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From Multisensory Integration to Multisensory Decision-Making

Qihao Zheng and Yong Gu

Abstract

Organisms live in a dynamic environment in which sensory information from multiple sources is ever changing. A conceptually complex task for the organisms is to accumulate evidence across sensory modalities and over time, a process known as multisensory decision-making. This is a new concept, in terms of that previous researches have been largely conducted in parallel disciplines. That is, much efforts have been put either in sensory integration across modalities using activity summed over a duration of time, or in decision-making with only one sensory modality that evolves over time. Recently, a few studies with neurophysiological measurements emerge to study how different sensory modality information is processed, accumulated, and integrated over time in decision-related areas such as the parietal or frontal lobes in mammals. In this review, we summarize and comment on these studies that combine the long-existed two parallel fields of multisensory integration and decision-making. We show how the new findings provide insight into our understanding about neural mechanisms mediating multisensory information processing in a more complete way.

Keywords

Multisensory integration · Decision-making · Vestibular · Optic flow

Animals live in a sensory world where they are exposed to different types of information from the surrounding environment, as well as from oneself. However, noise is always accompanied with information, more or less, causing uncertainties when animals detect or discriminate signals. The brain has evolved two strategies to overcome the uncertainty embedded in the sensory channels. One is to reduce the uncertainty of individual modalities by integrating sensory inputs from different modalities, and the other is to reduce the interference of transient noise by integrating signals over some time. The process of information integration across modalities is the so-called multisensory integration (Stein et al. 2020; Hou and Gu 2020; Chandrasekaran 2017; Ursino et al. 2014; Seilheimer et al. 2014; Fetsch et al. 2013; Angelaki et al. 2009; Stein and Stanford 2008), whereas the process of information integration over time is the so-called decision-making, or more specifically, perceptual

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decision-making (Najafi and Churchland 2018; Hanks and Summerfield 2017; Raposo 2016; Summerfield and de Lange 2014; Shadlen and Kiani 2013; Gold and Shadlen 2007). The combination of these two processes is thus defined as multisensory decision-making (Bizley et al. 2016; Raposo 2016).

The two fields of multisensory integration and decision-making have developed in parallel for a long time in the past. In particular, the field of multisensory integration mainly focuses on comparison of neuronal activity across different stimulus conditions in polysensory cortices (Smith et al. 2017; Gu et al. 2016; Yau et al. 2015; Fetsch et al. 2013; Chen et al. 2008, 2011a, b, c, 2013; Angelaki et al. 2011; Gu et al. 2006, 2008). By contrast, the field of perceptual decision-making commonly uses a single sensory modality (e.g., visual for most of the time) paradigm to study accumulation of sensory evidence over a temporal domain in sensory-motor transformation cortices such as the posterior parietal cortex or the prefrontal cortex (Li et al. 2016; Churchland et al. 2011; Kravitz et al. 2011; Bisley and Goldberg 2010; Churchland et al. 2008; Gold and Shadlen 2007; Roitman and Shadlen 2002; Shadlen and Newsome 1996, 2001). Recently, the two fields start to fuse, developing the cross-cutting field of "multisensory decision-making" (Coen et al. 2021; Hou et al. 2019; Nikbakht et al. 2018; Raposo et al. 2012, 2014; Sheppard et al. 2013).

This chapter reviews recent research advances in the field of multisensory decision-making at the behavioral, neurophysiological, and computational modeling levels and provides an outlook on the future of this field.

2.1 Computational Modeling

The computational essence of multisensory decision-making can be understood with the help of normative models (Fetsch et al. 2013) that has been used in multisensory integration and perceptual decision-making separately.

