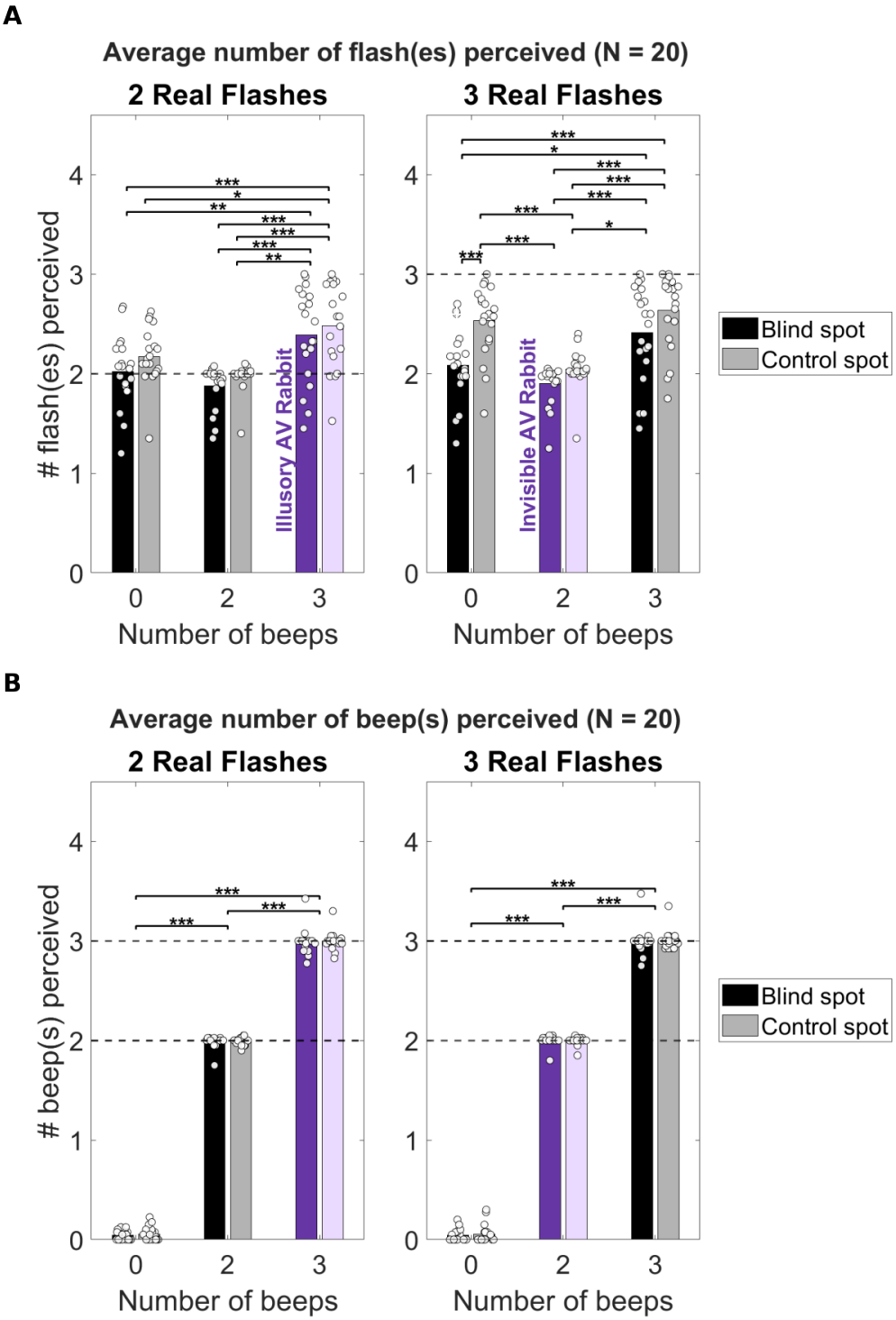

Figure 2: **Average number of flashes (A) and beeps (B) perceived across conditions, all movement directions combined.** Left: Two true flashes were presented, paired with different number of beeps (F2B0, F2B2, and F2B3); right: Three true flashes were presented, paired with different number of beeps (F3B0, F3B2, and F3B3). Bar represents group mean; one dot represents one participant's mean. Darker bars represent trials presented on blind spots; lighter bars represent trials presented on control spots. Statistical significance of the comparisons is indicated by stars: $p < 0.05(*), p < 0.01(**), p < 0.001(***)$.

