Multisensory Integration and Causal Inference in Typical and Atypical Populations

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Abstract

Multisensory perception is critical for effective interaction with the environment, but human responses to multisensory stimuli vary across the lifespan, and appear changed in some atypical populations. In this review chapter we consider multisensory integration within a normative Bayesian framework. We begin by outlining the complex computational challenges of multisensory causal inference and reliability-weighted cue integration, and discuss whether healthy young adults behave in accordance with normative Bayesian models. We then compare their behaviour with various other human populations (children, older adults, and those with neurological or neuropsychiatric disorders). In particular, we consider whether the differences seen in these groups are due only to changes in their computational parameters (such as sensory noise or perceptual priors), or whether the fundamental computational principles (such as reliability weighting) underlying multisensory perception may also be altered. We conclude by arguing that future research should aim explicitly to differentiate between these possibilities.

Keywords

multisensory integration; perception; Bayesian causal inference; lifespan; atypical

The Challenges of Multisensory Processing

Our ability to interact effectively with the word around us relies on precise, up-to-date sensory information. We therefore have an array of sensory organs that are optimised for detecting different types of information. Our eyes, for example, provide high precision when locating and identifying an object, but are of limited value for determining its temperature. The nose is an excellent tool for identifying whether food is rotten, but can tell us little about how much it weighs. Usefully, most objects and events produce signals that may be detected by several sense organs simultaneously, and the brain is able to combine these to enhance our perception and reduce our uncertainty about the world around us. Sometimes this information is separate and complementary; other times, the information provided by multiple senses overlaps. Consider a conversation with a friend in a loud room: we are far more likely to understand what they are saying if we can both listen to their voice and watch their lips form the words. Specifically, multisensory percepts afford two major benefits. First, they are more salient, facilitating faster and more accurate detection (Diederich & Colonius, 2004; Vroomen & de Gelder, 2000). Second, they are more precise, improving our estimates of an object or event's properties (Ernst & Bülthoff, 2004).

It is important to note, however, that our senses are constantly flooded with a mass of signals—many of them conflicting and/or unrelated—and the apparent effortlessness with which we sort and process this information belies the astounding complexity of the necessary underlying computations (and the neural processes involved in performing them). To integrate multisensory signals in an effective way, the brain needs to identify which of them belong together; only those signals that emanate from the same object or event should be processed together. This is a nontrivial process, as the observer has no access to the true causal structure of the world. Instead, sensory inputs must be matched based on *correspondence cues*—shared properties that suggest they were produced by the same source, such as appearing in the same place or at the same time (Parise & Spence, 2013)—and prior beliefs and expectations about which signals belong together. This complex operation is known as *causal inference*, as it involves attempting to infer the causal structure (i.e. one source versus several) that produced the signals (Acerbi et al., 2018; Körding et al., 2007; Rohe & Noppeney, 2015a). Once multiple signals have been determined to share a source, the sensory system should then integrate them into a more reliable percept that maximises the potential benefits (Alais & Burr, 2004; Ernst & Banks, 2002; Fetsch et al., 2012).

In this chapter, we consider these computational challenges within the framework of Bayesian probability theory (Ernst and Bülthoff, 2004; Fetsch et al., 2013; Meijer & Noppeney, 2020; Noppeney, 2020; 2021). This is a useful approach for evaluating how humans (and other organisms) process and respond to multisensory stimuli, as it enables the specification of an ideal observer that exhibits "optimal" behaviour against which actual responses may be compared. Within this framework, the observer is said to form a generative model of how sources in the environment may have produced the signals, which is inverted during perceptual inference.

The chapter includes two parts. Part 1 discusses how observers weight and combine multiple signals that were unambiguously produced by a single source (so-called "forced-fusion" scenarios). Part 2 moves beyond these forced-fusion cases and considers more complex situations in which signals can arise from common or different sources; this requires observers to infer the signals' causal structure, in order to arbitrate between sensory integration and segregation. Each part first introduces the normative Bayesian model that describes how ideal observers should combine signals during perceptual inference. We then discuss whether healthy young adults behave in accordance with these models, and compare their behaviour with various other human populations (children, older adults, and those with neurological or neuropsychiatric disorders). In particular, we consider the specific ways in which these groups can diverge: populations may differ only in their computational parameters, such as sensory noise (i.e. variances) or prior expectations about environmental properties (e.g. spatial location) and structures (e.g. number of sources) that are incorporated in model priors; alternatively, some groups may vary even in the computational principles (such as reliability weighting) underlying multisensory integration (Huys et al., 2021; Jones & Noppeney, 2021). At the end of each part, we briefly discuss the neural systems and mechanisms that support multisensory integration and causal inference. Though our review focuses on human work, we also briefly highlight the most relevant research in other species (for in-depth reviews, see Fetsch et al., 2013; Stein et al., 2014; Stein & Stanford, 2008; Witten & Knudsen, 2005).