Firstly, multisensory integration is considered as a Bayesian inference process (Ma 2019). Assuming that the probability of occurrence of stimulus s is $P(s)$, an observer makes two estimates of the same stimulus s using both senses, denoted as r_1 and r_2, respectively. Due to sensory uncertainty, the observation of r_1 and r_2 in the case of stimulus s is also a probabilistic event, denoted as $P(r_1, r_2 | s)$. Now, how should the observer infer the value of stimulus s based on senses r_1 and r_2? Mathematically, this can be solved by maximizing the posterior probability: $P(s | r_1, r_2)$. The posterior could be expanded by Bayesian formula as $P(r_1, r_2 | s)P(s)/P(r_1, r_2)$, where $P(r_1, r_2 | s)$ is likelihood function and $P(s)$ is the prior. Since our ultimate goal is to solve for s, and $P(r_1, r_2)$ does not contain s, this term can be ignored. Thus, the formula can be further written as $P(s | r_1, r_2) \propto P(r_1, r_2 | s)P(s)$. If it is assumed that r_1 and r_2 are conditionally independent with respect to s and s is uniformly distributed, then the above equation is further simplified as: $P(s | r_1, r_2) \propto P(r_1 | s)P(r_2 | s)$. Under the uniform prior, the maximum posterior probability method is also known as the maximum likelihood estimation because the posterior probability has been reduced to a likelihood function. As long as we take the s that maximizes this probability, then we have completed the solution and can prove that this approach is optimal. Such an observer is also known as an "ideal observer" (Landy et al. 2011; Doya et al. 2006; Knill and Pouget 2004; Knill and Richards 1996).

If we further assume that the likelihood functions $P(r_1 | s)$ and $P(r_2 | s)$ follow a Gaussian distribution, then using the maximum likelihood method, we can obtain that s inferred from a single cue r_i also follows a Gaussian distribution, which can be noted as a Gaussian distribution with mean μ_i and variance σ_i^2 $i = 1, 2$, respectively. And the s inferred from the two modality cues also follow a Gaussian distribution, denoted as a Gaussian distribution with mean μ_{comb} and variance σ_{comb}^2, with the following relations (Ursino et al. 2014; Fetsch et al. 2013; Angelaki et al. 2009; Ernst and Banks 2002):

$$\mu_{\text{comb}} = \frac{\sigma_2^2}{\sigma_1^2 + \sigma_2^2}\mu_1 + \frac{\sigma_1^2}{\sigma_1^2 + \sigma_2^2}\mu_2$$

$$\frac{1}{\sigma_{\text{comb}}^2} = \frac{1}{\sigma_1^2} + \frac{1}{\sigma_2^2}$$

To date a large number of behavioral experiments have demonstrated that integration between different species and modalities approximately satisfies Bayesian optimal integration theory. For example:

1. Visual-tactile integration in humans (Knill and Saunders 2003; Ernst and Banks 2002).
2. Visual-auditory integration in humans (Sheppard et al. 2013; Raposo et al. 2012; Alais and Burr 2004; Battaglia et al. 2003).
3. Visual-proprioceptive integration in humans (Sober and Sabes 2005; van Beers et al. 1999).
4. Visual-vestibular integration in macaques (Zheng et al. 2021; Hou et al. 2019; Chen et al. 2013; Fetsch et al. 2011; Gu et al. 2008).
5. Integration of visual and electrical stimulation-evoked proprioception in macaques (Dadarlat et al. 2015).
6. Visual-auditory integration in rats (Raposo et al. 2012, 2014; Sheppard et al. 2013).

These studies suggest that multisensory integration mechanisms may be conserved across species and modality combinations.

Bayesian integration model explains the behavior of multisensory integration very well in many cases; however, this model ignores an important factor—time. Bayesian models do not consider the time course of multisensory integration (Drugowitsch and Pouget 2012) and only predict two time-independent parameters, psychophysical thresholds and biases. In fact, however, the stimuli and the corresponding reliability may vary over time in the experiment, and parameters like reaction-time is an important performance indicator in many situations.

In perceptual decision models, time is an essential and critical parameter. The process of making a decision based on sensory input is considered as the temporal integration of the decision variable with noisy sensory input and finally reaching a decision bound to make a decision. This decision model is called the drift-diffusion model (DDM) (Ratcliff and McKoon 2008; Ratcliff and Smith 2004; Ratcliff and Rouder 1998; Ratcliff 1978). For example, in a typical random-dots direction discrimination task, subjects observe stimulus whose intensity is modulated by a parameter called coherence, which is the proportion of dots that represent consistent motion direction. Higher the coherence, easier for subjects to discriminate motion directions. In addition, while observing the stimuli, subjects were disturbed by Gaussian noise with mean 0 and variance σ^2. According to the DDM, the slope of the accumulation curve is equal to the coherence. This accumulation process is called “drift.” Due to the noise, the accumulated signal is disturbed by the noise, and the disturbance causes the fluctuation of the decision variable, which is called “diffusion.” The DDM describes the decision process and explains decision-related phenomena. DDM has been used successfully to explain the ramping activities of neurons in LIP (Roitman and Shadlen 2002; Shadlen and Newsome 1996, 2001), FEF (Kim and Shadlen 1999), SC (Horwitz and Newsome 1999, 2001), and so forth, suggesting that these brain areas may encode decision variables.