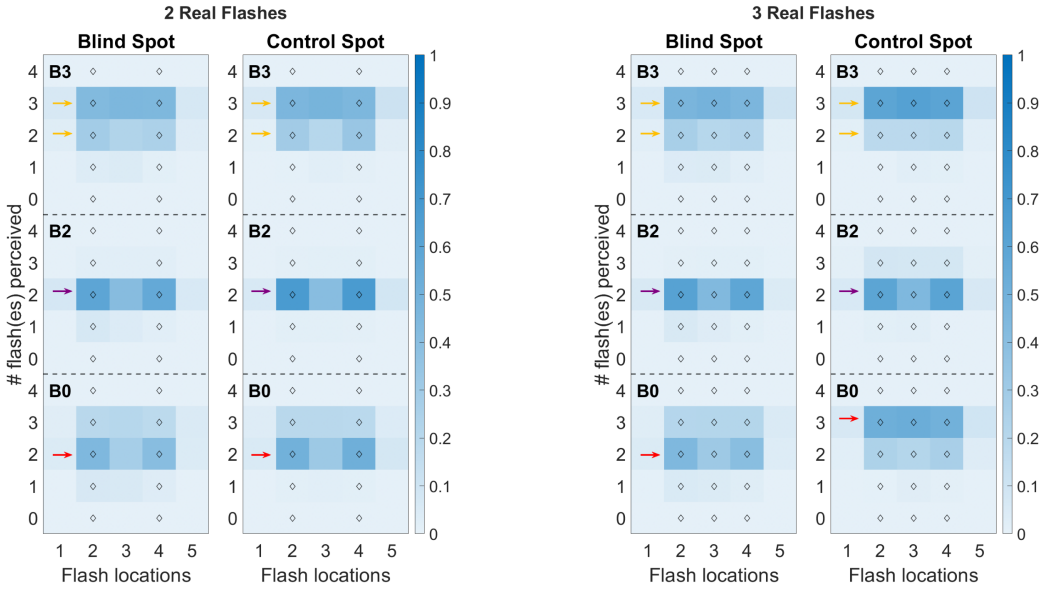

Figure 3: **Heatmaps displaying the proportion of trials certain flash locations were picked.** Within beep conditions, when 2 real flashes (left) and 3 real flashes (right) were presented (bottom: B0 – 0 beeps, middle: B2 – two beeps, top: B3 – three beeps). Number of flash locations reported equals to number of flash(es) perceived. For example, if participants reported two flash locations, they perceived two flashes, etc. Trials were grouped according to stimuli locations (left column: blind spot; right column: control spot), and real number of flashes presented (left: two; right: three). Diamonds indicate true locations of flashes presented. The y-axis represents number of flashes perceived (0-4), the x-axis represents flash locations 1-5. For example, across F2B2 conditions (left, middle section), participants mostly reported seeing 2 flashes, locations 2 and 4 were the most selected locations. For more details regarding flash locations, refer to Figure 5D. Arrows point to flash responses that were reported in the majority of trials (Yellow: F2B3/F3B3 conditions; Purple: F2B2/F3B2 conditions; Red: F2B0/F3B0 conditions).

