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of the Self in Motion****Jean-Paul Noel<sup>1</sup> and Dora E. Angelaki<sup>1,2</sup>**<sup>1</sup>Center for Neural Science, New York University, New York, NY 10003, USA;  
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**Keywords**

Bayesian inference, population probabilistic coding, multisensory, body, peri-personal space, navigation

**Abstract**

Navigating by path integration requires continuously estimating one's self-motion. This estimate may be derived from visual velocity and/or vestibular acceleration signals. Importantly, these senses in isolation are ill-equipped to provide accurate estimates, and thus visuo-vestibular integration is an imperative. After a summary of the visual and vestibular pathways involved, the crux of this review focuses on the human and theoretical approaches that have outlined a normative account of cue combination in behavior and neurons, as well as on the systems neuroscience efforts that are searching for its neural implementation. We then highlight a contemporary frontier in our state of knowledge: understanding how velocity cues with time-varying reliabilities are integrated into an evolving position estimate over prolonged time periods. Further, we discuss how the brain builds internal models inferring when cues ought to be integrated versus segregated—a process of causal inference. Lastly, we suggest that the study of spatial navigation has not yet addressed its initial condition: self-location.

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## INTRODUCTION

Successful navigation is central to adaptive behavior, as it underpins our ability to trade off between exploiting our current location in the environment with exploring novel ones. Traditionally, navigation has been divided into two broad classes: landmark-based navigation and path integration. The former relies on fixed environmental anchors for visual homing, reorientation, and way-finding. The latter, instead, involves integration of evolving estimates of heading, angular, and linear velocity derived from visual, vestibular, proprioceptive, and motor-efference signals into a best guess of position. In a sense, landmark-based navigation can be allocentric (e.g., turn left at the refrigerator), while path integration cannot—it relies on self-motion information derived from an egocentric perspective (e.g., an optic-flow field radiating from a focus of expansion). As such, the study of path integration and self-motion may allow us to further understand not only navigation but also our subjective and egocentric sense of self-location.

Here, we contextualize recent findings of path integration and self-motion while highlighting novel and interesting developments in neighboring and interdependent fields of study. First, we sketch the visual and vestibular neural pathways involved. We start with the vestibular pathways, as these are commonly less known to the general audience. Second, we highlight that the visual and vestibular systems are in isolation incapable of accurate self-motion perception. Thus, much of our focus is in outlining the computational and neural principles that underpin visuo-vestibular Bayes near-optimal integration. Further, we review initial findings and suggestions regarding the mechanism behind Bayesian causal inference. In the last section we highlight an area of study that is seldom incorporated into the study of navigation yet constitutes its initial condition: the sense of self-location.

## NEURAL PATHWAYS FOR SELF-MOTION

A multitude of sensory systems contribute to our subjective sense of self-motion. The strongest of these are likely vision and the vestibular system. In this section we briefly outline these neural pathways.

## The Vestibular System in Self-Motion

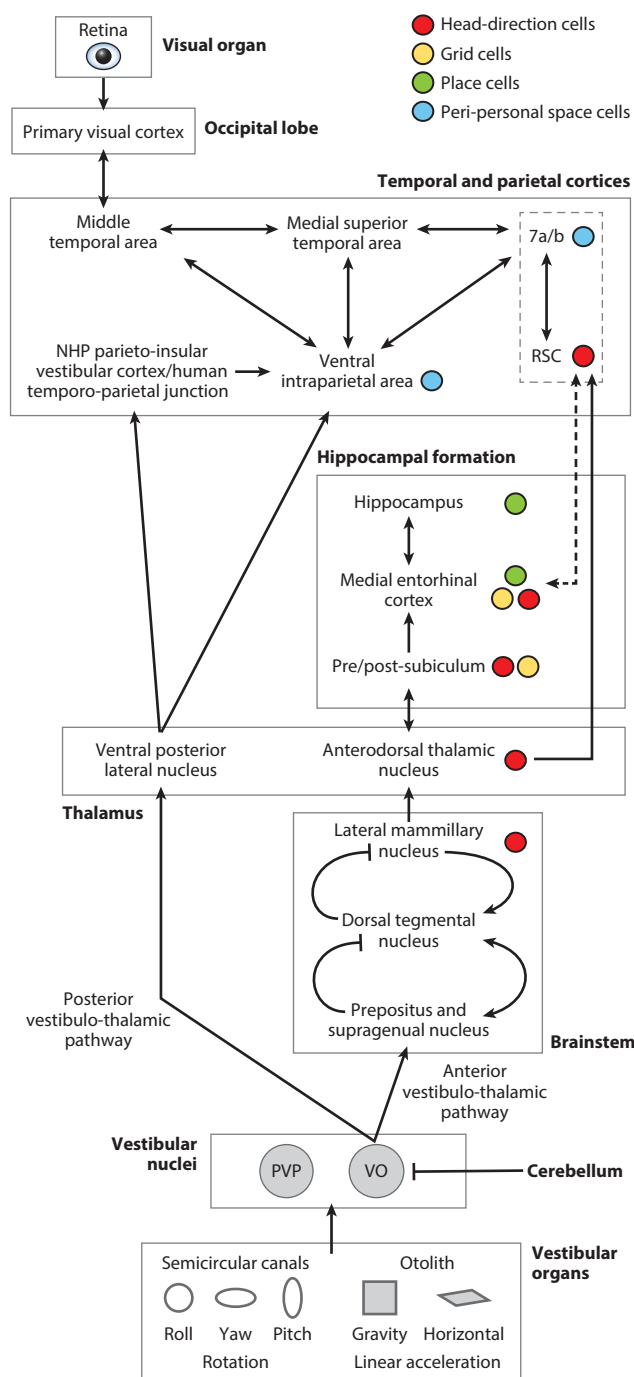
The vestibular peripheral organ is located in the inner ear and comprises two components: the otolith organs and the semicircular canals (**Figure 1**). The former detect linear head acceleration, both horizontally and vertically (i.e., gravity). The latter sense head rotation in three orthogonal planes. In turn, the afferent fibers of the vestibular nerve project to central vestibular areas, in particular the vestibular nuclei. This area is composed of many cell types; some are involved in gaze stabilization, while others [e.g., vestibular-only (VO) cells] are thought to be involved in posture, self-motion, and navigation (see Cullen 2019 for a recent review). VO neurons respond to passive (i.e., externally applied) head motion, but responses are suppressed during active head motion, translation (Carriot et al. 2013), or rotation (Roy & Cullen 2001, 2004).

The suppression of VO neurons during active self-motion is predicted by a Kalman filter-based model of self-motion (Laurens & Angelaki 2017). More specifically, the cerebellum is generally thought to form a forward internal model that predicts the sensory consequences of self-generated movement (Krakauer & Mazzoni 2011). Hence, theoretical models (Laurens & Angelaki 2017) of the vestibular system have similarly suggested that during active movement the cerebellum may compute an internal model of the expected sensory consequences of a motor command. This estimate is then compared with the observed sensory inflow to generate sensory prediction errors. When expectations are violated, as is the case during passive head movements, vestibular reafference cancellation signals from the cerebellum to the vestibular nuclei are not suppressed, and thus activity in VO neurons is enhanced (**Figure 1**). In addition to VO neurons in the vestibular nuclei, recordings from the rostral fastigial nucleus of the primate cerebellum confirm the computation of sensory predictions that enable the distinction between self-generated and externally applied self-motion (Brooks et al. 2015). Remarkably, therefore, already at this early stage, signals mediating self-motion estimation are multisensory (i.e., vestibular, motor efference copy, and likely proprioception from the neck).

From the vestibular nuclei, information is sent to the cortex via two ascending thalamocortical pathways. The anterior vestibulo-thalamic pathway projects first to the prepositus and supragenual nucleus, then to the dorsal tegmental nucleus, and finally to the lateral mammillary nucleus—all within the brainstem (**Figure 1**). The association between the latter two areas is postulated to encode a ring attractor (reviewed in Knierim & Zhang 2012) that leads to head-direction cells in their downstream area, the anterior dorsal nucleus of the thalamus (ADN) (see Hulse & Jayaraman 2020 for a recent review). These head-direction cells are egocentric in nature, in that they encode the direction of heading. The ADN outputs to the retrosplenial cortex and the dorsal presubiculum before this anterior pathway converges onto the well-known spatial codes of the entorhinal cortex and hippocampus (Moser et al. 2008). The entorhinal cortex is heterogeneously composed of, and multiplexes (Hardcastle et al. 2017), head-direction, place (O'Keefe & Nadel 1978), speed (Kropff et al. 2015), border (Solstad et al. 2008), and grid cells. It is likely best known for this latter cell type, tiling space in a hexagonal pattern (Hafting et al. 2005). The hippocampus possesses place cells, neurons that fire when the animal is within a particular location of space (O'Keefe 1976). Thus, interestingly, while supported by the vestibular system—an idiothetic sense—the anterior vestibulo-thalamic pathway ultimately is involved in building an allocentric map in limbic areas (**Figure 1**).

