(1) Introduction

Spatial perception presents a unique problem for neural systems: different sensory modalities initially encode space in different frames of reference, and these must be reconciled to produce coherent perception of the environment (Andersen 1997). For example, in audiovisual spatial perception, visual stimuli are encoded with respect to the retina (in an "eye-centered" frame of reference) (Fetsch et al. 2007), auditory stimuli are encoded with respect to the head (in a "head-centered" frame of reference) (Peña and Konishi 2001), and the brain must determine whether to use an eye-centered reference frame, a head-centered reference frame, or hybrid reference frame to combine information from the two modalities and derive the location of objects and events in space (Pouget, Deneve, and Duhamel 2002). As stimuli in the world are generally multisensory (Matusz et al. 2018), the question of how the brain decides which representational space to use to integrate sensory signals extends across a wide range of environmental scenarios.

Several studies, some of them with very large sample sizes (ranging from 130 to 380 observers), have shown that human audiovisual spatial localization can be accounted for remarkably well by Bayesian causal inference (Odegaard, Wozny, and Shams 2015; Wozny, Beierholm, and Shams 2010; Beierholm, Quartz, and Shams 2009; Körding et al. 2007). In this model, an observer's percept is a function of the reliabilities of unisensory encoding (likelihoods), a prior reflecting the *a priori* probability of inferring a common cause for sensory stimuli (the "binding tendency"; Odegaard and Shams 2016; Odegaard, Wozny, and Shams 2017), a spatial prior reflecting any bias to particular regions of space, and the decision-making strategy. In all of these studies, the spatial prior was shown to account for specific localization biases, such as the tendency to localize visual responses closer to the center of gaze. However, in these previous studies, the eyes and head of the observers were aligned. Therefore, it remains unclear whether the spatial bias is centered in the eye-centered or head-centered frame of reference, or even a combination of these frames. Changing eye position in either a transient or sustained manner has been shown to strongly influence auditory spatial perception (Dobreva, O'Neill, and Paige 2012; Cui et al. 2010; Razavi, O'Neill, and Paige 2007). Therefore, in this investigation, we asked the following question: how does eye position influence the spatial prior?

Three possibilities exist for how eye position may influence the spatial prior (Fig. 1). If the frame of reference of amodal representation of space is head-centered, then the direction of gaze will not affect the spatial prior (Fig 1A). Alternatively, the brain may use an eye-centered frame of reference in audiovisual spatial perception, and therefore this prior, which has previously been shown to be centered at the middle of gaze in most participants (Körding et al. 2007; Odegaard, Wozny, and Shams 2017), may shift to align itself with each new gaze position (Fig. 1B). Finally, it remains possible that this prior is encoded in some hybrid reference frame and may only exhibit partial shifts as the gaze position changes (Fig. 1C).