Integrating Signals that Share a Source: Forced Fusion

All sensory inputs are corrupted to some degree by both external and internal noise, reducing their reliability or precision. The brain can attenuate this uncertainty by integrating multiple cues that contain redundant information, leading to a final multisensory percept with greater precision/reliability (i.e. less variance/noise) than any of the individual unisensory estimates. Early approaches to Bayesian modelling of sensory integration focused on situations in which all sensory cues are assumed to originate from the same source, avoiding the causal inference problem. These forced-fusion models address the question of how to weight and combine multiple cues in a way that increases the precision of the final joint percept (Alais & Burr, 2004; Ernst & Banks, 2002; Hillis et al., 2002; Jacobs, 1999; Meijer et al., 2019).

Bayesian modelling of forced-fusion integration

Forced-fusion integration of multisensory signals can be illustrated using the example of locating a single object using both auditory and visual cues. In this example, the generative model specifies that a single audiovisual source (S_{AV}) simultaneously emits an auditory (x_A) and a visual signal (x_V), and that each of these unisensory signals is independently corrupted by some amount of noise. During perception, the observer computes the (posterior) probability of the source location by combining the estimates (likelihoods) of the auditory and visual signals with prior spatial expectations, according to Bayes' rule:

$$P(S_{AV}|x_A, x_V) \propto P(x_A|S_{AV}) * P(x_V|S_{AV}) * P(S_{AV})$$

If we specify a uniform spatial prior $P(S_{AV})$, such that the source of the signals may be anywhere in space with equal probability, this computation is equivalent to maximum-likelihood estimation (MLE):

$$P(S_{AV}|x_A, x_V) \propto P(x_A|S_{AV}) * P(x_V|S_{AV})$$

Assuming that the noise corrupting the unisensory signals is Gaussian, the maximum-likelihood estimate for the audiovisual source $\hat{S}_{AV}$ is the average of the unisensory estimates $\hat{S}_A$ and $\hat{S}_V$, weighted by their respective reliabilities:

$$\hat{S}_{AV} = w_A\hat{S}_A + w_V\hat{S}_V$$

where each unisensory signal's reliability is defined as the inverse of its variance, $r = 1/\sigma^2$, and the sensory weights are normalised to sum to one:

$$w_A = \frac{r_A}{r_A + r_V}$$

and

$$w_V = \frac{r_V}{r_A + r_V} = 1 - w_A$$

When a multisensory estimate is calculated in this way, the reliability of the final combined estimate is equal to the sum of the unisensory reliabilities:

$$r_{AV} = r_A + r_V = \frac{\sigma^2{}_A + \sigma^2{}_V}{\sigma^2{}_A * \sigma^2{}_V}$$

An optimal observer's integrated percept, under forced-fusion assumptions, therefore has two important properties. First, the final combined location estimate is an average of the auditory and visual estimates, weighted by their relative reliabilities. Second, the reliability of the final estimate will always be equal to, or greater than, the most reliable unisensory estimate. Though we focused here on the example of audiovisual spatial integration, the model may equally be applied to other stimulus properties, other sensory modalities, multiple cues within one modality, or situations with more than two signals (e.g. Bresciani et al., 2008; Ernst & Banks, 2002; Jacobs, 1999).

Forced-fusion integration in healthy young adults

As discussed above, Bayesian forced-fusion models describe the way in which a theoretical "optimal" observer integrates multiple sensory cues that share a common source. They make predictions (reliability weighting and enhanced precision) against which human behaviour may be tested. To do so, we can measure the reliability of participants' responses to unisensory signals, and use these measured reliabilities as known parameters in a forced-fusion model. The model predictions may then be compared with participants' true responses to multisensory stimuli.