Since Bayesian integration model describes integration across modalities and drift-diffusion model describes integration across time, can these two models be combined and used to describe multisensory decision-making? The answer is yes. In fact, Drugowitsch and colleagues used the combination of these two models (i.e., extended DDM) to explain subjects’ speed-accuracy tradeoff behavior in a reaction-time version of heading discrimination task based on visual and vestibular cues (Drugowitsch et al. 2014). In particular, velocity profile of the motion was set as a Gaussian profile. The transient evidence of vestibular input was assumed to be generated by acceleration $a(t)$, whereas the transient evidence of visual input was generated by velocity cues $v(t)$. Visual and vestibular cues contain spatially consistent heading information, and both are presented synchronously in time. Therefore, both visual and vestibular cues are time-varying signals, and thus their reliability also vary over time. Let $X_{\text{vis}}(t)$ be the cumulative evidence of visual cues (optic flow) and $X_{\text{ves}}(t)$ be the cumulative evidence of vestibular cues, then $X_{\mathrm{vis}}(t)$ and $X_{\mathrm{ves}}(t)$ are the time integrals of the noisy velocity and acceleration signals at $[0, t]$, respectively. Let k_{vis} be a constant representing the intensity of the visual signal and k_{ves} be a constant representing the intensity of the vestibular signal, the joint signal $X_{\mathrm{comb}}(t)$ is the sum of these two signals weighted by the corresponding reliability.

$$X_{\mathrm{comb}}(t) = \frac{k_{\mathrm{vis}}}{\sqrt{k_{\mathrm{vis}}^2 + k_{\mathrm{ves}}^2}} X_{\mathrm{vis}}(t) + \frac{k_{\mathrm{ves}}}{\sqrt{k_{\mathrm{vis}}^2 + k_{\mathrm{ves}}^2}} X_{\mathrm{ves}}(t)$$

In short, the extended DDM does the time integration of the sensory signals weighted by the time reliability, and then calculate the weighted sum of the two signals according to the modal reliability. This extended DDM is so far, to our knowledge, the only normative model for optimal multisensory decision-making (Drugowitsch et al. 2014).

2.2 Physiological Studies

2.2.1 Brain Regions Associated with Multisensory Decision-Making

Physiological studies of multisensory integration began with Barry Stein and colleagues in anesthetized cats in the 1980s. The researchers identified neurons in the superior colliculus (SC), a structure located in the midbrain that processes multiple types of information such as visual and auditory. Three empirical principles were proposed (Stein and Stanford 2008; Stein and Meredith 1993), including the temporal principle (Meredith et al. 1987), the spatial principle (Meredith and Stein 1986a), and the principle of inverse effectiveness (Meredith and Stein 1986b).

In addition to SC, studies on awake macaques using visual (e.g., optic flow) and vestibular stimuli to study how multisensory heading perception is mediated by neurons in the cerebral cortex. A series of multisensory brain regions have thus been identified (Fig. 2.1), including the dorsal medial superior temporal area (MSTd) (Maciokas and Britten 2010; Morgan et al. 2008; Takahashi et al. 2007; Gu et al. 2006; Page and Duffy 2003; Bremmer et al. 1999; Duffy 1998), the ventral intraparietal area (VIP) (Chen et al. 2011a, b, c, 2013; Zhang and Britten 2004; Zhang et al. 2004; Bremmer et al. 2002a, b; Schlack et al. 2002), the visual posterior sylvian area (VPS) (Chen et al. 2011b), the smooth eye movement area of the frontal eye field (FEFsem) (Yang and Gu 2017; Gu et al. 2016), and area 7a (Avila et al. 2019). Among all these, MSTd has received the highest attention. Numerous studies investigated basic integration properties in this area, as well as how they are linked to perception when the animals are trained to perform behavioral discrimination task at the same time (see following sections for more detail).