The second ascending thalamocortical pathway is the posterior one. This pathway projects from the vestibular nuclei and the cerebellum to the ventral posterior lateral thalamus (VPL). The VPL is also a hub for somatosensory information (Jones 1985), and thus it is not surprising that this area is highly multisensory, encoding for vestibular, somatosensory, proprioceptive, visual, and motor signals. From here, the posterior vestibulo-thalamic pathway projects directly to the

Egocentric perspective  
 Allocentric map  
 Egocentric perspective



(Caption appears on following page)

**Figure 1** (*Figure appears on preceding page*)

Visual and vestibular pathways leading to allocentric coding in parahippocampal formation. Vestibular-only cells in the vestibular nuclei project via the anterior vestibulo-thalamic pathway to hippocampal formation, first reflecting an egocentric code and ending in an allocentric code (e.g., place fields). Via the posterior vestibulo-thalamic pathway, vestibular signals permeate much of the posterior parietal cortex. The exact nature and strength of the message-passing across much of this schematic network remain to be fully described, and this schematic coalesces evidence from a number of species: macaques, rodents, and fruit flies. Thus, there are likely species-specific variations [e.g., head-direction cells exist in RSC in rodents (Keshavarzi et al. 2021), yet it is unknown whether this is true in macaques]. Nonetheless, overall area 7 and RSC seem to be strong points of contact between egocentric coding in cortex and allocentric coding in the hippocampal formation (e.g., Whitlock et al. 2008, Keshavarzi et al. 2021). Abbreviations: NHP, nonhuman primate; PVP, position-vestibular pause; RSC, retrosplenial cortex; VO, vestibular only.

parieto-insular vestibular cortex (PIVC), the ventral intraparietal area (area VIP), and the vicinity of the central sulcus near the face representation, among many others (see Lopez & Blanke 2011 for an extensive review). Thus, while the anterior thalamocortical pathway ultimately aids in building an allocentric map of external space, the posterior pathway is seemingly involved in the perception of the body in space (Lopez & Blanke 2011).

In addition to the abovementioned areas receiving vestibular input directly from the VPL, the medial superior temporal area (MST), particularly the dorsal subdivision (MSTd) (Duffy 1998) but also the lateral one (Sasaki et al. 2019), and area 7a (Avila et al. 2019) also respond to vestibular stimulation. Thus, seemingly much of the dorsal stream (e.g., MSTd, VIP, 7a) is generally responsive to vestibular self-motion stimuli. Further, until recently it was thought that the response patterns in these areas showed a progressively stronger correlation with heading discrimination behavior [e.g., MSTd (Gu et al. 2008) versus VIP (Chen et al. 2013)], at least insofar as measured by choice probabilities (i.e., a measure indicating how well an ideal observer can predict the animal's choice given the distribution of a neuron's discharge rate; see, e.g., Britten et al. 1996). However, recent causal experiments where chemical inactivation was performed have brought into question the causal role of MSTd and VIP in vestibular heading perception, as there is no or little impairment in heading discrimination when these areas are shut down (Gu et al. 2012, Yu & Gu 2018).

Interestingly, while the posterior parietal cortex is widely considered to be a hub for egocentric spatial navigation, and its tuning to allocentric variables (e.g., route information) is weak (e.g., Chen et al. 1994), area 7a—being downstream from most of the posterior parietal cortex—shows properties that suggest a gradual transformation toward cues amenable for allocentric encoding. That is, 7a seems to show weak visuo-vestibular convergence and distinct subpopulations of neurons code for either linear or angular velocity (Avila et al. 2019). Given that the distinctive characteristic of 7a relative to its parietal neighbors is its anatomical connection to the retrosplenial cortex and indirect connection to hippocampal formation (Pandya & Seltzer 1982), we speculate that the neural codes in 7a and the retrosplenial cortex (showing progressive divergence as opposed to convergence of linear and angular velocity signals) may be best suited for readout in the hippocampus (see Kravitz et al. 2011 for a similar argument linking the caudal inferior posterior lobule with hippocampal formation spatial codes). Similarly supporting this conjecture, Avila and colleagues (2019) recently reported that 7a is most readily driven by vestibular and not visual optic flow information, and this former sensory modality is tuned to acceleration. Along this line, Kropff et al. (2021) recently demonstrated that contrary to popular belief, theta rhythms organizing neural activity across the hippocampus and entorhinal cortex in running rats are modulated by the acceleration, and not speed, of the rats.

We speculate that while two ascending thalamocortical vestibular pathways exist (anterior and posterior), these in fact form a loop, being separate and egocentric at their outset (in the thalamus

and cortical areas) and converging in the hippocampal formation where they employ an allocentric code (see Herweg & Kahana 2018 for a similar argument, and see Andersen et al. 1985 and Bicanski & Burgess 2016 for arguments regarding the involvement of the retrosplenial cortex in allo-/egocentric transformation).

## The Visual System in Self-Motion

When a stationary observer views clouds move past her, a river flow by her, or a train departing on the adjacent track, she may experience an illusory sense of self-motion. This phenomenon is called *vection* (Tschermak 1931), and as these examples illustrate, it is a sensation that occurs in nature. As such, it has long been appreciated that visual cues alone can generate self-motion perception (Mach 1875). In particular, it is well established that large-field, coherent, and global motion mimicking the pattern of flow that occurs on our retinæ as we move relative to the environment is capable of eliciting vivid sensations of self-motion (see Dichgans & Brandt 1978). This pattern of motion was denominated *optic flow* (Gibson 1950) and has served as the backbone for much of the modern-day study of self-motion.

The striate and extrastriate cortices are well studied, in particular for their motion responses (Maunsell & Van Essen 1983). Hence, natural contenders for the processing of optic flow emerged rapidly. A subset of cells in the primary visual cortex (V1) are highly selective for direction, but these cells have small spatiotemporal receptive fields and encode motion of local features (Hubel & Wiesel 1968)—thus, they are likely not ideally suited for self-motion processing (but see Vélez-Fort et al. 2018). The middle temporal area (MT) likely integrates motion cues inherited from V1 (Adelson & Movshon 1982), and cells in this area can encode two-dimensional motion, such as patterned motion (e.g., vertical bars moving north and southeast yielding a rightward percept). MT is also thought to estimate velocity (Adelson & Movshon 1982). However, this area does not seem tailored for complex and whole-field flow processing. Instead, the subsequent stages of the visual dorsal stream—MSTd, VIP, and area 7a (**Figure 1**)—all seem to show properties well suited for optic flow processing: (a) large and often bilateral receptive fields, (b) selectivity for complex visual motion patterns, and (c) often partial remapping of reference frames allowing for heading representation independent of eye position (Avillac et al. 2005, Duffy & Wurtz 1991). These latter areas have therefore been the most extensively studied in the processing of optic flow and self-motion (see Britten 2008 for an earlier review focusing on MSTd and VIP).

Early studies suggested a weak but consistent correlation between spiking activity in MSTd and trial-to-trial fluctuations in heading perception derived from optic flow (Britten & van Wezel 1998, Gu et al. 2008). This small correlation has recently also been shown in MT (Yu & Gu 2018). In contrast, the downstream VIP shows substantially larger correlations between brain activity and heading perception (Chen et al. 2013). To the best of our knowledge the correlation between neural activity and heading judgments has not been reported in 7a. While it would be tempting to suggest that higher levels of the visual hierarchy (e.g., from MT to VIP) have a stronger role in guiding heading perception, recent experiments do not support this simple view. Causal experiments bilaterally suppressing MSTd showed a threefold increase in the psychophysical threshold for visual heading perception (Gu et al. 2012). Remarkably, however, bilateral suppression of VIP had no effect on heading perception as derived from optic flow (Chen et al. 2016). Supporting the conclusion linking MSTd but not VIP to heading perception, Zaidel and colleagues (2017) dissociated sensory-driven and choice-driven components to choice probabilities. This analysis suggested a preponderance of heading signals in MSTd and of choice signals in VIP. Recordings in the vestibular and deep cerebellar nuclei (Bryan & Angelaki 2008), as well as the PIVC (Chen et al. 2010), showed a lack of responsiveness to optic flow.