Accumulating research has shown that humans behave in a way that is consistent with these predictions (i.e. "optimally") in many situations (Fetsch et al., 2013). For example, Ernst and Banks (2002; also Helbig & Ernst, 2007) demonstrated statistically optimal integration of visual and haptic shape cues. Similar has also been shown for audiovisual localisation (Alais & Burr, 2004) and rate discrimination (Raposo et al., 2012). However, it is becoming increasingly clear that this is not universal: people sometimes respond in ways that are *not* consistent with the predictions of Bayesian forced fusion models. For example, in a paradigm similar to that used by Alais and Burr, Battaglia et al. (2003) found that participants overweighted the visual information. This was later replicated by Meijer et al. (2019), and overweighting of vestibular (Butler et al., 2010) and auditory (Burr et al. 2009) cues has also been demonstrated.

Forced-fusion integration in other populations

A large amount of past research has compared multisensory integration behaviour between various populations, addressing how responses to multisensory stimuli change across the lifespan (Burr & Gori, 2012; Jones and Noppeney, 2021) and whether/how they are impacted by various pathologies (Ding et al., 2017; Feldman et al., 2018; Tseng et al., 2015). Studies often do this by comparing different groups in terms of, for example, reaction times to forced-fusion stimuli, or the strength and frequency of illusions created by conflicting cues. Though these approaches provide useful information about differences in the *outcomes* of multisensory integration, they are often unable to identify whether the integration process itself has changed. As outlined above, the outcome of forced-fusion integration is determined by both the computational process itself and by the reliabilities of the incoming unisensory signals. It is therefore possible that any observed group differences in behavioural responses to identical multisensory stimuli result from changes to unisensory reliabilities, or even response strategies, rather than from changes in the integration process itself. By applying Bayesian models, we can determine whether and how changes in computational parameters or principles can lead to group differences in responses to multisensory stimuli.

In this section, we briefly discuss research that has directly investigated population differences in forced-fusion integration by taking the approach described in the previous section on younger adults: estimating unisensory reliability from participants' responses to unisensory stimuli alone, using these reliabilities as known (i.e. fixed) parameters in a forced fusion model to predict participants' responses to multisensory stimuli, and comparing those predictions to actual behaviour.

Children

Current evidence suggests that the ability to fuse and benefit from congruent, redundant multisensory cues is not present at birth, but develops throughout childhood (Burr & Gori, 2012). Nardini et al. (2008), for example, found that four-to-eight-year-olds did not integrate cues in a navigation task that relied on visual and self-motion signals, instead alternating between cues on a trial-by-trial basis. Gori et al. (2008) similarly showed that children younger than eight years old were extremely sub-optimal for cue weighting in visual haptic size discrimination tasks, with one of the cues dominating entirely, while those aged ten or older performed similarly to adults (i.e. in line with the predictions of Bayesian cue integration). Children younger than 12 have also been found to overweight the visual information in audiovisual spatial tasks (Gori et al., 2012).

These differences are not confined to integration of cues from different sensory modalities. Nardini et al. (2010) assessed integration of multiple visual cues to depth. The authors found that, while six-year-olds responded accurately to each cue individually, they did not appear to fuse the cues to improve the precision of their responses; this only occurred in those aged twelve years and older. In agreement with these behavioural findings, evidence of cue integration in visual cortex is only apparent in children older than around ten years old (Dekker et al., 2015).

This late development of Bayes-optimal cue integration may be explained by the fact that correspondences between senses evolve constantly throughout childhood (Burr & Gori, 2012). Relevant physical properties such as interocular distance, limb length, and head size are continually changing, and the development of individual senses does not occur at the same rate. It has therefore been suggested (by e.g. Burr & Gori) that the brain retains flexibility—at the expense of some precision—by not fusing cues until the development of the individual senses has slowed and the correspondences between them stabilised. In later sections, we discuss how this decreased tendency to integrate may be accounted for within the parameters of a more complex Bayesian causal inference model.