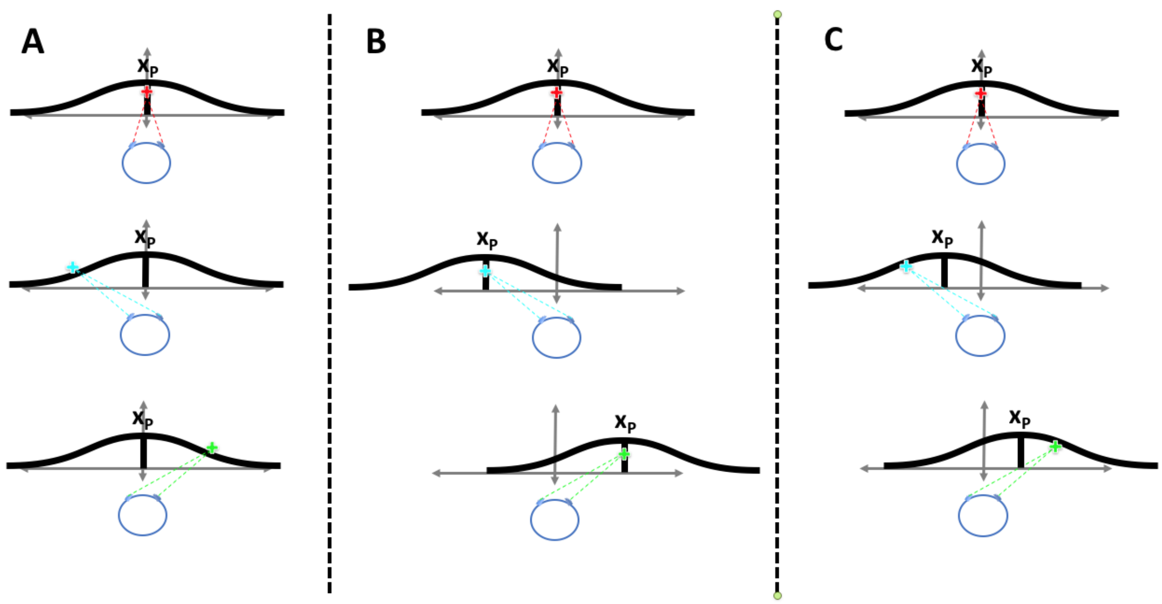

Fig. 1. Hypotheses about the frame of reference for the spatial prior. (A) Head-centered frame of reference. The mean of the spatial prior (x_P) is consistent across different fixation positions. (B) Eye-centered frame of reference. The mean of the spatial prior moves to match the change in gaze angle. (C) Hybrid frame of reference. The mean of the spatial prior exhibits a partial shift in response to different gaze positions.

In order to shed light on this question, we examined the reference frame used by the brain for encoding the prior bias in perception of space by employing an audiovisual spatial localization task and changing the location where participants fixated across trials. We examined spatial localization of simple auditory and visual stimuli in three different gaze conditions for each observer. On every trial, participants were presented with either a flash of light, a burst of sound, or a simultaneous presentation of both stimuli, which could either be spatially congruent or incongruent. Participants were asked to localize any stimuli that were presented as quickly and as accurately as possible. By fitting the parameters of our Bayesian model (see Supplemental Materials, Section 1) to each participant's data in each of the gaze conditions, we could estimate the optimal value for the mean of the spatial prior and determine which of the three aforementioned scenarios best characterizes the frame of reference for this computational element.

(2) Methods

2.1 Participants

Twenty-three individuals participated in our experiment (7 males, 16 females). All participants were undergraduate research volunteers participating for course credit at the University of California-Los Angeles, were older than 18 years of age, had normal or corrected-to-normal vision and hearing, and did not have a neurological condition (e.g., seizures, epilepsy, or stroke).

2.2 Apparatus and Materials

Participants were seated in a chinrest located 52cm in front of a large, acoustically transparent black cloth that covered most of the visual field (134° width x 60° height). A ceiling-mounted projector (resolution: 1,280 x 1,024 pixels; refresh rate: 75Hz) was located above participants and could display visual stimuli at one of nine locations along a horizontal display axis in front of participants: -24.8°, -19.1°, -13°, -6.5°, 0°, 6.5°, 13°, 19.1°, and 24.8°. Our display was a two-dimensional screen and not a semicircle; therefore, as stimuli were presented further away from the central midpoint, distance from the observer changed very slightly based on the stimulus position. This influenced the computation for visual degrees and prevented stimuli from being spaced equidistantly in degrees. Visual stimuli were a white disk (0.41 cd/m^2) masked with a Gaussian envelope of 1.5° and were displayed for 35ms.

Nine speakers (5 x 8 cm; extended range paper cone) were mounted on a shelf located behind the black cloth and were positioned at the same locations as visual stimuli (i.e., from -24.8° to 24.8°). While the black cloth was acoustically transparent, the color was dark enough that participants could not see the speaker positions behind the screen and were thus unaware of the exact spatial positions of the speakers. Auditory stimuli consisted of ramped white-noise bursts emitted from a single speaker on each trial. These noise bursts registered 59dB at a distance of 52cm from the speakers and were played for 35ms.

A ViewPoint Eyetracker (Arrington Research, Scottsdale, AZ) was fixed to the chinrest to monitor participants' fixation locations throughout the start of each trial in the experiment. The eyetracker was connected to a Dell PC using PC-60 software (version 2.8.5,000). Viewing of all stimuli in our experiment was binocular, but the eyetracker was only used to track monocular movements of the right eye. Stimuli were not displayed until the recorded gaze angle was within 3.0° of the fixation cross, and fixation time was greater than 250ms. All experimental stimuli were displayed using a custom script written in MATLAB (version 7.6.0, R2008a) and a wireless mouse was used to record the behavioral responses. Participants were allowed to place the wireless mouse wherever they felt most comfortable, but the approximate location of the mouse remained the same throughout the experiment for each participant.

2.3 Procedure

Our experiment was conducted over two days, with each day spaced exactly one week apart. Each session lasted for approximately 90 minutes. During the first day, participants began the session with a practice block of 10 trials containing visual, auditory, and audiovisual stimuli. Every trial in both the practice block and the real experiment proceeded in the following manner: first, a white fixation cross was presented at either -13°, 0°, or 13°. Once fixation was established by the eyetracker, stimuli were presented after a delay of 750ms. 450ms after the stimuli, the fixation cross was removed, and the mouse cursor appeared at a random location on the screen along the horizontal, one-dimensional axis where stimuli could be displayed. The location of this cursor could be controlled by scrolling with the red trackball on the wireless mouse. On each trial, participants were instructed to "move the cursor as quickly and as accurately as possible to the location of the stimuli and click the mouse." The participants were not required to fixate during the response period.

