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Bayesian-based integration of multisensory naturalistic perithreshold stimuli

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ABSTRACT

Most studies exploring multisensory integration have used clearly perceivable stimuli. According to the principle of inverse effectiveness, the added neural and behavioral benefit of integrating clear stimuli is reduced in comparison to stimuli with degraded and less salient unisensory information. Traditionally, speed and accuracy measures have been analyzed separately with few studies merging these to gain an understanding of speed-accuracy trade-offs in multisensory integration.

In two separate experiments, we assessed multisensory integration of naturalistic audio-visual objects consisting of individually-tailored perithreshold dynamic visual and auditory stimuli, presented within a multiple-choice task, using a Bayesian Hierarchical Drift Diffusion Model that combines response time and accuracy. For both experiments, unisensory stimuli were degraded to reach a 75% identification accuracy level for all individuals and stimuli to promote multisensory binding. In Experiment 1, we subsequently presented uni- and their respective bimodal stimuli followed by a 5-alternative-forced-choice task. In Experiment 2, we controlled for low-level integration and attentional differences.

Both experiments demonstrated significant superadditive multisensory integration of bimodal perithreshold dynamic information. We present evidence that the use of degraded sensory stimuli may provide a link between previous findings of inverse effectiveness on a single neuron level and overt behavior. We further suggest that a combined measure of accuracy and reaction time may be a more valid and holistic approach of studying multisensory integration and propose the application of drift diffusion models for studying behavioral correlates as well as brain-behavior relationships of multisensory integration.

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1. Introduction

During everyday perception, we are challenged to simultaneously process a plethora of relevant information stemming from different modalities. From that information, we make fast judgments on an object's identity, e.g. when hearing sounds from the bushes and simultaneously seeing an object which is running towards us – is that a bear, a cat, our friend, or are we altogether mistaken? Whether we attribute these noisy signals to a meaningful and coherent common source, or assign separate sources to each of them, depends on a probabilistic process following Bayesian causal inference (Rohe et al., 2015; Seilheimer et al., 2013). Our brain solves perceptual problems, similar to the one described above, by factoring in the probability of each sensory cue after weighting it by prior experience to minimize the precision error (Kayser et al., 2015). This fast occurring causal inference, based on the unisensory probabilities of the perceptions, results in an optimal estimate (Kayser et al., 2015) and has been demonstrated to correctly characterize behavioral multisensory integration (MSI) in a dichotomized choice task. However, whether a Bayesian model can explain behavioral MSI in a naturalistic multiple-choice context, as the one outlined above, is presently unknown.

Behavioral MSI is characterized by better basic detection and localization abilities toward multisensory objects in rodents (Stein et al., 1988), and superior object detection and identification accuracy in humans (Stevenson et al., 2014), compared to unisensory

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ones. A vital factor for MSI is the perceptual clarity of the unisensory stimuli. Differences in neuronal response amplitudes between multisensory and unisensory information are larger when unisensory inputs are degraded and less salient compared to when they are clear and salient. This 'Principle of Inverse Effectiveness' was first documented on a neural level in rodents (Meredith et al., 1983, 1986) but does also apply to non-human and human behavior (Stein et al., 1988; Stevenson et al., 2014), e.g. in studies using degraded stimuli (Senkowski et al., 2011; Stevenson et al., 2006; Werner et al., 2010b). Degraded stimuli may be of special importance when assessing MSI for dynamic and complex rather than static and simple stimuli (Chandrasekaran et al., 2013; Sella et al., 2014; Senkowski et al., 2007; Soto-Faraco et al., 2004). Using dynamic and complex stimuli enhances the ecological validity (Collignon et al., 2008) and helps to identify higher-order MSI in object identification; at the same time, might mask MSI by virtue of ceiling effects (task becomes too easy) and therefore obscure the point of optimal integration that seems to be located in between the extremes of a clear and a fully degraded stimulus (Ross et al., 2007). Using degraded video clips therefore seems an adequate solution to incorporate the advantages of dynamic stimuli and avoid ceiling effects.

Multisensory integration is commonly defined as performance in response to a multisensory stimulus that is greater than the sum of performances to its unisensory parts (Stein et al., 2009; Stevenson et al., 2014). One of the criteria, 'superadditivity', has traditionally been statistical assessed using a wide range of approaches. Accuracy and reaction time (RT) are, however, commonly handled as separate aspects of a behavioral response and are independently analyzed for MSI (but see Collignon et al., 2010). This approach of dividing the data fails to account for the full information contained within the data (Rach et al., 2011; Seubert et al., 2014); in other words, the fact that task-difficulty dependent speed differences may exist requires a more holistic approach of analyzing the observable markers of human perception.