In addition to visuo-vestibular, other multisensory signals have been found including tactile and visual signals in mice' dorsal striatum (Reig and Silberberg 2014), or in macaques' VIP (Avillac et al. 2007). These regions are essentially part of the association cortex, but there is evidence that the neural basis of multisensory integration extends into early sensory processing (Ghazanfar and Schroeder 2006). For example, primary auditory cortex (A1) in macaques encodes not only auditory but also visual (Ghazanfar et al. 2005) and tactile signals (Lemus et al. 2010). Primary somatosensory cortex (S1) in macaques encodes not only tactile but also proprioceptive (Kim et al. 2015) and auditory (Lemus et al. 2010) sense.

In parallel, many brain regions are related to perceptual decision-making, particularly under the oculomotor paradigm such as the lateral intraparietal area (Roitman and Shadlen 2002; Shadlen and Newsome 1996, 2001), the frontal eye field (FEF) (Kim and Shadlen 1999), the superior colliculus (SC) (Horwitz and Newsome 1999, 2001), and the caudate (CD) in the basal ganglia (Ding and Gold 2010). In these sensory-motor transformation areas, ramping activities have been found during delay period and its rising slope depends on task difficulty and therefore

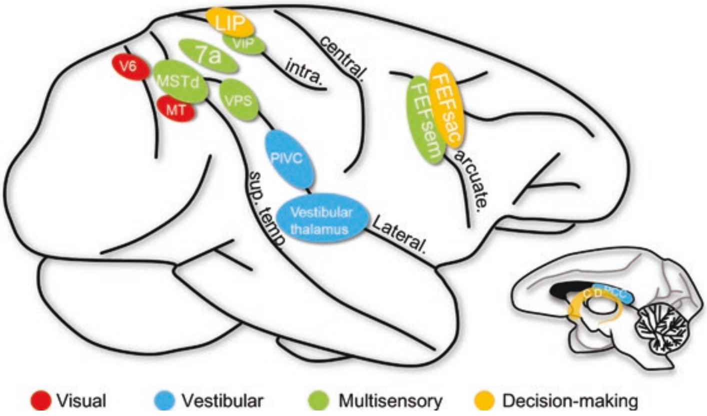

Fig. 2.1 Self-motion perception-related brain areas in macaque. Red: sensory area encoding visual information only, blue: sensory area encoding vestibular information only, green: sensory area encoding both visual and vestibular information, yellow: decision-related areas. *MT* middle temporal cortex, *V6* sixth visual area, *PIVC* parieto-insular vestibular cortex, *PCC* posterior cingulate cortex, *MSTd* dorsal medial superior temporal area, *VIP* ventral intraparietal area, *VPS* visual posterior sylvian area, *FEFsem* smooth eye movement/pursuit area of the frontal eye field, *7a* Brodmann area 7a, *LIP* lateral intraparietal area, *FEFsac* saccade area of the frontal eye field, *CD* caudate

cannot be interpreted as a pure sensory signal or a pure motor signal (Shadlen and Newsome 1996). Instead, evidence from manipulation experiments such as electrical microstimulation (Hanks et al. 2006) and pulse perturbation (Huk and Shadlen 2005) suggest that this signal may reflect a process of accumulation of sensory information that favors one of the decisions over the other choices, i.e., decision variables, and thus these brain areas are considered to be decision-related.

Recently, a few studies combining the two fields, that is, multisensory integration in decision-making-related areas, begin to emerge. These studies have been conducted in posterior parietal cortex (PPC) in rats (Nikbakht et al. 2018; Raposo 2016; Raposo et al. 2014), LIP (Hou et al. 2019) and FEF (Zheng et al. 2021) in macaques, and the secondary motor area (MO) in mice (Coen et al. 2021). Although there are not many of them, these studies already make interesting and valuable insights into how cross-modal information is accumulated, and integrated in sensory-motor transformation areas, reflecting how multisensory signals are propagated and decoded along the sensory channels.

2.2.2 Modality and Category-Free Coding

In sensory cortex, it is frequently seen that single neurons in the same brain region tend to be homogeneous by exhibiting clear tuning that can be described by some descriptive models like basis functions. For example, in MSTd, many neurons have visual or vestibular heading tuning (Fetsch et al. 2007; Gu et al. 2006; Duffy 1998) that can be modeled by a cosine or wrapped Gaussian function. Interestingly, many neurons coded a labeled-line of left and rightward heading preference (Gu et al. 2006), leading to the strongest discriminability of headings varied in fine steps around straightforward (Gu et al. 2010). Furthermore, temporal dynamics of MSTd neurons typically show single-peaked peristimulus time histogram (PSTH), indicating a velocity quantity (Gu 2018; Laurens et al. 2017; Chen et al. 2011a; Gu et al. 2008).