Inside the cursor was a small letter which indicated the stimulus that participants needed to localize. If only a visual stimulus was displayed, the cursor would denote a blue "L," indicating participants needed to localize the light. If only a sound stimulus was displayed, the cursor would denote a red "S," indicating participants needed to localize the sound. If *both* a sound and a light were displayed on a given trial, for half of the participants, when the cursor first appeared, it would denote an "L." Following localization of the light, the cursor position was randomized again, and would change to a red "S," indicating they needed to localize the sound next. For the other half of the participants, the response order on bisensory trials was sound first, and then light; thus, the response order was counterbalanced across participants. No feedback about the correctness of their responses was given.

Following the practice session, participants began the real experiment, which consisted of 630 trials on day 1 and 735 trials on day 2, for a total of 1365 trials in the experiment. There were three conditions in the experiment: a left-fixation condition, where the fixation cross was presented at -13° to start each trial, a center-fixation condition where it was presented at 0° to start each trial, and a right-fixation condition where it was presented at 13° to initiate each trial. The fixation cross was 7 degrees above the axis where stimuli were displayed. Within the 455 trials for each fixation condition, there were three types of stimuli: unisensory visual stimuli, unisensory auditory stimuli, and bisensory stimuli. Unisensory stimuli were always presented at a single location, but bisensory stimuli could either be presented from the same location, or from different locations. This yielded 35 different trial locations for each condition: five unisensory visual locations, five unisensory auditory locations, and twenty-five different bisensory locations, with the permutations of all possible visual & auditory combinations in the five-location array. This stimulus presentation design ensured that all possible combinations of stimuli for the five locations surrounding the fixation cross were included, as in previous studies using this modeling framework (Körding et al. 2007; Wozny, Beierholm, and Shams 2010; Odegaard, Wozny, and Shams 2015) (see Supplementary Material, Section 4 for further discussion). Each of these 35 trial types were presented 13 times during the experiment in a pseudo-random order, yielding the 455 trials for a given fixation condition. This design provides equal and sufficiently large number of trials per stimulus condition needed for a reliable estimation of model parameters.

Stimuli were always presented at the five locations surrounding each fixation cross. For example, for the left-fixation condition, stimuli were presented at -24.8°, -19.1°, -13°, -6.5°, or 0° relative to the center of the head; for the center-fixation condition, stimuli were presented at -13°, -6.5°, 0°, 6.5°, and 13°; for the right-fixation condition, stimuli could be presented at 0°, 6.5°, 13°, 19.1°, and 24.8° relative to the head center (see Fig. 2).