Older adults

Older adults are known to respond to multisensory stimuli differently from younger age groups in a variety of ways (see Jones & Noppeney, 2021, for a review). They differ in how they perceive multisensory illusions (e.g. Bedard & Barnett-Cowan, 2015; Chancel et al., 2018; DeLoss et al., 2013), and have previously been found to receive more multisensory benefit to reaction times (e.g. Laurienti et al., 2006; Peiffer et al., 2007). Despite this, research that explicitly assesses reliability weighting of multisensory cues in older adults is limited, and has produced mixed results. In some cases, ageing has been found to have little impact. Braem et al. (2014), for example, found no differences between younger and older adults' cue integration performance on a visual-haptic verticality judgement task; nor did Couth et al. (2019) for visual-haptic size judgement. However, in an audiovisual rate perception paradigm, Brooks et al. (2015) found that only the younger age group received an accuracy benefit from the integration of redundant cues, despite both groups weighting them appropriately. Bates and Wolbers (2014) showed the opposite in a task that required the integration of visual and self-motion cues: while both younger and older adults' accuracies benefitted from cue integration, the latter group consistently overweighted visual information. Finally, one study of visual-haptic verticality judgement by Billino and Drewing (2018) found that older adults weighted the signals in a way that was *more* consistent with the predictions of a forced-fusion model than the younger group, who underweighted the visual signal.

Atypical populations

Changes in multisensory perception have been reported for several neurological and neuropsychiatric disorders, but the mechanisms underlying these differences are currently unclear. As noted above, perceptual differences could arise in the absence of any changes to the computational principles (e.g. reliability weighting) as a result of, for example, reduced unisensory precision, or even due to impairments in related functions such as selective attention and response selection. Alternatively, it may be that some disorders do directly affect the computational principles governing multisensory integration. For instance, participants with neuropsychiatric disorders may resort to approximate algorithms or simple heuristics. Here we focus on autism spectrum disorder (ASD), schizophrenia (SZ), and Parkinson's disease (PD), as diverse examples that have been shown to cause some changes to multisensory perception, and consider research that has attempted to distinguish between these possibilities.

Perceptual changes are a common symptom of ASD (American Psychiatric Association, 2013), and a variety of autism-related differences in multisensory perception have been reported. Collignon et al. (2013) found that, unlike non-autistic controls, autistic participants did not benefit from additional auditory cues in a visual search task. Autistic children also appear to be less able to use visual information to improve their comprehension of auditory speech stimuli (Foxe et al., 2015; Iarocci et al., 2010; Stevenson et al., 2014; Woynaroski et al., 2013), and receive less response time benefit for multisensory versus unisensory stimuli (Brandwein et al., 2013). Several differences in perception of multisensory illusions have also been documented: autistic children were found to be less susceptible to the McGurk illusion (Bebko et al., 2014; Stevenson et al., 2014), but experienced the rubber-hand (Greenfield et al., 2015) and sound-induced flash (Foss-Feig et al., 2010) illusions over a wider range of stimulus asynchronies. See Feldman et al. (2018) for a comprehensive review.

There is growing evidence that these differences in multisensory perception may not be caused by changes to sensory cue weighting. Bedford et al. (2011) compared autistic and non-autistic teenagers in their weighting of visual cues to depth, and report that both performed in a way that was consistent with Bayesian forced-fusion integration. Zaidel et al. (2015) and Miller and McIntosh (2013) found similar for visual-vestibular integration. In the later section on Bayesian causal inference in atypical populations, we therefore discuss alternative explanations for multisensory processing changes in autistic individuals, particularly in terms of the role of perceptual and causal priors that define their tendency to integrate signals across the senses.

Changes in multisensory processing have also been reported in schizophrenia patients, particularly for speech cues. For example, Pearl et al. (2009) found that adolescents with schizophrenia were less susceptible to the McGurk illusion, and de Gelder et al. (2003) showed that SZ patients were impaired in an audiovisual lipreading task (despite performing similarly to controls at audiovisual localisation). Integration of multisensory emotional stimuli also appears to be changed: de Gelder et al. (2005) and de Jong et al. (2009) found that cross-sensory influence of vocal affect on emotional face categorisation (and vice-versa) was diminished in SZ patients.

The effects of schizophrenia on integration of lower-level multisensory cues appear more mixed. As noted above, de Gelder et al. (2003) found no differences between SZ patients and healthy controls in an audiovisual localisation (ventriloquist) task, but schizophrenia *has* been shown to reduce multisensory reaction time benefits in classical redundant target paradigms (e.g. Williams et al., 2010). Schizophrenia patients also appear to integrate temporally incongruent audiovisual stimuli over a wider range of SOAs, as tested by sound-induced flash illusion (Haβ et al., 2017) and simultaneity judgement (Foucher et al., 2007) paradigms. See Tseng et al. (2015) for a systematic review of multisensory integration effects in SZ.