The spatial relation between the two sensory modality is also clear in most of cases on individual neurons. Difference in heading preference between visual and vestibular for multisensory MSTd neurons shows a bimodal pattern (Gu et al. 2006, 2008; Morgan et al. 2008; Takahashi et al. 2007), such that the majority of cells are either “congruent” or “conflict.” The congruent and conflict patterns are so clear that it is straightforward to speculate that two categories may execute different functions. Specifically, congruent cells may facilitate multisensory integration, for example, during natural navigation when optic flow arisen from self-motion registers well with vestibular signals. By contrast, conflict cells may be associated with multisensory segregation, for example, when estimate of self-motion is confounded by independently moving objects in the environment (Zhang et al. 2019; Gu et al. 2008).

In sum, single neurons in sensory cortices tend to show clear modulations, and these properties across neurons tend to show a high degree of homogeneity and aggregation. For example, similar tuning preference for both visual and vestibular tend to be spatially clustered in a local range in MSTd, or VIP (Shao et al. 2018; Yu and Gu 2018; Gu et al. 2012; Zhang and Britten 2004).

By contrast to the above-mentioned sensory domains, single neurons in decision-related regions are neither homogeneous nor clustered very much, a phenomenon of which is known as “category-free.” Even worse, studying multisensory integration in decision-related regions involves a higher dimensional space in which both decision-related and modality signals need to be represented in certain ways. One of the earliest studies of this issue is from Raposo and colleagues (Raposo et al. 2014), who trained rats to perform an audio-visual frequency recognition task while recording the responses of PPC neurons. They found that PPC neurons are heterogeneous, with different neurons exhibiting different dynamics, and carrying different degree of decision and modality signals. With exception of a minor population of cells presenting only decision or only modality signals, most cells encode a mixture of the two signals, which is referred as mixed selectivity (Rigotti et al. 2013). Overall, the preference for choice (i.e., decision) and modality is randomly distributed across individual neurons and thus no correlation between the two exists per se. In conclusion, it is very difficult to immediately understand the function of a single neuron when just eyeballing them individually.

Despite that task-related variables are mixed at the level of individual neurons, encoding of task parameters at the PPC population level remains linearly separable, and the PPC network is able to decode the desired variables according to task demands (Raposo et al. 2014). Category-free phenomenon is recently observed in the macaque LIP in a task when the animals are trained to discriminate fine headings-based optic flow, vestibular, or the combination of both cues (Hou et al. 2019). In a motion direction-color mixed discrimination task, this phenomenon has also been observed in several frontal and parietal regions, allowing for flexible decision for certain type of information according to task needs (Siegel et al. 2015; Ibos and Freedman 2014; Mante et al. 2013).

2.2.3 Modality-Dependent Dynamics of Decision Signals

The “decision” part of multisensory decision-making emphasizes the importance of time, over which pieces of instantaneous information is integrated. Looking into temporal dynamics of different modality signals may provide useful insight into how sensory signals are decoded and are ultimately integrated across time and modality. A good example comes from the visuo-vestibular studies. First of all, it is notable that vestibular channel is unique among all sensory systems in terms of its dramatic temporal dynamics. In particular, peripheral vestibular organs, especially the otolith apparatus, only encodes self-motion with the physical quantity of acceleration (Fernandez and Goldberg 1976; Goldberg and Fernandez 1971). The acceleration information is then temporally integrated to different extent when being propagated to the central nervous system, resulting in a broad distribution from acceleration to velocity in the brain (Laurens et al. 2017). In contrast to plentiful vestibular dynamic signals, visual signals are typically represented in velocity rather than acceleration (Gu et al. 2006; Liu and Newsome 2005; Lisberger and Movshon 1999; Rodman and Albright 1987; Maunsell and Van Essen 1983). Thus, a question arises: does the brain integrate visual and vestibular with temporally identical signal of velocity, or with temporally incongruent signal (velocity and acceleration) during self-motion? Notably, it would be difficult to address this question by looking only into the psychophysical data. Instead, neurophysiological data would give us useful hints.