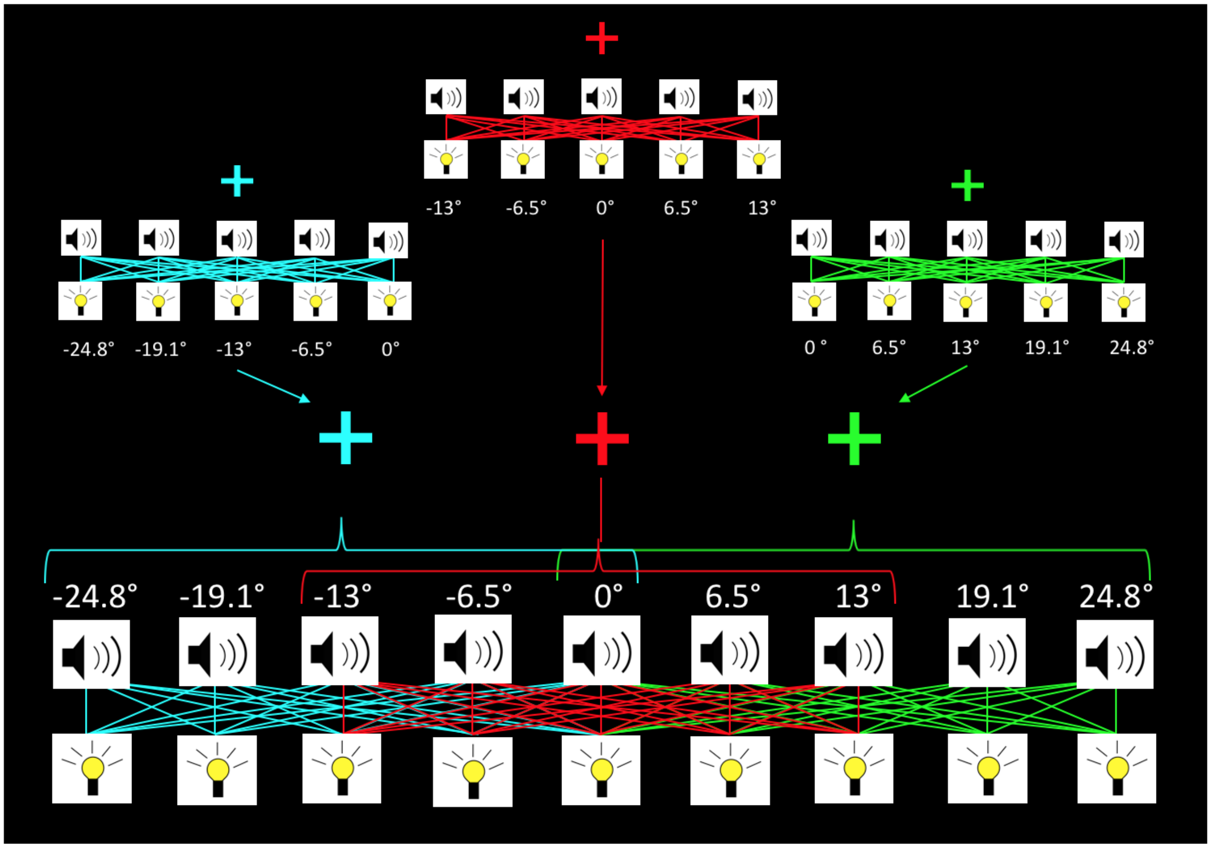

Fig. 2. The three fixation conditions. In our spatial localization task, audiovisual stimuli were presented from one of five locations which were centered around a given fixation point. Participants were required to start each trial with their eyes on the fixation cross, which could appear in one of three positions: -13 degrees, 0 degrees, or 13 degrees. The cyan, red and green plus signs represent the fixation point in the left-fixation, center-fixation, and right-fixation conditions, respectively.

Results

In Figure 3, response distributions across all observers (N=23) for the visual-alone conditions, auditory-alone conditions, and audiovisual conditions, are plotted separately for the left (A), middle (B), and right (C) fixation conditions.