Importantly, however, there has (to our knowledge) been no research to date that has applied forced-fusion modelling to systematically test sensory cue weighting in schizophrenia.

Parkinson's disease is a neurodegenerative disease predominantly affecting the basal ganglia, which have been shown to be involved in low-level integration of multisensory signals (Nagy et al., 2006; Reig & Silberberg, 2014). Ren et al. (2018) found, using a race-model analysis of reaction times, that PD patients do not benefit from multisensory stimuli in the same way as healthy controls. Parkinson's patients also seem to experience the rubber hand illusion more strongly, under a wider range of conditions (Ding et al.; 2017), and to over-rely on visual information for postural and motor control (Azulay et al., 2002; Bronstein et al., 1990; Cook et al., 1978; Halperin et al., 2021). A recent study by Yakubovich et al. (2020) found that Parkinson's patients overweighted visual cues significantly more than controls in a visual-vestibular navigation task, despite reductions in the reliability of these visual cues that correlated with the severity of disease, providing early evidence that PD may directly impact the computational processes underlying multisensory processing.

Neural mechanisms of reliability-weighted integration

Integration of multisensory signals has been observed across the brain. In their seminal early work, Stein and colleagues recorded from single neurons in cat superior colliculus, finding enhanced responses to audiovisual stimuli (Meredith & Stein, 1983; 1985). Since then, human neuroimaging research and neurophysiological recordings in non-human primates, rodents and other animals has shown that multisensory integration occurs pervasively throughout the cortex (Dahl et al., 2009, 2010; Foxe et al., 2002; Gau et al., 2020; Kayser et al., 2008; Lee & Noppeney, 2014; Lehmann et al., 2006; Martuzzi et al., 2007; Noppeney et al., 2010; Rohe & Noppeney, 2015b; Ghazanfar & Schroeder, 2006; Werner & Noppeney, 2010, 2011). The question of how and where reliability-weighted integration arises within this hierarchy is yet to be fully resolved; growing evidence points towards parietal and temporal association cortices, though the specific regions involved are likely to vary depending on the type of information being integrated. Neurophysiological research in non-human primates has found neurones in medial superior temporal area (MST) that respond in a way that closely approximates Bayesian integration of visuovestibular heading information (Fetsch et al, 2012; Gu et al., 2008; 2012). In humans, Helbig et al. (2012) used functional magnetic resonance imaging (fMRI) to assess neural responses during a visual-haptic shape discrimination task. The amplitude of blood-oxygen-level-dependent (BOLD) responses in areas of parietal and occipitotemporal cortices was seen to modulate in line with the weights given to the unisensory signals (derived based on behavioural responses). More recently, Rohe and Noppeney (2018) investigated the weighting of auditory and visual signals during a spatial localisation task, finding BOLD responses in intraparietal sulcus that were consistent with reliability-weighted integration.

Processing Signals from Multiple Sources: Causal Inference

In the first half of this chapter, we discussed how an optimal observer should combine sensory cues that were unambiguously generated by the same object or event, and compared this with the behaviour of various human populations. In the real world, an observer does not know which signals belong together, and needs to infer this from noisy sensory information: only those signals that originate from a common source should be integrated, while those from different sources must be segregated. Forced-fusion models do not provide insights into this causal inference process, as they assume that all signals are generated by one source. In this second part we introduce the Bayesian causal inference (BCI) model, which moves beyond these approaches and accounts for the possibility that some of the incoming signals have separate causes. It does so by explicitly modelling each of the potential causal structures that could have generated the various incoming sensory signals (Körding et al., 2007; Sato et al., 2007; Shams & Beierholm, 2010).

Prior to the use of BCI, research had already begun to investigate the conditions under which an observer integrates signals, finding those that are more (e.g. spatially, temporally, or semantically) congruent are more likely to be fused into a single percept or otherwise influence each other (Shams et al., 2000; Slutsky & Recanzone, 2001; Thurlow & Jack, 1973). BCI moves beyond these descriptive approaches to provide a principled explanation for the complex, interacting influences on observers' responses to multisensory stimuli. It models how, with increased sensory uncertainty, observers are less precise at arbitrating between integrating and segregating signals. The model also incorporates a causal prior, which quantifies the prior expectation of multiple inputs sharing a source. All else being equal, a participant with a stronger causal prior is likely to integrate stimuli under a wider range of conditions, and the presence of this parameter allows us to assess the relative contributions of past experience and incoming signal properties to the causal inference process.