In general, therefore, there is a convergence of visual and vestibular signals for self-motion in the parietal dorsal stream (e.g., MSTd, VIP, 7a). However, their exact functional roles are not yet fully understood. It seems as if the strongest signals relating to the encoding of self-motion from vision are in MSTd, but after this stage, information may be most strongly related to decision-making processes and visuo-vestibular cue combination, while being highly distributed and redundantly coded (see Zhang et al. 2016 for a similar argument and modeling effort, and see Bizley et al. 2016, for an argument that distributed networks underlie multisensory decision-making).

## **VISUO-VESTIBULAR INTEGRATION: COMPUTATION, ALGORITHM, AND IMPLEMENTATION**

Despite their clear contribution to self-motion processing, in isolation the visual and vestibular systems are ill-equipped to guide spatial navigation. As mentioned above, given that self-motion is relative, during full-field visual motion observers may misinterpret global world motion as self-motion (i.e.,vection; see Dichgans & Brandt 1978 for an early and extensive review). Similarly, optic flow may be caused by true translation or rotation of the head in the environment, but it may also be due to rotation of the eyes in orbit, or a confluence of signals that have to be parsed (i.e., the rotation problem). The vestibular system also has inherent limitations. For instance, given that the inner ear detects acceleration, in the absence of visual cues we cannot sense movement after a prolonged period of constant velocity (e.g., closing one's eyes on a moving train). Likewise, given that otolith afferents encode linear acceleration and changes in head orientation relative to gravity in an identical manner, this system in isolation cannot distinguish between these [Einstein's equivalence principle (Einstein 1907)]. Thus, the integration of visual and vestibular signals not only supposes a redundancy of encoding that via multisensory integration is likely to ameliorate perceptual sensitivity (see Fetsch et al. 2013 for a review) but also overcomes fundamental deficits in each of these systems.

In this section we first summarize behavioral and computational evidence specifying how signals ought to be combined, from a principled perspective. Then, we highlight probabilistic population codes (PPCs) as a theoretical framework detailing how optimal cue combination may occur in the brain and review the evidence for this sort of neural code in visuo-vestibular integration for heading perception (see the sidebar titled Neural Instantiation of Probabilistic Inference for a broader discussion on the neural instantiation of statistical inference). We highlight important advances that have (a) developed ideal observers who integrate signals over an undetermined period of time and with time-varying reliabilities and (b) sketched the putative neural implementation of this computation. Lastly, we discuss causal inference as a more general computation toggling between different internal models (e.g., dictating the integration or not of visuo-vestibular cues) and point to theoretical proposals as well as recent findings from cognitive and systems neuroscience that together promise to ultimately elucidate the neural underpinning of this fundamental and ubiquitous computation.

### **Bayesian Observers**

Our brains are locked inside dark and silent skulls. They understand the language of spikes and not that of visual objects and vestibular events. Thus, as Helmholtz (1867) most famously stated, perception is a process of (unconscious) inference. We do not have direct access to the external world, and instead we must make our best guesses based on available sensory evidence and prior knowledge.

## NEURAL INSTANTIATION OF PROBABILISTIC INFERENCE

The central tenet of the Bayesian framework is that the brain represents uncertainty about the environment in the form of probability distributions. In the main text we emphasize probabilistic population codes (PPCs) (Beck et al. 2008, Hou et al. 2019, Ma et al. 2006) as a putative neural implementation of probabilistic inference, given that these have a strong history of accounting for cue combination, and their application to this problem has produced much of their empirical support. Walker et al. (2020) have also recently shown strong support for this framework in demonstrating that trial-to-trial changes in the shape of likelihood functions as derived from a population of V1 neurons can account for fluctuations in behavior.

PPCs suggest that the response of a neural population is proportional to parameters of probability distributions. Given this distributed format (i.e., a spatial code), this framework is thought to represent probabilities almost instantaneously, a great strength. However, this code has also been criticized, most commonly for only being able to represent a restrictive class of distributions and for its prohibitive computational cost for performing exact inference (e.g., Savin & Denève 2015). On the other end of the theoretical spectrum lie sampling models suggesting that the activity of each neuron within a population encodes a different random variable, and that neural activity represents samples drawn from a latent probability distribution (Hoyer & Hyvarinen 2003). This second framework, relying on a temporal code, is slower than PPCs but is said to allow for easier marginalization, and it accounts for trial-to-trial variability in single-unit neural variability (Fiser et al. 2010). Strong empirical support for the sampling framework comes from spontaneous and evoked V1 activity of developing ferrets showing a progressive adaptation of internal models (i.e., spontaneous activity) to the statistic of natural stimuli with age (Berkes et al. 2011). Relatedly, Sohn et al. (2019) recently argued that Bayesian computations depend on the shape (i.e., curvature) of cortical dynamics within a latent low-dimensional space, thus also suggesting that neural activity defines a latent space where Bayesian computations occur.

More broadly, it must be noted that PPCs are a theory of statistical inference that occurs at the population level, while sampling puts the burden on single neurons. As such, these may not be mutually exclusive. In fact, Festa et al. (2021) recently suggested that sampling in V1 might account for Poisson-like variability of single neurons. The outset of PPCs is exactly this form of variability, and thus we may conjecture that certain statistical inferences occur at the single-neuron level and via sampling while others occur at the population level via PPCs and Poisson-like variability, the latter being inherited from the individual neurons and sampling.

More formally, and taking the example of heading discrimination, on a particular trial  $T$ , an observer is presented with a specific heading,  $\theta_T$ . This stimulus is encoded by noisy and stochastic biological elements, and thus our measurements or observations,  $m$ , of the environment may change on a trial-by-trial basis, even for a fixed  $\theta_T$  (Tolhurst et al. 1982). The resultant distribution,  $p(m|\theta_T)$ , is called a measurement distribution and is defined for a fixed stimulus. It is typically considered to be Gaussian and centered on the true  $\theta_T$ . The relation between (a) the different headings that we may experience,  $p(\theta)$ , and (b) the measurement distribution specifies a generative model. This model is an explanation of how sensory data were generated by the world and our sensory systems and is the schema the brain is tasked with inverting to perceive. That is, we make a hypothesis to explain the observed data. The process of translating external stimuli to internal measurements,  $\theta_T \rightarrow m$ , is referred to as neural encoding and has a rich computational history (i.e., efficient coding; Barlow 1961), yet it is unfortunately typically considered separately from decoding processes, such as Bayesian inference (but see Wei & Stocker 2015 for an exception).

In a first step of inference, observers generate a degree of belief (Ramsey 1926) about  $\theta$  based on their measurements. This belief is characterized by likelihood functions,  $L(\theta_T)$ , that effectively take the same shape as  $p(m|\theta_T)$  but in this case are functions of  $\theta_T$  and not  $m$  (see Ma 2019

for details). Next, an observer may incorporate beliefs that are independent from current sensory observations (i.e., at time  $t$ ) and instead based on expectations (for instance, derived from long-term environmental statistics or immediately preceding states, e.g., the heading at  $t - 1$ ). These expectations are the prior distribution,  $p(\theta)$ . In different contexts this distribution is typically considered to be Gaussian, uniform, or broad enough to be negligible. According to the Bayes Rule (Equation 1), by combining the likelihood and prior we can compute posterior distributions—the probability of  $\theta$  given  $m$ .

$$p(\theta|m) \propto L(\theta_T)p(\theta) \quad 1.$$

In a last step, the observer must make a decision or take action. This requires a cost function (i.e., penalties and rewards for hits, misses, etc.) and a mapping from posterior distributions to a concrete action. In the general case where priors and likelihood distributions are Gaussian, the posterior will be so as well, and thus the mean, median, and mode of the posterior specify the same value, the same action. However, posteriors need not be Gaussian, and thus loss functions and action-selection must be carefully considered (Rahnev & Denison 2018). What characterizes an observer as optimal is the use of the correct generative model and computations that minimize cost or maximize reward (see Daptardar et al. 2019 for a description of rational observers as those making optimal decisions within an incorrect generative model).