Firstly, evidence from the polysensory area of MSTd appears to support the temporal-identical (i.e., velocity for both visual and vestibular) integration hypothesis. In particular, vestibular signals in MSTd are predominantly velocity, making it seemingly ideal for integration with visual (Gu 2018; Laurens et al. 2017; Gu et al. 2006, 2008). Secondly, however, recent studies in macaques have found that the temporal dynamics of visuo-vestibular signals in decision-related region like LIP and FEF are not consistent across modalities (Zheng et al. 2021; Hou et al. 2019). Specifically, vestibular signals ramp up early, roughly corresponding to the peak of the acceleration profile of the stimulus, and the visual signals ramp up relatively late, roughly corresponding to the peak of the velocity profile. This divergent temporal dynamics between the two types of signals suggests that the brain accumulates different physical quantities for different modalities. To further verify this, researchers broaden the motion profiles such that the peak moment of velocity remains the same, which is still the middle point of the stimulus duration, whereas the peak moment of the acceleration was advanced by some time compared to that before being adjusted. If decision neurons do accumulate velocity signals in the visual condition and acceleration signals in the vestibular condition, then the timing for steepest rising slope should remain unchanged for visual, yet should move earlier for the vestibular. Indeed, LIP responses are consistent with these expectations, supporting that LIP accumulates momentary evidence from vestibular acceleration and visual velocity (Hou et al. 2019).

To distinguish how exactly the brain employs visual and vestibular signals for estimate of heading, researchers introduced temporal offset at a step of 250 ms between the two sensory inputs (Zheng et al. 2021). The rationale is that if the brain has used a temporal-identical model to combine heading cues, introducing cross-modal temporal offset would misalign the two signals and presumably reduce the efficiency of integration. Otherwise, temporal-offset manipulation could artificially better align the two dynamics and may instead boost cue integration. Surprisingly, in conditions when optic flow was adjusted to lead vestibular by 250–500 ms, benefit of multisensory integration in macaques' heading performance was indeed further improved compared to that under zero-offset condition. Such an effect was not observed under other offset conditions, for example, when visual stimuli led vestibular by 750 ms, or lagged vestibular by 250 ms, suggesting that the 250–500 ms offset window was specific with respect to further-enhanced cue combination effect. Moreover, simultaneous recordings revealed that under this specific offset window (250–500 ms visual leading), difference in temporal dynamics between the two modality signals in FEF and LIP was reduced. Thus with the more synchronous signals across modality, neural activity was enhanced more than that under zero-offset condition, which exactly explains the behavior. In sum, these results support that under natural conditions, the brain combines optic flow and vestibular with inconsistent physical quantities for multisensory heading perception (Fig. 2.2).

2.2.4 Causality Issue

Causal manipulation studies are few, especially when compared to the large number of studies based on a correlation measurement as described above. The causal experiments, however, are critically important for pinning down circuits that mediate multisensory processing. For example, a few possible models have been envisioned for multisensory decision-making (Bizley et al. 2016):