Bayesian modelling of multisensory causal inference

If we again focus on audiovisual localisation as an example, the BCI generative model specifies that one auditory and one visual signal could have been produced either by a single object or event ($C = 1$) or by two separate objects/events ($C = 2$). These possible causal structures are sampled from a binomial distribution determined by a causal or common-source prior, P_{common}, which describes the prior probability of signals sharing a common cause. If $C = 1$ (one cause) is drawn, a single source S_{AV} is sampled from a normal distribution that quantifies the prior probability of signals originating from different areas of space. If $C = 2$ (two causes) is drawn, two separate sources S_A and S_V are sampled from the same spatial prior distribution. These sources then generate auditory and visual signals, x_A and x_V, that are independently corrupted by some amount of Gaussian noise.

This generative model is said to be inverted by the observer during perceptual inference to obtain the posterior probability over the possible causal structures and spatial locations of sensory sources. The probability of the received signals sharing a common cause is estimated by applying Bayes' rule to combine the available sensory information with the causal prior.

$$P(C = 1|x_A, x_V) = \frac{P(x_A, x_V|C = 1) * P_{common}}{P(x_A, x_V)}$$

In general, the possibility that the signals share a source is greater when they are closer together in space, and when the prior probability of signals sharing a source is higher.

If the observer is required to indicate whether the signals shared a source (an *explicit* causal inference judgement), a response may then be calculated based on a decision rule:

$$\hat{C} = \begin{cases} 1 \; if \; P(C = 1|x_A, x_V) > \alpha \\ 2 \; if \; P(C = 1|x_A, x_V) \leq \alpha \end{cases}$$

where α is a criterion value between 0 and 1 (often set as 0.5), above which the observer responds that the signals shared a source.

As there is always some level of uncertainty about the true causal structure of the signals, auditory and visual location estimates are calculated for both possible causal structures. For the case that the signals share a common cause, reliability-weighted integration occurs in the same way as it does under forced fusion. For the case that signals have different sources, separate (segregated) spatial estimates are calculated for each modality. These two sets of estimates are then combined according to some decision strategy (Wozny et al., 2010) to provide final estimates of the auditory ($\hat{S}_A$) and visual ($\hat{S}_V$) stimulus locations.

One possible decision strategy, known as model averaging, combines the integrated and segregated estimates by weighting their influence according to estimated posterior probabilities of the possible causal structures (i.e. if it is more likely that the signals had a shared source, the integrated estimate is given more weight, and vice versa).

$$\hat{S}_A = P(C = 1|x_A, x_V) * \hat{S}_{AV,C=1} + \left(1 - P(C = 2|x_A, x_V)\right) * \hat{S}_{A,C=2}$$

$$\hat{S}_V = P(C = 1|x_A, x_V) * \hat{S}_{AV,C=1} + \left(1 - P(C = 2|x_A, x_V)\right) * \hat{S}_{V,C=2}$$

Another possible decision strategy is probability matching. This approach assumes that the observer reports either the integrated or the segregated percepts probabilistically, depending on the posterior probability of a common cause.

$$\hat{S}_A = \begin{cases} \hat{S}_{AV,C=1} \; if \; P(C = 1|x_A, x_V) > \xi \\ \hat{S}_{A,C=2} \; if \; P(C = 1|x_A, x_V) \leq \xi \end{cases}$$

$$\hat{S}_V = \begin{cases} \hat{S}_{AV,C=1} \; if \; P(C = 1|x_A, x_V) > \xi \\ \hat{S}_{V,C=2} \; if \; P(C = 1|x_A, x_V) \leq \xi \end{cases}$$

The Bayesian causal inference model thus builds upon forced fusion models by modelling each of the possible causal structures that may have produced a set of signals, and generates responses by combining these estimates based on their relative probabilities.