## Bayes Optimal Cue Fusion

Borrowing from insights in computer vision (Knill & Richards 1996) and within the Bayesian framework detailed above, Ernst & Banks (2002) (among others) specified an ideal observer for multisensory cue combination. They assumed a flat prior, Gaussian likelihoods, and that measurements are conditionally independent across modalities (i.e., signals may covary, but their noise does not). Under these assumptions, it can be shown that the likelihood function of a combined (e.g., visuo-vestibular) condition  $L^{\text{comb}}(\theta)$  is the product of the unisensory likelihoods  $L^{\text{vis}}(\theta) L^{\text{vest}}(\theta)$ , and the maximum-likelihood estimate will be

$$\hat{\theta}_{\text{comb}} = w_{\text{vis}}\hat{\theta}_{\text{vis}} + w_{\text{vest}}\hat{\theta}_{\text{vest}}, \quad 2.$$

with  $\hat{\theta}_{\text{vis}}$  and  $\hat{\theta}_{\text{vest}}$  being the unisensory estimates and  $w_{\text{vis}}$  and  $w_{\text{vest}}$  being weights that are proportional to inverse variances  $\sigma_{\text{vis}}^2$  and  $\sigma_{\text{vest}}^2$ :

$$w_{\text{vis}} = \frac{\frac{1}{\sigma_{\text{vis}}^2}}{\frac{1}{\sigma_{\text{vis}}^2} + \frac{1}{\sigma_{\text{vest}}^2}}, \quad 3.$$

and similarly for  $w_{\text{vest}}$ . The variance of the combined estimate is

$$\sigma_{\text{comb}}^2 = \frac{\sigma_{\text{vis}}^2 \sigma_{\text{vest}}^2}{\sigma_{\text{vis}}^2 + \sigma_{\text{vest}}^2}. \quad 4.$$

Thus, if individuals are combining information across cues, their combined estimate will intuitively fall in between the unisensory estimates, weighted by the relative reliability of each cue. More importantly, given that a weighted average estimate across trials could also emanate from following a given estimate at some times and the other estimate in the remaining trials, the true hallmark of optimal cue combination is a reduction in uncertainty (predicted by Equation 4). Humans have been shown to combine cues optimally or near optimally within senses (Hillis et al. 2004) and across visuo-tactile (Ernst & Banks 2002), audio-visual (Alais & Burr 2004), visuo-proprioceptive (van Beers et al. 1996), and visuo-vestibular (Fetsch et al. 2009, Prsa et al. 2012) pairings, among others.

## Neural Instantiation of Bayes Optimal Cue Fusion

Armed with a principled account of multisensory behavior, researchers' next step was to derive how such a computation could be instantiated algorithmically—what operations and set of rules may neurons follow in accomplishing the computation at hand?

In an influential theoretical contribution, Ma and colleagues (2006) highlighted that neural populations have to represent the reliability associated with environmental cues in order to perform an inference of the type  $p(\mathbf{S}|\mathbf{r})$ , where  $\mathbf{S}$  is the cue and  $\mathbf{r}$  is a vector of neural responses for a given presentation. In analogy to the Bayesian observers described above,  $p(\mathbf{r}|\mathbf{S})$  is proportional to  $p(\mathbf{S}|\mathbf{r})$ , and the former is something we can measure. In fact, we know that cortical neurons tend to show Poisson-like variability (Tolhurst et al. 1982), meaning that their average activity is monotonically related to their variance. Taking this property into account, it can be shown that the posterior distribution  $p(\mathbf{S}|\mathbf{r})$  approximates a Gaussian function, its mean closely corresponds to the peak of population activity, and importantly, its variance is implicitly encoded in the amplitude of the population response, or gain,  $g$ , such that  $Kg = 1/\sigma^2$ , where  $K$  is a constant.

In turn, regarding cue combination and again with the example of visuo-vestibular integration, this PPC (Ma et al. 2006) renders the hypothesis that if unisensory populations have the same number of neurons, identical tuning functions, and independent Poisson-like variability, optimal conservation of information [e.g.,  $I_{\text{comb}} = I_{\text{vis}} + I_{\text{vest}}$  (Clark & Yuille 1990)] equates to a simple sum of neural activities,  $r_{\text{comb}} = r_{\text{vis}} + r_{\text{vest}}$ . Since the unisensory areas are characterized by Poisson-like variability, so will the multisensory, and  $\frac{1}{\sigma_{\text{comb}}^2} = \frac{1}{\sigma_{\text{vis}}^2} + \frac{1}{\sigma_{\text{vest}}^2}$ , which is equivalent to the uncertainty reduction outlined in Equation 3. Many of the assumptions outlined (e.g., equal number of neurons) can be relaxed in more general formulations (e.g.,  $w_{\text{comb}}r_{\text{comb}} = w_{\text{vis}}r_{\text{vis}} + w_{\text{vest}}r_{\text{vest}}$ ), but the important take-home message is that by incorporating the known distribution of single-unit variability, PPCs are able to accomplish a multiplication required at the computational level,  $L^{\text{vis}}(\theta)$   $L^{\text{vest}}(\theta)$ , by simple summation—convergence of unisensory populations onto a multisensory one (see Ma et al. 2006 for mathematical details).

Angelaki, DeAngelis, and colleagues performed a series of experiments to detail the neural code underlying visuo-vestibular integration and to specifically ascertain whether PPCs are indeed biologically implemented. First, Gu et al. (2008) demonstrated that nonhuman primates perform a discrimination task where they are required to indicate their direction of heading relative to straight-head in line with optimal cue combination, their sensitivity during visuo-vestibular conditions improving consistently with theoretical predictions (Ernst & Banks 2002). Second, Fetsch et al. (2009, 2012) showed that these animals also took into account the relative uncertainty between cues in generating estimates when visual and vestibular cues were incongruent. In addition to the behavioral observations, these authors performed single-neuron recordings in MSTd and observed two classes of neurons: those with congruent visual and vestibular tuning functions and those with opposite preferences. Neurometric curves constructed from receiver operating characteristic analysis of spiking activity of congruent cells had visuo-vestibular discrimination thresholds in line with predictions from optimal cue combination (Gu et al. 2008; see Chen et al. 2013 for a similar result in VIP). We return to the opposite cells below.

These behavioral and physiological studies set the stage for questioning whether optimal cue combination in fact occurs in the brain as predicted by PPCs. However, the headings probed in the early reports were fairly restricted and thus did not allow for sketching a neural combination rule—the set of weights  $\mathbf{A}$ , such that  $\mathbf{R}_{\text{comb}} = \mathbf{A}_{\text{vis}}\mathbf{R}_{\text{vis}} + \mathbf{A}_{\text{vest}}\mathbf{R}_{\text{vest}} + \mathbf{C}$ , where  $\mathbf{R}$  is neural responses and  $\mathbf{C}$  is a constant. To remedy this situation, Morgan et al. (2008) recorded from MSTd while presenting nonhuman primates with the full gamut of visual, vestibular, and visuo-vestibular headings—including incongruent presentations. Results demonstrated that a linear combination of

unisensory visual and vestibular responses was indeed well able to predict multisensory responses (i.e., the addition of nonlinear components did not significantly improve fits). However, somewhat surprisingly, weights  $A_{\text{vis}}$  and  $A_{\text{vest}}$  were smaller than 1 (i.e., subadditive as opposed to the additive), and perhaps most vexingly, they varied with changes in cue reliability. This latter observation was at face value incongruent with the framework of PPCs, as this theory in essence suggests that the weighting of likelihood functions by their reliability is accomplished at the unisensory level, where, for example, visual responses are modulated by coherence, and thus Poisson statistics imply that there is no need to update neural weights,  $A$ , with changes in stimulus coherence.