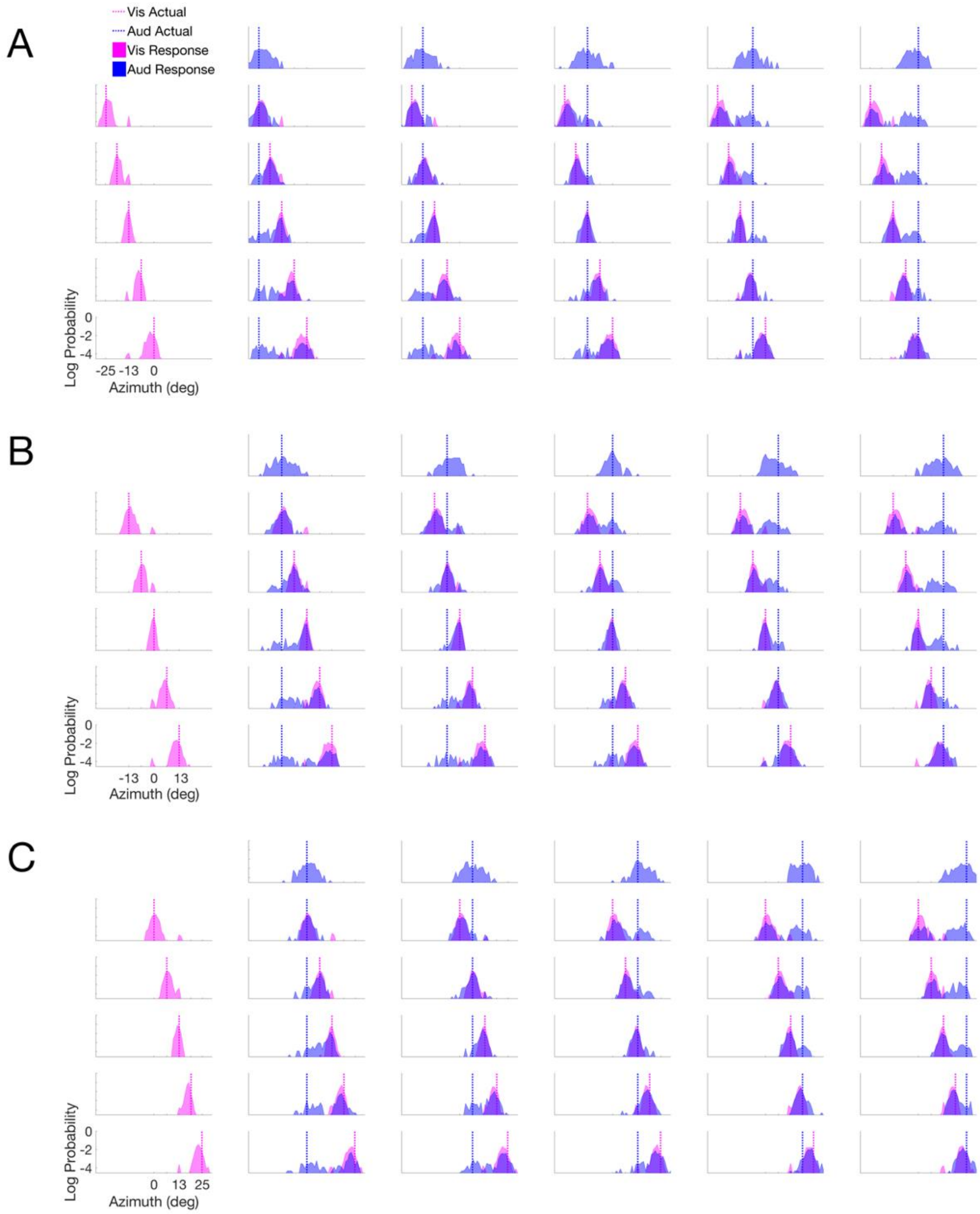

Fig. 3. Observers' response distributions (combined across all 23 subjects) for each stimulus condition. Auditory responses are shown in blue, and visual responses are shown pink; all 35 stimulus conditions are shown. (A) Observers' response distributions in the left-fixation conditions. (B) Observers' response distributions in the center-fixation conditions. (C) Observers' response distributions in the right-fixation conditions

Shown in Table 1 are the optimized parameter values from our Bayesian causal inference model (see Supplemental Materials, Section 1). The parameter of interest in this study was the mean of the spatial prior (x_p). As can be seen in the table, the mean of the spatial prior changed as a function of fixation location. A one-way repeated-measures ANOVA indicated that these differences were significant ($F(2,44) = 55.64$, $p < .001$). Post-hoc t-tests revealed that differences between the means of the spatial prior for all three fixation conditions were significantly different from one another: left fixation and center fixation ($t(22) = 5.80$, $p_{bonf} < .001$); center fixation and right fixation ($t(22) = 6.22$, $p_{bonf} < 0.01$); left fixation and right fixation ($t(22) = 8.77$, $p_{bonf} < 0.001$)). The one-way repeated measure ANOVAs conducted on the prior probability of a common cause parameter (p_c), visual likelihood variance parameter (σ_V), and auditory likelihood variance parameter (σ_A) did not reveal any significant changes across fixation conditions ($p > .05$ for all ANOVAs). However, the one-way repeated-measures ANOVA conducted on the prior variance (σ_p) did reveal a significant change across fixation conditions ($F(2,44) = 4.56$, $p = .016$), which was driven primarily by the difference in variance between the left and right fixation conditions (post-hoc t-test, $t(22) = 2.56$, $p_{bonf} = 0.053$).

	Priors			Likelihoods	
	x_P	σ_P	p_C	σ_V	σ_A
Left Fixation	-11.51 ± 1.90	10.90 ± 1.20	0.73 ± 0.06	2.36 ± 0.37	12.86 ± 2.09
Center Fixation	-0.09 ± 1.97	13.25 ± 1.40	0.73 ± 0.06	2.37 ± 0.39	14.05 ± 2.41
Right Fixation	10.81 ± 2.61	16.45 ± 2.84	0.72 ± 0.06	2.62 ± 0.46	13.25 ± 2.04

Table 1. Optimized model parameter values for the 23 participants. Values represent the average across participants for each parameter, +/- SEM across participants.

To gain a better understanding of how the prior expectation of spatial information (which is captured by the spatial prior) influences localization behavior, we conducted an analysis of localization biases across different fixation conditions. The main effect of the spatial prior is to attract localizations of sensory stimuli towards the mean of the prior. Thus, as our model's estimates of the mean of this prior change across fixation locations, there should be an observable change in localization behavior across conditions. For example, for sensory stimuli at the same location, as the fixation location changes, the mean of this prior shifts, and therefore different sensory biases should emerge across fixation conditions. As shown in Fig. 4, the behavior that would be predicted by the model's estimates is indeed borne out in the localization data. When fixation is towards the left (blue), the prior shifts towards the left. Stimuli to the left of the mean will be localized closer to the center of the prior by exhibiting a bias towards the right, and stimuli to the right of the mean will similarly be localized closer to the center of the prior by exhibiting a bias towards the left. When fixation is at the center (red), the prior remains at the center of space, and the attractive effects on localization behavior are shown by the red arrows. When fixation is towards the right (green), the prior is shifted towards the right, and the attractive effects on localization behavior are shown by the green arrows.