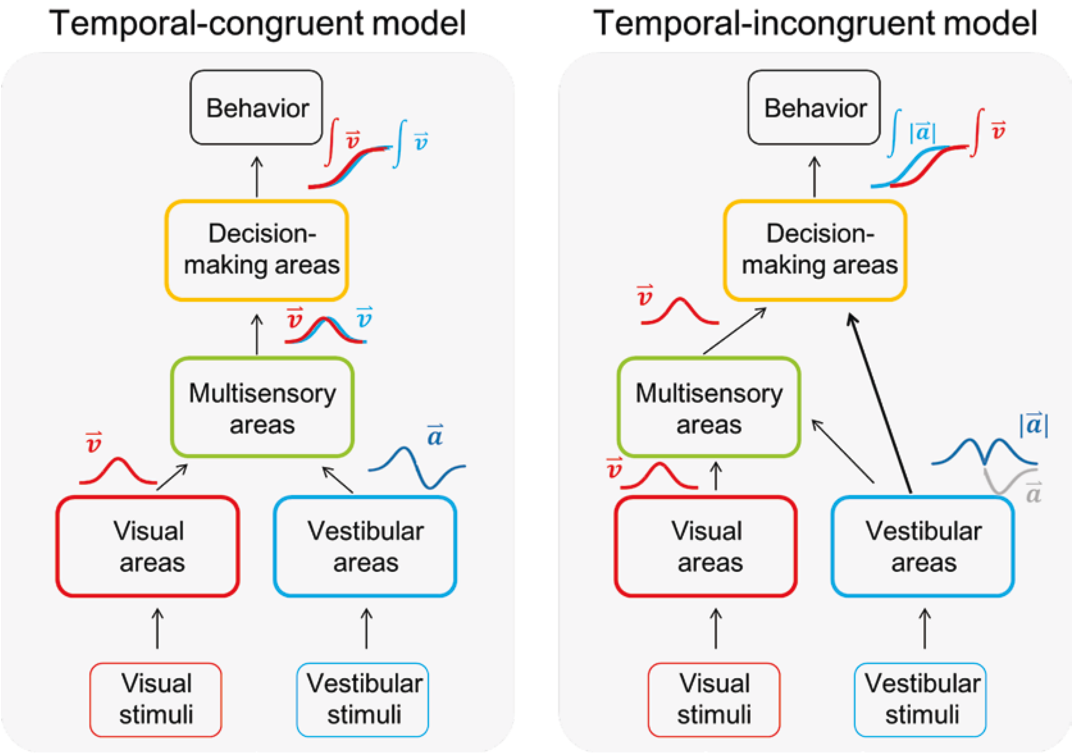

Fig. 2.2 Two models of visual-vestibular integration for self-motion perception. Velocity (v) follows Gaussian-shape profile; acceleration (a) is derivative of velocity and follows a peak-and-trough profile. In temporal-congruent model, multisensory areas convert vestibular acceleration signal to velocity signal and then decision-making areas receive and accumulate this vestibular velocity signal. In temporal-incongruent model, decision-making areas receive and accumulate absolute vestibular acceleration signal from vestibular areas

1. Late integration model: signals from different modalities are first transmitted to decision-making areas along each individual pathway, after which unimodal decision signals are integrated.
2. Early integration model: signals from different modalities are first converged in the same sensory area for integration, and then the integrated signals are transmitted to the decision-making area.

So in self-motion perception, how exactly are visual and vestibular signals converged and integrated in the brain along hierarchical level? A number of casual experiments have been conducted to examine whether and how optic flow and vestibular signals in cortices contribute to macaques' heading judgments. For example, inactivating MSTd with reversible drugs dramatically impairs vision-based heading perception but has a much weaker effect on vestibular discriminability. Consistent with this result, microcurrent stimulation applied in MSTd biases the animals' perceptual judgment on heading based on optic flow, but not on vestibular (Gu et al. 2012). By contrast, inactivating PIVC causes large deficits in vestibular heading perception (Chen et al. 2016). Surprisingly, inactivation of VIP does not generate any significant influence on either visual or vestibular-based heading judgments although this area contains robust vestibular and visual motion signals (Chen et al. 2016). Thus, it is likely that the coexistence of visuo-vestibular signals in MSTd and VIP may be for some other functions rather than heading estimate. Such techniques and methods should be applied in other areas to examine their roles in self-motion perception.

To our knowledge, there is so far only one study reporting that causal manipulations affect both modality signals. Specifically, optogenetic inactivation of the secondary motor cortex (MO), a multisensory region in rodents that encodes both visual and auditory information, impairs mice's performance in spatial localization tasks based on either modality (Coen et al. 2021). This result suggests that MO in mice is critical for processing cross modality information, and consequently, for its integration and evidence accumulation.

Finally, it should be noted that results from causality manipulation experiments should be explained with cautiousness. For example, due to the trait of highly redundant information coding in the brain, inactivating one of the nodes could be quickly compensated by other nodes within the network, and thus may not cause observable changes in the behavior. For activation experiments on the other hand, it is likely to activate passing fibers, leading to results that could be misleadingly explained by links with the manipulated areas. Furthermore, region of interest (ROI) may be involved in different task context. For example, while inactivation and electrical microstimulation in VIP fail to evoke significant effects on the animals' heading judgments during central fixation (Yu and Gu 2018; Chen et al. 2016), microstimulation does produce more salient effects when smooth pursuit eye movements are accompanied during heading perception (Zhang and Britten 2011). In decision-related areas, inactivation of LIP (Katz et al. 2016) or PPC (Erlich et al. 2015; Raposo et al. 2014) typically does not influence the animals' ability much in accumulation of sensory evidence, yet this effect is much stronger when novel stimuli are involved, suggesting that LIP may be involved more in the early phase of task-learning (Zhong et al. 2019). In sum, cross-discipline methods, as well as more task contexts need to be used to reveal a clearer picture about neural circuits mediating multisensory decision-making in the future.

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