Two subsequent reports proposed why, and how, neural weights might change as a function of visual coherence and hence reinstated PPCs as a putative neural mechanism of optimal cue integration. Fetsch and colleagues (2012) first showed that Poisson statistics do not entirely account for how neural responses in MSTd change with visual motion coherence. Instead, with increasing coherence in visual stimuli there is both a multiplicative scaling of neural responses and a change in baseline firing. Taking these properties into account, the researchers derived the optimal neural weights for visuo-vestibular integration in MSTd and showed a correlation between mathematically derived optimal and measured neural weights (see Hou et al. 2019 for a suggestion that incorporating neural correlations could have strengthened the agreement between PPC theory and empirical observations). Secondly, Ohshiro and colleagues (2011) suggested that both the subadditivity in neural weights (i.e.,  $A < 1$ ) and rapid changes of these weights on a trial-by-trial basis could be accounted for by divisive normalization acting at the stage of multisensory integration. Divisive normalization is a ubiquitous neural computation wherein the output of each neuron is divided by the summed activity of a normalization pool (Carandini & Heeger 1994, 2011). Thus, the strength of the normalization pool depends on unisensory firing rates; hence, as firing rates covary with stimuli coherence, so will the neural weights. In fact, divisive normalization can give rise to a neural combination rule similar to that measured by Morgan et al. (2008) and Fetsch et al. (2012). Further, this property is likely critical for appropriate function of the nervous system as a whole in that it prevents neural saturation—a ceiling effect in firing rates—and hence potentially explain why neural weights in fact need to be subadditive. Lastly, in a beautiful convergence of evidence, divisive normalization at a multisensory layer is not only able to account for population level properties in cortex (Ohshiro et al. 2011) but is equally able to account for properties of individual multisensory neurons in subcortex, such as their supra-additive responses during weak stimuli presentations (inverse effectiveness), or presentations within colocalized receptive fields (spatial principle; see Stein & Stanford 2008 for a review summarizing early work detailing the properties of multisensory neurons in superior colliculus). The divisive normalization conjecture makes a strong and testable prediction: Nonpreferred sensory input from one modality should suppress the response to a preferred input in another modality. Recent recordings have confirmed the presence of this form of cross modal suppression in MSTd and not in MT (Ohshiro et al. 2017).

Broadly, therefore, a multitude of visuo-vestibular phenomena (e.g., vection) and the basic peripheral properties of the visual and vestibular system implied that appropriate self-motion perception requires the integration of visual and vestibular information. Normative approaches to modeling behavior then suggested how these signals ought to be integrated, and landmark theoretical studies bridged the gap between behavioral cue combination and neural integration. Physiological recordings in MSTd then largely confirmed predictions from theory, while iteratively adding caveats—e.g., MSTd responses are further from Poisson-like than initially suggested, and neural weights may vary trial-to-trial with changes in stimuli reliability. These empirical observations lead to the conjecture of a network-level operation that may account for the inconsistencies between theory and empirical observations. And in turn, this circuit property (i.e., divisive

normalization) was able not only to account for population-level responses in cortex but also to incorporate traditional properties of single neurons in subcortex (see Fetsch et al. 2013 and Hou & Gu 2020 for insightful reviews).

### Time and Time-Varying Reliabilities

An important and more recent extension to the study of optimal cue combination is the incorporation of time as a critical variable. Indeed, the publications in the human literature on multisensory integration appear to be divided between those employing estimation tasks and optimal cue combination as a theoretical framework on one side (e.g., Fetsch et al. 2009, Gu et al. 2008) and those using reaction time tasks and race models (Miller 1982, Raab, 1962) or principles derived from early single-unit electrophysiology (Stein & Stanford 2008) on the other. The former have ignored a critical dimension present in all perceptual and decisional processes—time—while the latter have ignored the perceptual sensitivity benefits derived from multisensory integration and have not been able to connect behavior with neurons; nor can they establish whether multisensory inputs are combined optimally.

Drugowitsch et al. (2014) closed the gap between multisensory precision and speed by deriving an extension to the traditional drift diffusion model (DDM). The conventional DDM (Ratcliff & Rouder 1998) is based on particle dynamics accumulating evidence until hitting a decision bound. This model can account well for stereotypical distributions of reaction times, and changes in the speed of evidence accumulation (i.e., drift rate) and/or the initial distance of particles to the decisional boundary can accommodate speed accuracy trade-offs during decision making. Additionally, these diffusion models are known to optimally integrate evidence over time given that the reliability of the evidence is time-invariant (Bogacz et al. 2006). However, in their standard implementation, DDMs are not optimal when the speed of evidence accumulation changes over time (within or across trials), nor are they designed to integrate disparate sources of information. In Drugowitsch and colleagues' (2014) extension, a multisensory DDM's drift rate is determined by a weighted combination of unisensory drift rates, each weighted in proportion to its relative and momentary (i.e., time-evolving) sensitivities.

This version of DDMs is optimal despite time-varying reliability of cues (see Drugowitsch et al. 2014 for mathematical detail). Within the context of a speeded version of the visuo-vestibular heading discrimination task, the multisensory DDM can account for apparent suboptimal behavior as indexed by standard analyses not incorporating time as a factor. It also suggests a near-optimal speed-accuracy trade-off in maximizing reward rate across trials (Drugowitsch et al. 2015). Further, in analogy, this framework specifying accumulation of evidence both across time and across the senses may be able to account not only for apparent suboptimal behavior (Drugowitsch et al. 2014) but also for recent reports of supraoptimal behavior, most common in the rodent literature (Nikbakht et al. 2018, Raposo et al. 2012; but see Shalom & Zaidel 2018 for an alternative explanation). Finally, and perhaps most interestingly from a neural implementation standpoint, the extended DDM suggests that in natural self-motion visual and vestibular signals may each play an outweighed role during different time periods. As alluded to above, vestibular signals are most sensitive to acceleration while visual signals are tuned to velocity, and thus their weight during visuo-vestibular motion may vary accordingly. This conjecture would also suggest that there is no need to integrate vestibular acceleration into a velocity signal, a process that could in principle be costly in terms of signal-to-noise (Bogacz et al. 2006; but see Laurens et al. 2017 for evidence that vestibular acceleration seems to indeed be transformed into velocity estimates as it climbs the neuraxis).

In the most recent physiological recordings attempting to further delineate the neural underpinning of optimal visuo-vestibular integration, Hou and colleagues (2019) took on the challenge of determining whether in fact cue combination is dependent on momentary evidence (e.g., visual velocity and vestibular acceleration) and whether such a code is compatible with PPCs (Ma et al. 2006). These authors presented nonhuman primates with translations of a Gaussian velocity profile, naturally dissociating moments of maximal vestibular information (early and late in the motion profile, due to its encoding of acceleration) versus visual information (peaking with maximal velocity). Single-unit recordings were performed in the lateral intraparietal (LIP) cortex. This area receives anatomical input from MSTd and VIP (Boussaoud et al. 1990), two areas heavily implicated in the coding of self-motion (Chen et al. 2011, 2013; Gu et al. 2006, 2008). However, while a majority of neurons in LIP are in fact tuned to visual motion direction, this selectivity is very broad [ $>120^\circ$  (Fanini & Assad 2009)]. Thus, in keeping with the general thought of LIP as an area reflecting evidence accumulation (but see Huk et al. 2017, Katz et al. 2016, and Zhou & Freedman 2019 for recent controversy), recording in LIP (as opposed to earlier areas) likely allowed Hou et al. (2019) to examine a neural node that is a good candidate for one performing a computation akin to integration in the multisensory DDM (Drugowitsch et al. 2014). Further, recording from LIP implicitly supports the hypothesis that multisensory integration occurs at a decisional stage (see Bizley et al. 2016). Hou and colleagues (2019) demonstrated that LIP indeed harbors heading discrimination choice signals that peak in accordance with vestibular acceleration and visual speed. Moreover, the authors demonstrated that a network performing decisions by summing spikes across time and cues via an invariant linear PPC (Beck et al. 2008) was able to perform optimal multisensory decisions. Finally, a linear approximation of the optimal model showed responses similar to those of LIP, while decreasing its time constant of integration did not. In other words, this report suggests that (a) PPC is the algorithm supporting optimal cue combination even for time-varying reliabilities, (b) this algorithm is housed (at least partially) in LIP, and (c) a defining characteristic of LIP versus its neighbors is its time constant of integration.

Novel path integration studies employing optic flow alone (Lakshminarasimhan et al. 2018, 2020; Noel et al. 2020a, 2021a) or visuo-vestibular signals (Stavropoulos et al. 2020) during protracted timelines ( $\sim 2\text{--}4$  s) will be ideally suited to further examine the circuit motifs sustaining long versus short integration time constants. Initial results within this domain suggest there is no leak in the integration of self-motion information into a position estimate, and instead errors in path integration may be due to initial mis-estimations of velocity (Lakshminarasimhan et al. 2018, Noel et al. 2020a).