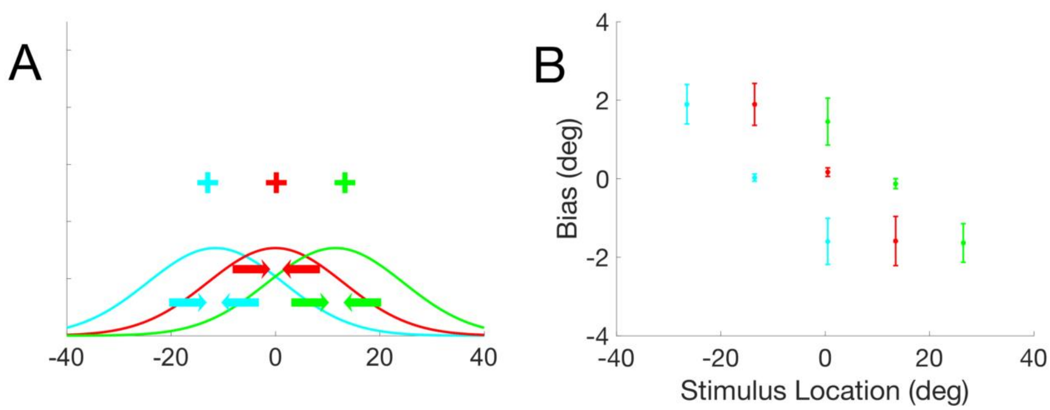

Fig. 4. The effect of the spatial prior on visual localizations. (A) Schematic of how the central prior influences localization responses. As shown in this panel, the mean of the spatial prior changes across the three fixation conditions (shown by the locations of the "+" in each color). Arrows indicate how localization of stimuli at different locations are influenced by the spatial prior.   (B) Visual localization behavior displaying the effects of the spatial prior. Positive values on the y-axis represent localization biases towards the right, and negative values represent localization biases towards the left.   When fixation is towards the left (cyan), stimuli presented at fixation (-13 deg) do not exhibit any localization bias. However, when stimuli are presented to the left of fixation (e.g., -24.8 deg), they exhibit biases towards the right, and when stimuli are presented to the right of fixation in this condition (e.g., 0 deg) they exhibit biases towards the left. This general pattern is maintained for both the central fixation (red) and rightward fixation (green) conditions. Dots represent average bias across participants; error bars represent SEM across participants.

These results indicate that the direction of gaze influences the spatial prior. To quantify the support for each of the three hypotheses with respect to the nature of the relationship between gaze direction and spatial prior, we conducted a simple regression analysis with fixation position as the predictor variable and optimized spatial prior mean as the outcome variable. As shown in Fig. 5, the basic idea behind this analysis was to fit a linear model to the values from the three fixation conditions for each subject, and then to evaluate the magnitude of the Beta weight as evidence for a given hypothesis. Beta weights near one could be interpreted to support the hypothesis that the spatial prior was encoded in an eye-centered reference frame, as the mean of this prior shifted fully with eye position; beta weights near zero could be interpreted to support the hypothesis that the spatial prior was encoded in a head-centered reference frame, as the mean of the prior did not change with eye position.

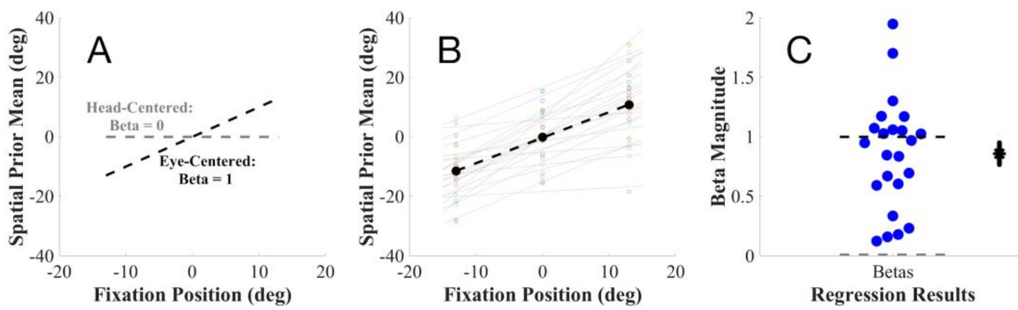

Fig. 5. Linear regression analysis to arbitrate among reference frame hypotheses. (A) Schematic of how Betas can be used to provide support for each hypothesis. As shown in this panel, with fixation position as the predictor variable, and spatial prior mean as the outcome variable, a line fit to these three data points can provide evidence for a given hypothesis. If the slope (Beta) of the line is near one, the prior changes with eye position, and this provides support that the prior is encoded in an eye-centered reference frame. If the slope of the line is near zero, the prior does not change with eye position, and this can be interpreted as evidence for a head-centered reference frame. (B) Individual linear fits and average linear fit. Each individual subject's linear fit is shown in gray, and the average linear fit is shown in black. (C) The Beta values from each of the linear fits for each participant from panel B. The black dotted line centered at 1 represents strong support for the eye-centered reference frame, and the gray dotted line around 0 represents strong support for the head-centered reference frame. As can be seen in this panel, a majority of participants exhibited Beta values (shown in blue) near 1, consistent with the prior being encoded in an eye-centered reference frame. The black dot on the right represents the average Beta value, with the standard error of the mean across Betas also shown.