Bayesian causal inference in healthy young adults

A substantial body of literature shows that young, healthy adults generally perform multisensory integration in a way that is consistent with the principles of Bayesian causal inference (Acerbi et al., 2018; Körding et al., 2007; Rohe & Noppeney, 2015a; Shams & Beierholm, 2010; Wozny et al., 2010). To evaluate this, participants are usually presented with multisensory signals that have varying degrees of conflict, and their behavioural responses compared to those predicted by a suitable BCI model. The model makes predictions for both *explicit* causal inference tasks, in which observers decide whether two signals come from a common source, as well as for tasks in which observers need to estimate a particular environmental property (such as the location or size of an object). We refer to the latter as *implicit* causal inference because the perceptual estimates are implicitly informed by causal inference. For instance, if an observer infers that an auditory and visual signal share a common source, the perceived location of the auditory stimulus will be informed by the estimate of the visual signal's location.

In practice, such tests often involve the use of multisensory perceptual illusions that arise when two or more conflicting signals are integrated. For example, the ventriloquist illusion occurs when the perceived location of a sound is altered by a simultaneously presented visual stimulus, as with a ventriloquist and their dummy: the movement of the dummy's mouth creates the perception that the voice is emanating from the dummy itself. This illusion exploits the fact that, in humans, visual information is generally far more spatially reliable than auditory information (our eyes are much better than our ears at determining *where* something happened). It can occur even for simple stimuli, such as a simultaneous beep and flash of light. In the laboratory, stimulus properties such as the spatial reliability of the unisensory signals, and the distance between them, may be randomised on every trial. Participants are asked to make explicit ("Were the sound and the flash caused by the same source?") and/or implicit ("Where did the sound/flash come from?") causal inference judgements about each set of stimuli. BCI predicts that multisensory interactions become weaker, and are less likely to occur, as the amount of conflict between signals increases: a beep and flash that appear to originate from different locations are unlikely to share a source, and should therefore have little or no influence on each other. Behavioural testing (e.g. Bertelson & Radeau, 1981; Körding et al., 2007; Lewald & Guski, 2003; Mohl et al., 2020; Rohe & Noppeney, 2015a; Wallace et al., 2004) has repeatedly shown that this accurately describes human localisation responses to spatially discrepant audiovisual stimuli: as audiovisual spatial disparity increases, the influence of the visual stimulus on the perceived sound location declines nonlinearly (implicit causal inference) and observers are progressively less likely to perceive the two signals as sharing a common source (explicit causal inference).

The sound-induced flash illusion (SIFI; Shams et al., 2000) instead relies on *temporal* binding of signals. It involves presenting, for example, one brief flash sandwiched between two short beeps. If the onsets of these stimuli are sufficiently close together in time, participants will incorrectly report perceiving two flashes. This occurs because humans' temporal reliability is greater for auditory than visual stimuli (we are more precise at hearing, than at seeing, *when* something happened), so the auditory signals are weighted more heavily in the final percept. The illusion has also been demonstrated for more than two beeps, and for multiple flashes and one beep (resulting in fusion, rather than fission, of the visual stimuli; Anderson et al., 2004). Again, the probability of the effect occurring diminishes as the temporal distance (stimulus onset asynchrony, or SOA) between the stimuli increases, in a way that closely approximates the predictions of BCI (Shams et al., 2005).

Bayesian causal inference modelling has been successfully applied to several other paradigms and stimulus combinations, including visuovestibular heading and verticality judgement (Acerbi et al., 2018; de Winkel et al., 2018), and audiovisual speech perception (Magnotti & Beauchamp, 2017; Magnotti et al., 2013).

Bayesian causal inference in other populations

As with forced-fusion models, Bayesian causal inference allows us to differentiate between several possible causes of inter-individual differences in multisensory integration. With BCI, we are no longer constrained to situations in which multiple signals unambiguously share a source, but can also assess the causes of atypical arbitration between sensory integration and segregation. We can, for example, test whether an increase in the tendency to bind conflicting signals is due to greater sensory noise, or to a stronger causal prior. In each case, we can then consider the underlying cognitive and neural mechanisms. Reduced unisensory reliability can, for instance, be caused by changes to both peripheral and central sensory processing (see Jones & Noppeney, 2021, for a discussion of how this can apply to older adults). Similarly, a stronger binding tendency could potentially be the result of attentional abnormalities that impair the ability to selectively attend to stimuli from a specific modality (for evidence of attentional effects on multisensory integration see e.g. Alsius et al., 2005; 2007).