## Causal Inference

In addition to the reliability of different sensory signals, the world around us and the objects and events in our surroundings change dynamically over time. The approach of optimal cue combination (Ernst & Banks 2002) outlined above is sometimes referred to as a forced fusion model, given that its main limitation is that it can only consider one alternative; the signals must be combined. However, in the real world there are instances when multiple signals refer to the same source (e.g., auditory and visual signals conveying speech and mouthing of an interlocutor) and thus should be combined, and in other instances these signals relate to different sources (e.g., an unskillful ventriloquist) and should be separated. To appropriately perceive and act in the world, therefore, we must first use the samples we draw from our environment (i.e., observations) to build an internal model specifying the likely causal structure of the environment [building the generative model (**Figure 2**)]. Then, we can use this deduced generative model in perceiving. This process is

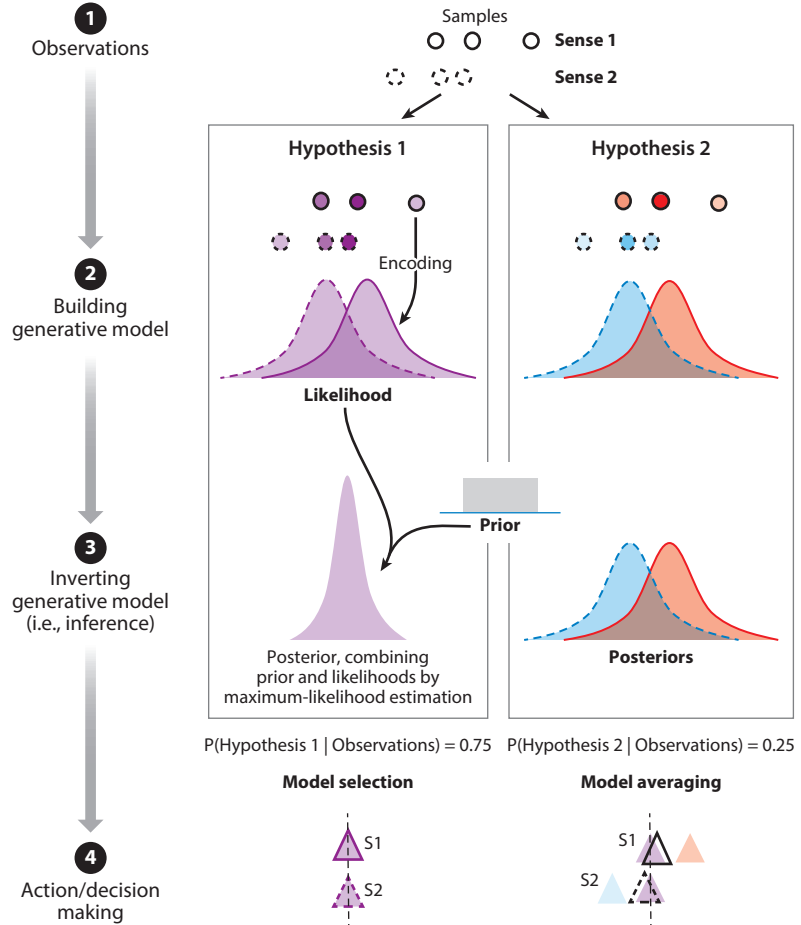
referred to as Bayesian causal inference (Kording et al. 2007) (**Figure 2**) and is again based on the Bayes Rule:

$$p(C|x_{\text{vis}}, x_{\text{vest}}) = \frac{p(x_{\text{vis}}, x_{\text{vest}}|C)p(C)}{p(x_{\text{vis}}, x_{\text{vest}})}, \quad 5.$$

where  $x_{\text{vis}}$  and  $x_{\text{vest}}$  refer to sensory measurements and  $C$  is a categorical variable whose value depends on the state of the world. In an example where visual and vestibular signals index either the same ( $C = 1$ ) or separate causes ( $C = 2$ ),

$$p(C = 1|x_{\text{vis}}, x_{\text{vest}}) = \frac{p(x_{\text{vis}}, x_{\text{vest}}|C = 1)p(C = 1)}{p(x_{\text{vis}}, x_{\text{vest}}|C = 1)p(C = 1) + p(x_{\text{vis}}, x_{\text{vest}}|C = 2)(1 - p(C = 1))}. \quad 6.$$

Solving  $p(x_{\text{vis}}, x_{\text{vest}}|C = 1)$  and  $p(x_{\text{vis}}, x_{\text{vest}}|C = 2)$  allows establishing the likelihood of signals emanating from a single cause,  $p(C = 1|x_{\text{vis}}, x_{\text{vest}})$ , and these have closed-form analytical solutions assuming measurement distributions and priors are Gaussian or uninformative (see Kording et al. 2007 for mathematical detail). In turn, the maximum a posteriori estimate of the different signals  $\hat{\theta}_{\text{vis}}$  and  $\hat{\theta}_{\text{vest}}$  can be computed under either of the hypotheses,  $C = 1$  or  $C = 2$  [inverting the generative model (**Figure 2**)]. Now, exactly how these estimates and the inferred causal structure



(Caption appears on following page)

**Figure 2** (*Figure appears on preceding page*)

Causal inference. (●) Our sensory periphery redundantly samples from the environment (*solid and dashed white circles* represent samples for Sense 1 and Sense 2, respectively). (●) Based on these samples, we build an internal model of the potential causal structure of the world that may have given rise to the observed sensory data (Equation 5). In the first hypothesis illustrated here (Hypothesis 1), the two senses index a common object in the environment (*purple circles; colored circles* indicate a sample under a particular hypothesis). As such, the samples that best reflect the state of affairs is the middle sample for Sense 1, and the rightmost for Sense 2 (darker color indicates the sample falling closer to the mean of the inferred distribution). (●) Since signals from both Sense 1 and Sense 2 are taken to come from the same source, we can integrate this information, together with a prior, according to maximum-likelihood estimation (Equation 2). Conversely, we might hypothesize that the two senses reflect different objects in the external environment (represented by *red and blue*). If this were the case, the central sample, both for Sense 1 and Sense 2 (*darkest red and blue circles*, respectively), would be best aligned with the mean of the inferred distribution (again, a darker color indicates the sample closest to the mean of its distribution). Under this hypothesis, we would not integrate the different signals. (●) Lastly, we can combine (or not) worldviews (i.e., hypotheses) in acting on the external world. Two potential solutions are illustrated here. In a model-selection strategy (*left*), we would commit to the most likely hypothesis. In this example, we assume Hypothesis 1 is most likely, and thus the final estimates (*triangles*) correspond to the estimates from this model (*purple triangles* indicate the mean of the posterior of Hypothesis 1, and *solid and dashed black triangles* indicate the final percept/response). In a model-averaging strategy (*right*), observers can weigh estimates according to the relative certainty of the hypothesis. Again, Hypothesis 1 is most likely in this example. Thus, the final estimates (*solid and dashed white triangles*) will fall somewhere in between the posteriors derived from Hypothesis 1 (*purple*) and Hypothesis 2 (*blue and red*), but they will be closer to the former.

are used in generating actions depends on the loss function, and this one is largely dependent on the specific task. The three decision strategies that are routinely considered are model averaging, probability matching, and model selection (e.g., Cao et al. 2019). Model averaging linearly combines estimates derived from integration and segregation, each weighted by the inferred posterior probability over the respective causal structure. On the other hand, probability matching and model selection commit to a certain worldview for a given trial. The final estimate is sampled from, say,  $\hat{\theta}_{\text{vis}, C=1}$  or  $\hat{\theta}_{\text{vis}, C=2}$ , with a proportion that is either stochastic (probability matching) or fixed (model selection) (**Figure 2**).

Causal inference has been shown to account well for a number of empirical observations, including low-level audio-visual localization (Odegaard et al. 2015), speech perception (Magnotti et al. 2013, Noel et al. 2018b), and heading discrimination (Acerbi et al. 2018; Dokka et al. 2019) among many others (see French & DeAngelis 2020 for a recent review, and below for further examples). However, the precise neural underpinning of this computation is less well established.

To tackle this gap in our knowledge, human neuroimaging studies based on functional magnetic resonance imaging (Rohe & Noppeney 2015, 2016) or time-resolved M/EEG (Aller & Noppeney 2019, Cao et al. 2019, Rohe et al. 2019) are starting to delineate the general principles putatively guiding the neural implementation of causal inference. By and large these reports all agree in describing causal inference as a hierarchical process where early sensory areas [e.g., V1 or A1 (Rohe & Noppeney 2015)] and early neural latencies [e.g., <100 ms (Aller & Noppeney 2019)] encode their preferred sensory modality independently. Intermediate areas (e.g., posterior parietal cortex) and latencies (e.g., <250 ms) show patterns most consistent with forced fusion (Ernst & Banks 2002). Finally, more anterior regions [e.g., anterior parietal cortex (Rohe & Noppeney 2015)] and later neural latencies (e.g., >250 ms) flexibly vary their response patterns in accordance with causal inference. An existing discrepancy regards whether groups emphasize anterior aspects of the parietal cortex (Rohe & Noppeney 2015) or the inferior frontal lobe (Cao et al. 2019) as the primary seat of causal inference.