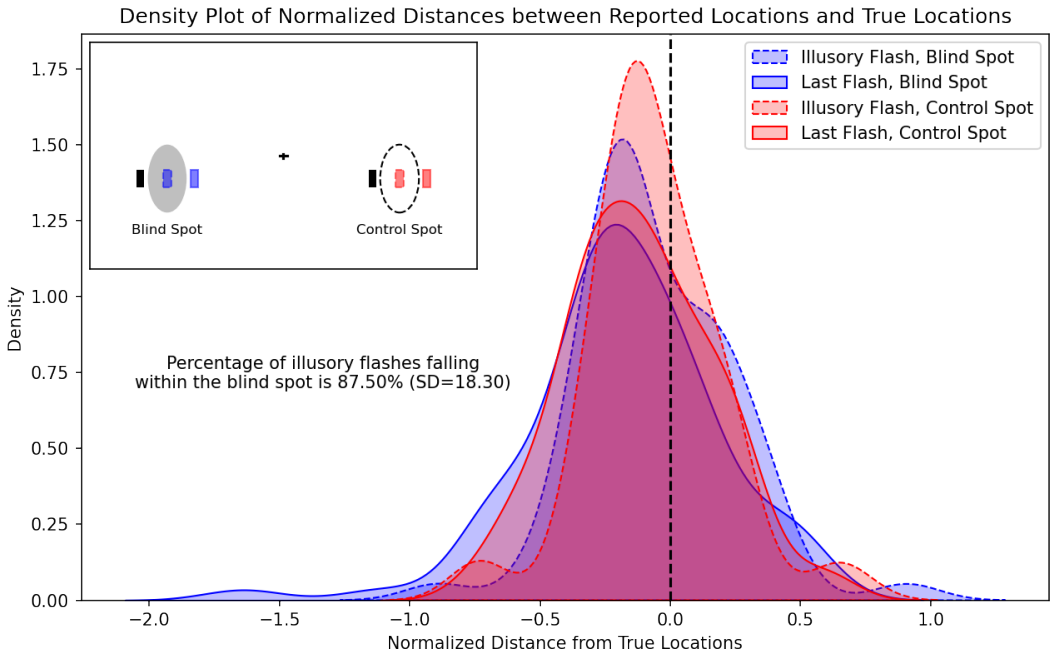

Figure 4: **Density plot displaying the distribution of response' normalized distances from the hypothesized location of illusory flash (center) and true location of the last flash in visual degrees.** Note this data comes from additional flash localization trials, where only 10 out of 20 participants completed this block. All trials were F2B3 "Illusory AV Rabbit" trials. Participants were instructed to report the location(s) of the illusory second flash (if any) and last flash. The illusory flash's location was hypothesized to be at the center of the blind and control spots, thus flash localization performance was evaluated based on normalized distances from center. We normalized the distances because the blind spot is often not a perfect circle. This allows us to do a fair comparison combining both vertical and horizontal trials.