Overall, the results support the hypothesis that the spatial prior is encoded in an eye-centered reference frame, as the mean of the spatial prior appears to shift with fixation towards peripheral locations (Fig. 5C). Some variability in the overall trend was evident, but clear modulation of the mean of the spatial prior with varying eye position was displayed by most participants. Additional analyses confirmed that our model could indeed tease apart eye and head-centered reference frames in data marked by visual dominance (see Supplemental Materials, Section 3).

Supplemental Materials

All data, figures, and code for this project can be found on the Open Science Framework site for this project (https://osf.io/mkxpw/) in a zipped directory labeled, “Article Materials.” A direct link to the data can be found in our Reference List [dataset] (Odegaard et al., 2018). The supplemental materials section is divided into four sections and includes the following information: a full description of our Bayesian causal inference model (Section 1), tables of the localization biases for each fixation condition and stimulus location (Section 2), analyses to evaluate the model’s ability to uncover the frame of reference (Section 3), and a brief discussion of whether exposure to spatially incongruent trials reduces PCommon (Section 4).

(3) Discussion

We investigated whether changing eye fixation position during an audiovisual localization task would result in a shift in participants’ prior bias for localization. Participants exhibited a localization bias towards the center of gaze, and the localization bias shifted in the same direction as the shift in gaze positions. Estimates of the prior bias for each individual observer obtained from a Bayesian model (Körding et al. 2007; Beierholm et al. 2013) indicated that the mean of the spatial prior (Körding et al. 2007; Wozny, Beierholm, and Shams 2010) shifted along with gaze.

In principle, the prior may be encoded in one of three ways: in an eye-centered reference frame, a head-centered reference frame, or a hybrid reference frame between the two. Our Bayesian model estimates together with a linear regression analysis revealed that most participants had a prior which was consistent with an eye-centered reference frame, which is consistent with previous findings in the literature (Engbert and Krügel 2010; Krügel and Engbert 2014). Some variability in the magnitude of the shift in the mean of the prior was evident across subjects.

One limitation in the present investigation can be found in the experimental design: as fixation position changes, so does the stimulus array that is used in the task. Since trials from the three conditions were randomly interleaved throughout each localization session, the potential for learning effects to occur seemed small, but remains possible. Ideally, the entire 9-position array would be used at all times with any given fixation position, with 81 possible conditions (9 visual x 9 auditory) for each fixation condition but acquiring enough localization trials per condition to perform the modeling work would require a prohibitive number of hours for each subject to complete the task. Moreover, keeping the stimulus array fixed with varying fixation points would introduce the confound that the distribution of stimuli relative to the fixation point would no longer be the same across fixation points. For example, if the gaze is to the left, there would be significantly more stimuli presented to the right of fixation, which could modify the bias for spatial position if learning occurs during the experiment. Thus, we opted for the design that maintained the same exact distribution of stimuli relative to the fixation point. However, future studies should explore the alternative design.

Additionally, we recommend that future investigations manipulate both eye and head position in a factorial design in a within-subjects manner, to tease apart head- and body-centered influences on the frame of reference, if any. The influence of mode of response on frame of reference should also be further investigated. For example, it is to be determined whether using a response device based on a different modality (e.g., an auditory cursor using sound that ramps across locations) would influence the frame of reference used in this task. While most localization tasks require use of visual or motoric response devices, use of an auditory response device could provide unique insights into the frame of reference utilized by the perceptual system.

Moving forward, research should aim to identify where in the perceptual pathway this prior is encoded. A recent study suggests that interactions between the eye and ear take place at remarkably early stages of perceptual processing (Gruters et al. 2018). Thus, it seems possible that the spatial prior exhibited by our participants may be encoded by either cortical or subcortical regions. Additionally, the origin or cause of this prior is not quite clear. Objective physical events are typically equally likely to happen at any angle around us, but events which we create and act upon tend to happen in front of us. While auditory perception is possible for all 360 degrees, vision is restricted to what is in front of our eyes, and due to poor visual acuity in periphery, gathering detailed and reliable visual information requires foveating the object/event of interest. As a result, events and objects of interest do tend to appear in the fovea most of the time. Future studies should investigate whether we encode a prior based on *subjective* visual experiences, rather than *objective* event probabilities.