Broadly, these neuroimaging studies are conceptually consistent with initial efforts to implement causal inference in biologically plausible neural networks. Early work in this area suggested

that a decentralized and interconnected network (e.g., MSTd and VIP) receiving input from pools encoding unisensory stimuli (e.g., MT and PIVC, respectively) could perform optimal cue combination (Zhang et al. 2016). This type of redundant encoding, not only of stimuli but also across neural areas, is robust to local failure (versus, e.g., postulating LIP as the sole region of multi-sensory integration) and seemingly consistent with the observation that while disrupting one area may alter unisensory encoding, optimal cue combination is preserved (see Hou & Gu 2020 for a review). More recently, this architecture has been updated to include known properties of areas computing visuo-vestibular heading. That is, in addition to cells with overlapping visual and vestibular tuning functions (congruent cells), there is a large fraction of neurons showing opposite tuning functions [offset by  $\sim 180^\circ$ ; opposite cells (Gu et al. 2008)]. Opposite cells have been postulated to be involved in (a) dissociating object motion during self-motion (e.g., Sasaki et al. 2017, 2019; see also Sasaki et al. 2020) [and recent neural network models suggest they may more generally compute Bayes factors (Zhang et al. 2020; ratio between a segregation and integration model of the world)] and (b) retaining access to unisensory likelihoods even after fusion (Zhang et al. 2019; also see Hillis et al. 2002).

Ultimately, the precise detailing of the neural implementation of Bayesian causal inference will depend on invasive neurophysiology, and thus on the development of behavioral paradigms capable of indexing causal inference in animal models. Along this line, Dokka and colleagues (2019) recently demonstrated that nonhuman primates perform causal inference in determining heading direction in the presence of independent object motion (i.e., object motion must be parsed from optic flow caused by self-location for appropriate heading perception). Mohl and colleagues (2020) similarly showed that both humans and rhesus monkeys make either a single or multiple saccades to audio-visual targets depending on their disparity and in line with causal inference. Interestingly, however, while human behavior was best explained by model averaging, nonhuman primate behavior was most consistent with model selection. Whether this latter effect is a true difference between humans and nonhuman primates, or whether it is a corollary of the fact that the monkeys were trained on the specific task—and the fact that during training animals are rewarded for committing to a single (and correct) worldview—will be an interesting area for future study (see Noel et al. 2021a for an example experimental ecosystem that should allow the study of causal inference without explicit training, and thus without putatively shaping task strategies).

Lastly, Fang and colleagues (2019) had nonhuman primates reach toward a target during different levels of visuo-proprioceptive disparities (i.e., real hand position versus visual rendering of a dummy hand). Results suggested no bias during congruent visuo-proprioceptive presentations, and a saturating level of reaching end-point error as the visuo-proprioceptive conflict grew. Moreover, these researchers recorded single units in the premotor cortex, and neural activity in this area was similarly modulated by visuo-proprioceptive conflict. Overall, therefore, they showed behavior and neural activity consistent with causal inference. Further, these results imply not only that visuo-vestibular self-motion perception may be rooted in causal inference—the example par excellence in the study of cue combination and probabilistic coding (Dokka et al. 2019; Fetsch et al. 2009, 2012, 2013; Gu et al. 2006, 2008; Hou et al. 2019; Ma et al. 2006)—but also that aspects more personal to the self, such as body ownership, may be rooted in this computation. Below we further explore the “self” in self-motion.

## SELF-LOCATION AS AN INITIAL CONDITION

As described so far, successful navigation via path integration depends on both the visual and vestibular sense and on the integration of these to generate accurate and precise self-motion and heading estimates. In turn, it is thought that the continual integration of self-motion velocity

estimates generates a dynamic sense of self-location (although this process is generally less studied, particularly within a computational framework; see Lakshminarasimhan et al. 2018 and Noel et al. 2020a for recent exceptions). These processes are routinely considered to be central in the study of spatial navigation. However, there is another critical condition that is seldom considered within the spatial navigation literature—an initial condition. Our initial sense of self-location must be correct to enable successful navigation.

Note, where “I” am and where my body is are typically one and the same. But they need not be, as demonstrated by neurological phenomena such as heautoscopy, autoscopic hallucinations, and out-of-body experiences (see Blanke & Metzinger 2009). Static (i.e., prior to movement) and egocentric self-location is typically studied within the broader study of bodily self-consciousness (Blanke 2012) and in conjunction with the subjective experience of body ownership and first-person perspective of the environment (Blanke & Metzinger 2009). [The study of the location of the body is also widely considered in the rodent literature, but mostly from an allocentric encoding point of view (see Barry & Burgess 2014 for a review), and the dissociation between body and self-position is difficult in rodents.] Philosophically, it has been argued that these three together—a sense of being encapsulated within a body that belongs to “me” (body ownership), that is located at a specific location within the external environment (self-location), and from where “I” perceive (first-person perspective)—constitute the minimal requirement for a pre-reflective phenomenal selfhood (Blanke & Metzinger 2009).

Empirically, this area of investigation was jump-started by a seminal contribution from Botvinick & Cohen (1998), who demonstrated that by providing touch on participants’ real hand while showing touch on a dummy hand, they could elicit ownership over a rubber hand (i.e., the rubber-hand illusion). Further, when subjects were asked to close their eyes and indicate the location of their real hand, they were systematically biased toward the rubber hand (i.e., they experienced proprioceptive drift). Over the following 20 years a number of similar illusions have been developed [e.g., with face, leg, tongue, and even tail in rodents (Wada et al. 2016, 2019)], and most importantly, the computational and neural correlates of the rubber-hand illusion are being established. Interestingly, recent models have casted the process of limb ownership as a process of Bayesian causal inference (Samad et al. 2015) and have postulated that neural networks dedicated to encoding the space near our bodies (see below) act as a coupling prior between our body and what is near us (Noel et al. 2018a). As such, the computational principles (e.g., Bayesian observer with particular priors and performing causal inference) underlying inferences of the world around us and of ourselves within it may largely overlap. The recent neurophysiology recordings from Fang and colleagues (2019) equally support this speculation by demonstrating that reaches during visuo-proprioceptive conflicts were in line with causal inference and that firing patterns in the premotor cortex reflected this computation.

Now, empirical results (Rohde et al. 2011) have shown that the subjective sense of embodiment over a limb and the sense of where it is located in external space do not necessarily covary. And more importantly, while studies derived from the rubber-hand illusion are interesting in and of themselves, a change in the subjective location of one’s hand is still described from an unmoved egocentric location and perspective. That is, it does not involve a manipulation of our reference frame as a whole, a global translation in space. To tackle this more general question—one that ought to impact the initial conditions during self-motion guided navigation—Blanke and colleagues as well as Ehrsson and colleagues devised a manipulation similar to the rubber-hand illusion but applied to the whole body. These researchers administered touch on either the back (Lenggenhager et al. 2007) or chest (Ehrsson 2007) of participants who viewed synchronous (or asynchronous in the case of controls) touch being applied far from their location (i.e., ~2 m in front of them). In both studies participants reported subjective experiences somewhat akin to

out-of-body experiences (Blanke et al. 2004, De Ridder et al. 2007). Further, in Lenggenhager and colleagues' (2007) protocol, subjects were blindfolded and moved backward from their original location. When asked to return to their initial spatial location via path integration, they overshooted their target, as if returning to a location in-between their initial physical location and that of the avatar they felt body ownership over. That is, a visuo-tactile manipulation was able to induce a subjective sense of embodiment over a virtual avatar and to perturb the subjective sense of self-location.

To the best of our knowledge, single-unit recordings during full-body illusions such as those described above have not been performed. This would be particularly interesting, not only for the full-body (versus body-part) ownership piece but more so for the corollary that these illusions have on what have been denominated the spatial aspects of bodily self-consciousness: self-location and first-person perspective (Blanke 2012). In this vein, there is a well-established neural circuit that largely overlaps with that for optic flow and self-motion processing that is widely considered to play a fundamental role in bodily self-consciousness generally, and in its spatial aspects in particular. Fang et al. (2019) recorded from ventral premotor and found correlates of arm-reaching errors. Approximately 20 years earlier, Graziano et al. (2000) recorded single-unit activity from parietal area 5 during a rubber-hand illusion and found that the activity of these neurons was influenced by the location of the rubber hand after synchronous but not asynchronous (control) visuo-tactile stroking. Both these reports concern body-part (i.e., hand) ownership and not self-location. Remarkably, however, these areas house neurons encoding for peri-personal space (PPS), and there seems to be a strong association between PPS and self-location.