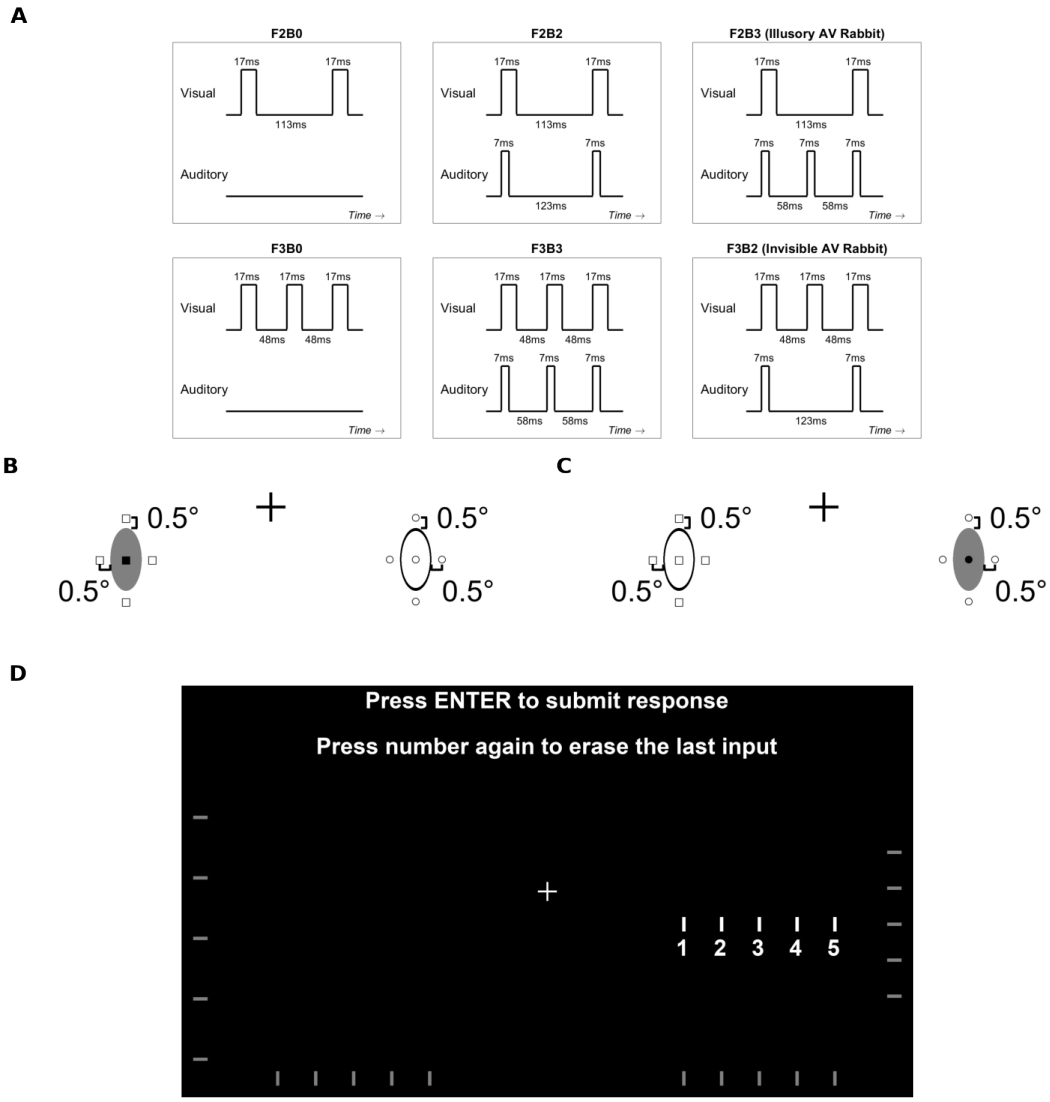

Figure 5: **Experiment design (A)** Schematics for all six conditions. Conditions were named using the FXBY convention - X: number of flashes, Y: number of beeps. The onset times of the beeps and flashes are simultaneous when paired. Left column: unimodal conditions; middle column: bimodal congruent conditions; right column: bimodal incongruent conditions. In the Illusory Audiovisual Rabbit condition (F2B3), participants perceive an illusory flash paired with the second auditory beep. In the Invisible Audiovisual Rabbit condition (F3B2), the middle flash is suppressed by the absence of the second auditory beep. **(B, C)** Stimuli locations when the testing eye is left eye **(B)** and right eye **(C)** respectively. Flashes were presented 0.5 visual degrees from the cardinal border points, as well as at the center of the blind spot (grey region) and the control spot (hollow region). All flashes presented in the experiment were identical among all locations. Here, we used squares and circles to indicate flashes to illustrate that stimuli were presented on the same locations on the visual field between eyes, even though sometimes the central flash fell on the blind spots, thus became invisible to participants (dark stimuli). **(D)** Prompt screen for flash location response. All five options are equidistant from each other. Locations 2 and 4 lie on the cardinal borders (North, East, South, West), location 3 lies right at the center. In F2BY (two physical flashes) conditions, visual stimuli were presented on locations 2 and 4; in F3BY (three physical flashes) conditions, visual stimuli were presented on locations 2, 3, and 4. Participants were allowed to select as many options as they would like.

Table 1: Results of one-sample t-tests comparing the observed percentage of location selections to the expected chance level for each location. Only significant results are reported. * $p < 0.01$, ** $p < 0.002$, *** $p < 0.0002$

Condition		**Stimuli presented on**	
		Blind spot	**Control spot**
		$t(39) =$	$t(39) =$
	3 flashes perceived		
F2B3	Location 2	5.62***	6.03***
	Location 3	5.63***	6.04***
	Location 4	5.83***	5.92***
	2 flashes perceived		
	Location 2	4.80***	4.43***
	Location 3	4.30***	3.02*
	Location 4	4.23***	5.42***
	2 flashes perceived		
F2B2	Location 2	13.3***	17.2***
	Location 3	8.91***	8.18***
	Location 4	12.3***	21.0***
	2 flashes perceived		
F2B0	Location 2	8.91***	11.9***
	Location 3	6.35***	6.70***
	Location 4	8.28***	13.0***
	3 flashes perceived		
F3B3	Location 2	4.69***	9.46***
	Location 3	3.79***	9.52***
	Location 4	4.17***	9.53***
	2 flashes perceived		
	Location 2	4.69***	2.70*
	Location 3	3.79**	n.s.
	Location 4	4.17***	2.68*
	2 flashes perceived		
F3B2	Location 2	16.2***	15.8***
	Location 3	9.81***	9.85***
	Location 4	13.2***	16.9***
	3 flashes perceived		
F3B0	Location 2	n.s.	9.02***
	Location 3	n.s.	8.56***
	Location 4	n.s.	8.45***
	2 flashes perceived		
	Location 2	8.97***	4.47***
	Location 3	7.29***	3.88***
	Location 4	9.00***	4.83***

Table 2: Results of chi-squared tests showing the top 3 location pairs selected across conditions, when participants reported perceiving 2 flashes. * $p < 0.005$, ** $p < 0.001$, *** $p < 0.0001$

Condition		**Stimuli presented on**	
		Blind spot	**Control spot**
		χ^2, df, N	χ^2, df, N
F2B3	**Locations 2, 4**	184***, 1, 111	552***, 1, 174
	Locations 2, 3	132***, 1, 99	-
	Locations 3, 4	46.1***, 1, 72	74.3***, 1, 86
F2B2	**Locations 2, 4**	705***, 1, 287	1192***, 1, 377
	Locations 2, 3	84.9***, 1, 144	-
	Locations 3, 4	80.5***, 1, 142	-
	Locations 1, 2	-	66.3***, 1, 5
F2B0	**Locations 2, 4**	595***, 1, 217	782***, 1, 271
	Locations 2, 3	80.1***, 1, 110	-
	Locations 3, 4	-	68.4***, 1, 121
	Location 1, 5	-	56.0***, 1, 1
F3B3	**Locations 2, 4**	199***, 1, 105	140*, 1, 82
	Locations 2, 3	146**, 1, 94	54.0***, 1, 60
	Locations 3, 4	47.2***, 1, 66	92.0***, 1, 71
F3B2	**Locations 2, 4**	749***, 1, 299	802***, 1, 307
	Locations 2, 3	137***, 1, 168	78.2***, 1, 144
	Locations 3, 4	86.9***, 1, 148	111***, 1, 158
F3B0	**Locations 2, 4**	497***, 1, 205	244***, 1, 118
	Locations 2, 3	112***, 1, 123	41.8***, 1, 67
	Locations 3, 4	51.0***, 1, 99	87.2***, 1, 83