References

Andersen, R. A. 1997. “Multimodal Integration for the Representation of Space in the Posterior Parietal Cortex.” *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 352 (1360): 1421–28.

Beierholm, Ulrik, Marc Guitart-Masip, Marcos Economides, Rumana Chowdhury, Emrah Düzel, Ray Dolan, and Peter Dayan. 2013. “Dopamine Modulates Reward-Related Vigor.” *Neuropsychopharmacology: Official Publication of the American College of Neuropsychopharmacology* 38 (8): 1495–1503.

Beierholm, Ulrik R., Steven R. Quartz, and Ladan Shams. 2009. “Bayesian Priors Are Encoded Independently from Likelihoods in Human Multisensory Perception.” *Journal of Vision* 9 (5): 23.1–9.

Cui, Qi N., Babak Razavi, William E. O’Neill, and Gary D. Paige. 2010. “Perception of Auditory, Visual, and Egocentric Spatial Alignment Adapts Differently to Changes in Eye Position.” *Journal of Neurophysiology* 103 (2): 1020–35.

Dobreva, Marina S., William E. O’Neill, and Gary D. Paige. 2012. “Influence of Age, Spatial Memory, and Ocular Fixation on Localization of Auditory, Visual, and Bimodal Targets by Human Subjects.” *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale* 223 (4): 441–55.

Engbert, Ralf, and André Krügel. 2010. “Readers Use Bayesian Estimation for Eye Movement Control.” *Psychological Science* 21 (3): 366–71.

Fetsch, Christopher R., Sentao Wang, Yong Gu, Gregory C. Deangelis, and Dora E. Angelaki. 2007. “Spatial Reference Frames of Visual, Vestibular, and Multimodal Heading Signals in the Dorsal Subdivision of the Medial Superior Temporal Area.” *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience* 27 (3): 700–712.

Gruters, Kurtis G., David L. K. Murphy, Cole D. Jenson, David W. Smith, Christopher A. Shera, and Jennifer M. Groh. 2018. “The Eardrums Move When the Eyes Move: A Multisensory Effect on the Mechanics of Hearing.” *Proceedings of the National Academy of Sciences*, January. https://doi.org/10.1073/pnas.1717948115.

Körding, Konrad P., Ulrik Beierholm, Wei Ji Ma, Steven Quartz, Joshua B. Tenenbaum, and Ladan Shams. 2007. “Causal Inference in Multisensory Perception.” *PloS One* 2 (9): e943.

Krügel, André, and Ralf Engbert. 2014. “A Model of Saccadic Landing Positions in Reading under the Influence of Sensory Noise.” *Visual Cognition* 22 (3-4): 334–53.

Matusz, Pawel J., Suzanne Dikker, Alexander G. Huth, and Catherine Perrodin. 2018. “Are We Ready for Real-World Neuroscience?” *Journal of Cognitive Neuroscience*, June, 1–12.

Odegaard, Brian, and Ladan Shams. 2016. “The Brain’s Tendency to Bind Audiovisual Signals Is Stable but Not General.” *Psychological Science*, March. https://doi.org/10.1177/0956797616628860.

Odegaard, Brian, David R. Wozny, and Ladan Shams. 2015. “Biases in Visual, Auditory, and Audiovisual Perception of Space.” *PLoS Computational Biology* 11 (12): e1004649.

———. 2017. “A Simple and Efficient Method to Enhance Audiovisual Binding Tendencies.” *PeerJ* 5 (April): e3143.

Odegaard, Brian, Ulrik Beierholm, Jason Carpenter, & Ladan Shams (2018). “Article Material/Data/Actual.” Open Science Framework, 2018, https://osf.io/3yaut/.

Peña, J. L., and M. Konishi. 2001. “Auditory Spatial Receptive Fields Created by Multiplication.” *Science* 292 (5515): 249–52.

Pouget, Alexandre, Sophie Deneve, and Jean-René Duhamel. 2002. “A Computational Perspective on the Neural Basis of Multisensory Spatial Representations.” *Nature Reviews. Neuroscience* 3 (9): 741–47.

Razavi, Babak, William E. O’Neill, and Gary D. Paige. 2007. “Auditory Spatial Perception Dynamically Realigns with Changing Eye Position.” *The Journal of Neuroscience: The*

Official Journal of the Society for Neuroscience 27 (38): 10249–58.
Wozny, David R., Ulrik R. Beierholm, and Ladan Shams. 2010. “Probability Matching as a Computational Strategy Used in Perception.” *PLoS Computational Biology* 6 (8). https://doi.org/10.1371/journal.pcbi.1000871.