PPS is the space immediately adjacent to and surrounding one's body (Serino 2019). This space is encoded by a frontoparietal network composed of multisensory neurons in ventral premotor cortex (areas F4 and F5; Fogassi et al. 1996), VIP (Colby et al. 1993), and 7b (Hyvärinen 1981), among other areas (see Cléry et al. 2015b for a recent and extensive review). These neurons respond both to touch on the body and to visual or auditory stimuli when these are presented near, but not far, from one's body. That is, they map the body and the space near it (~30 cm in depth, but this is body-part specific and highly heterogeneous). The receptive fields of these neurons are anchored to the body, in that visual responses are largely independent of gaze position (particularly true in premotor areas) and instead follow the movement of specific body parts or the body as a whole (Graziano et al. 1997). These areas receive projections from earlier motion processing regions such as MSTd, and as a consequence it is no surprise that they are velocity (Fogassi et al. 1996, Noel et al. 2018c) and motion-direction (Duhamel et al. 1998) selective (particularly sensitive to looming stimuli). Similarly, both the premotor areas and VIP are activated by large-field optic-flow stimulation and by vestibular input (Chen et al. 2011). Finally, the premotor neurons in this network seem to preferentially respond during voluntary as opposed to passive head rotation (Graziano et al. 1997). As a whole, therefore, there is a spatial code that specifically maps the body and the space near it (and seems involved in body ownership; Graziano et al. 2000, Fang et al. 2019), and this code is largely overlapping and interdependent with the areas highlighted earlier as encoding self-motion and heading perception (e.g., optic flow and vestibular translation responses, differentiating between active and passive movement).

Psychophysical methods have been developed to study PPS in humans, and many of these rely on indexing tactile detection facilitation when exteroceptive sensory signals (audition or vision) are presented near as opposed to far from the body (Serino et al. 2015, 2018). Researchers have used these methods to replicate in humans many of the earlier findings from the monkey electrophysiology literature. In addition, these methods have advanced our understanding of PPS and self-location in two aspects. First, Noel et al. (2015) behaviorally mapped peri-trunk space encoding in the front and backspace during a full-body illusion. As expected, participants reported

feeling ownership over a virtual avatar placed in front of them, and more importantly, their PPS shrink in the back while it expanded in the front—as if translating forward to encode not the location of their physical body but their subjective self-location. This finding is similar to observations of neural responses during the rubber-hand illusion (Graziano et al. 2000) and has been replicated while rendering subliminal both the stimuli eliciting the full-body illusion and the stimuli used for mapping PPS (Salomon et al. 2017). Second, a plethora of results have highlighted the incredible plasticity of PPS (Noel et al. 2020b), remapping due to personality traits, and the perceived danger of our environment (e.g., Sambo & Iannetti 2013), our social context (e.g., Teneggi et al. 2013, Noel et al. 2021b), and the state space of potential actions (see Bufacchi & Iannetti 2018, Serino 2019 for reviews). Given these observations, the general agreement is that PPS serves as an interface between self and environment, is involved in defensive behaviors (see Graziano & Cooke 2006), and likely computes time-to-contact or impact prediction (Cléry et al. 2015a).

The latest interpretation of PPS as involved in impact prediction may be colored by the fact that PPS is most sensitive to looming stimuli and often studied in static individuals. In a more active setting, however, we would attribute cause to the agent and not to the external environment, and thus we may rephrase this interpretation as PPS predicting the future location of the body (and not the future location of objects in the environment). In fact, PPS remapping has been shown to anticipate arm movement (Brozzoli et al. 2010) and the PPS has been shown to enlarge during full-body actions, such as walking (Noel et al. 2014). This emphasis on PPS as (*a*) encoding subjective self-location and (*b*) anticipating future self-locations may be particularly fruitful in embedding the study of the bodily self within the study of self-motion, and conversely, in furthering our understanding of path integration. That is, incoming sensory evidence is by definition egocentric, and the parietal cortex seems outfitted to process this information: from edge detection to motion detection to a multisensory estimate of self-motion. However, eventually this egocentric information must converge with the spatial codes of the hippocampal formation (e.g., grid and place cells). Thus, just as clear spatial codes exist in the limbic system (e.g., place, grid, border, and speed cells), it is useful to define and identify spatial codes that exist in the parietal cortex. In PPS, we have an egocentric encoding of self-location and future potential locations (see Moon et al. 2020 for recent evidence suggesting that bodily self-consciousness impacts the tuning of spatial codes in the hippocampal formation). Relatedly, reinforcement learning models have emphasized that codes that represent future relations may be particularly useful in navigating state spaces (Dayan 1993), and within this framework some (Behrens et al. 2018) have reinterpreted place cells as encoding an animal's best estimate of where it will be in the immediate future, one step ahead, as opposed to its current location. Arguably, this desideratum is accomplished in parietal cortex by the PPS network. While subjective self-location may be encoded by a population of place cells (Robinson et al. 2020), it may be encoded in individual PPS neurons.

A last aspect worth briefly mentioning related to the study of self-location is that of first-person perspective. This can broadly be defined as one's outlook on the environment, an outlook that is directed at external components of the environment (see Blanke & Metzinger 2009 for more detail). Most often one navigates in their heading direction, and thus first-person perspective is thought to be an important component of self-location (but autoscopic hallucinations and out-of-body experiences are two neurological conditions defined by a differential relationship between self-location and first-person perspective; Blanke & Metzinger 2009). Importantly, however, first-person perspective is not exclusively defined by one's visual viewpoint. To demonstrate this, Ionta and colleagues (2011) had participants experience a full-body illusion while lying in a supine position. Subjects viewed an avatar in virtual reality that provided conflicting information; while gravity on the participant's real body suggested a vector pointing downward, the visual image suggested that gravity was pointing upward for the seen body. During the synchronous visuo-tactile

condition, participants reported feeling ownership over the virtual avatar. Most interestingly, approximately half of the subjects perceived themselves to be lying under the seen avatar, and thus during the illusion they perceived themselves as moving upward. The other half of the subjects were more influenced by observed rather than felt gravity, and thus in seeing the back of an avatar in front of them, they felt as if they were viewing this subject from above. During the illusory condition, they felt their self-location to be closer to the ground than in the asynchronous control condition (Ionta et al. 2011). Together, these data show that subjective self-location can generally be distorted by visuo-tactile stimulation, and further that experienced direction of first-person perspective depends on a balance between visual and vestibular cues, and this outlook may affect the perceived direction of self-motion.

## OUTLOOK AND CONCLUDING REMARKS

Admittedly, our review on the state of knowledge regarding the neural underpinning and computation of self-motion is broad in scope. Importantly, we find this to be an imperative toward building true knowledge and consider that the ability to leverage implementation, algorithmic, and computational (maybe even philosophical!) insights to reciprocally inform one another is a true asset—maybe even the envy of other fields of study.

We have detailed the known cortical circuit involved in visual optic-flow processing as well as the subcortical and cortical networks involved in vestibular processing. Perhaps more importantly, we have highlighted that visuo-vestibular integration is a necessity for accurate and precise self-motion-guided navigation. Gratifyingly, studying how these senses are combined for the purpose of self-motion estimation has allowed more general sketching of the common principles underlying cue combination as a whole, and hopefully it has informed the study of probabilistic coding.

Of course, however, for as much as we have learned, there is so much more we do not yet understand. As underlined in previous sections, the exact roles of different elements in the neural circuitry are not yet clear. Similarly, there seems to be an inherent tension between information converging in certain areas for or prior to integration (e.g., LIP) versus more distributed schemes. The neural underpinning of causal inference, a general computation for attributing likely causes to observations—particularly relevant for path integration during independent object motion, but applicable to all sorts of problems—is not understood. Further, our understanding of basic elements such as how self-motion velocity estimates get accumulated over protracted periods of time or how initial conditions are set (i.e., self-location) are only in their infancy and not always considered. In fact, a recent psychophysical study in humans has suggested that only optic flow with time-varying velocity (i.e., evolving sequence of flow) is informative vis-à-vis heading direction (Burlingham & Heeger 2020). This example highlights that we do not yet quite understand even which particular elements of visual signals guide self-motion. Thus, the challenges moving forward are numerous, and overcoming them will be important in furthering our understanding of brain function. The next decades should see major advances, and we couldn't be more excited to go along for the ride.

## DISCLOSURE STATEMENT

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