A progression of the classical diffusion decision model, the Hierarchical Drift Diffusion Model (HDDM), was recently put forward as an integrative solution of the speed-accuracy problem (Wiecki et al., 2013). Here, information leading to a decision are modeled as noisy observations that accumulate over time in order to reduce noise and facilitate a choice. Drift diffusion models (DDMs), as part of the sequential sampling model family (Townsend and Ashby, 1983), provide an unbiased assessment of the time taken to accumulate sufficient evidence to make a decision. The HDDM, specifically, quantifies uncertainty by allowing inference of the full posterior distribution of each choice data parameter, thereby applying a Bayesian scheme to perceptual decision data (Bitzer et al., 2014). In the HDDM, the parameters are hierarchically estimated on an individual trial-by-trial level and on a group-level while the number of trials per subject are accounted for. To date, only a few studies have used this more holistic approach to study MSI. Using a non-hierarchical DDM model, Drugowitsch and colleagues stated that multisensory speed/accuracy trade-offs are best represented by neural population codes rather than mediated by slower neuronal mechanisms, such as learning-dependent changes in synaptic weights (Drugowitsch et al., 2015). The same group demonstrated that visual-vestibular object integration can be well described using a DDM (Drugowitsch et al., 2014). These studies clearly demonstrate that DDMs provide an appropriate Bayesian model approach for investigating MSI of low-level feature stimuli. Whether this holds up in multiple-choice designs, where participants are presented with dynamic, degraded, and naturalistic objects to fulfill the requirements for the Principle of Inverse Effectiveness, was the focus of the present work. More specifically, the aim was to investigate higher-order object identification MSI (Stevenson et al., 2006) using naturalistic and degraded audio-visual objects (Senkowski et al., 2007; Stevenson et al., 2006; Werner et al., 2010a, 2010b) with individually-tailored perithreshold stimuli (Stevenson et al., 2006) within a Bayesian analysis scheme.

In two independent experiments, unisensory identification thresholds were initially determined for each participant by presenting participants with video clips (audio or video part only) in a staircase design. In the subsequent multisensory assessment, these perithreshold unisensory stimuli and their bimodal combinations were presented to participants, followed by a 5-alternativeforced-choice-task (5AFCT) assessing object identification. Single-trial accuracy and RT were analyzed with a HDDM and the group-level posterior drift rates were subsequently subjected to common statistical tests for MSI. In Experiment 1, we assessed MSI in degraded naturalistic and dynamic stimuli and hypothesized a superadditive MSI in HDDM-derived posterior choice data for the multisensory stimuli, therefore demonstrating object-related MSI in stimuli with high ecological validity. In Experiment 2, we extended this finding by further minimizing the differences in information load between the uni- and multisensory stimuli. When comparing unisensory to multisensory stimuli, mere 'energy summation'[1] (Bernstein et al., 1970; Nickerson, 1970, 1973) and low-level integration (Werner et al., 2010b) may all contribute to potential 'multisensory enhancements' and potentially blur the effects of interest. Further, there is an inherent problem with commonly used experimental designs assessing MSI effects. When task performance to pure unisensory stimuli is assessed, full attention can be devoted to the stimulus whereas in subsequent multisensory tasks, attention has to be divided between the senses (Körding et al., 2007), potentially biasing behavioral performance. To avoid these potential experimental problems and to focus on relative multimodal gain (Ross et al., 2007), differences between unisensory and multimodal stimuli were minimized in Experiment 2 by assessing unisensory identification performance with 100% of noise in the respective other modality (Werner et al., 2010a, 2010b). We hypothesized that the results of Experiment 2, where low-level integration effects and attentional demands were accounted for, would demonstrate significantly larger MSI effects than Experiment 1.

2. Experiment 1

2.1. Material and methods

2.1.1. Participants

Twenty-one healthy volunteers were initially recruited from a student population and received one movie ticket as enumeration. All participants provided written informed consent and the local institutional review board approved all aspects of the study. Two participants reported hearing and vision deficits which reduced the final sample size to $n=19$ (age $M=25.05 \pm 6.15$ years, 10 females).

2.1.2. Stimuli

Four sound and video clips depicting clear semantic descriptor characteristics of 'wood fire', lawn mower', 'popcorn', and 'flopping fish' were obtained from Shutterstock (http://www.shutterstock.com). These stimuli were selected to represent a range of visual movement and sound types. Using Audacity 2.0 (http://audacity.sourceforge.net/) and Adobe Audition, sounds were cropped to

[1] This describes the observation that even if stimuli that are irrelevant for each other are combined, the mere presence of another sensory inputs helps facilitate a behavioral answer.

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