Altered behavioural responses to multisensory stimuli may also/instead be due to differing response strategies and cost functions. Using sequential sampling models, we recently showed that older adults place a greater emphasis on accuracy when responding to multisensory stimuli in a speeded context (Jones et al., 2019). They accumulated evidence to a higher threshold before committing to a response, leading to a different speed-accuracy trade off.

Finally, individuals from atypical populations may deviate entirely from normative Bayesian principles, and instead resort to simple heuristics or approximate algorithms.

Children

In the earlier section on forced-fusion integration, we noted that children often do not benefit from congruent multisensory signals to the same degree as adults, instead relying primarily on a single sensory modality (Gori et al., 2008; 2012; Nardini et al., 2008). Within the framework of Bayesian causal inference, this decreased tendency to integrate signals would likely manifest as a weaker causal prior, which may be explained by limited multisensory experience during early neurodevelopment. Yet, children have also been reported to be more distracted by an irrelevant visual stimulus when attempting to locate a sound, which may suggest a *stronger* causal prior (Petrini et al., 2015). These considerations suggest that complex interactions between brain maturation and sensory experience must be taken into account when interpreting computational parameters of the BCI model in children. For instance, effective sensory integration and attentional mechanisms may rely on maturation of white matter tracts and frontoparietal cortices effectively. At the same time, the formation of causal priors (and other key sensory priors, such as the light-from-above prior; Stone, 2011) may require sufficient exposure to the sensory statistics of the real world.

Older adults

Two studies have recently investigated the influence of ageing on audiovisual integration for spatial localisation. In classical spatial ventriloquist paradigms, Jones et al. (2019) and Park et al. (2021) directly applied the Bayesian causal inference model to older adults' responses to multisensory stimuli. In each case, older adults were found to have lower unisensory reliabilities, but did not differ in their spatial or common-source priors and, crucially, still performed in a way that was consistent with the predictions of Bayesian causal inference.

As discussed earlier, there is also a substantial body of research assessing the effects of ageing on multisensory perception from other (i.e. non-Bayesian) perspectives, and older adults have been found to respond differently to multisensory stimuli under a variety of circumstances. In a recent review that considered this evidence alongside the limited computational research (Jones & Noppeney, 2021), we tentatively concluded that ageing can affect unisensory reliability, attentional control, and response strategies, but does not seem to impact the fundamental computational principles (including causal inference) that govern the integration of multisensory stimuli. However, further research that addresses this question directly is clearly required.

Atypical populations

In the earlier section on forced-fusion integration in atypical populations, we discussed evidence that the multisensory processing differences associated with ASD do not appear to be caused by abnormalities in sensory weighting. There is, however, increasing evidence from related areas that autism is associated with changes to perceptual (and other) priors. In an influential paper, Pellicano and Burr (2012) argue that weaker priors may be the primary cause of many perceptual symptoms of autism (see also responses by Friston et al., 2013, and Van de Cruys et al., 2012). The evidence for this view comes from studies demonstrating that autistic individuals perceive sensory stimuli in a way that is consistent with greater weight being placed on current sensory signals (the likelihood) than on past experience (the prior). For example, Skewes and Gebauer (2016) found that autistic participants were less likely to use relevant prior information when localising sounds. Similarly, when Skewes et al. (2015) presented observers with a perceptual learning task, those who scored higher for autistic traits placed more weight on the likelihood than the prior.

In the context of multisensory causal inference, this may mean that observers have a causal prior that favours neither integration nor segregation (i.e. close to 0.5). We might therefore expect autistic individuals to rely more directly on the properties of the incoming signals (conflict size, sensory noise) when arbitrating between integration and segregation. This is somewhat supported by evidence. For example, Stevenson et al. (2014; also Bebko et al., 2014) found that autistic children and adolescents with ASD are less susceptible to the McGurk illusion, which relies on the fusion of conflicting auditory and visual signals (though see Woynaroski et al., 2013, who did not find the same effect). Adolescents with ASD also appear less likely to integrate conflicting visual depth cues (Bedford et al., 2016).

Conversely, autistic individuals appear *more* likely to integrate multisensory stimuli that are spread out over time: Foss-Feig et al. (2010) report that children with ASD experienced the sound-induced flash illusion over a wider range of stimulus onset asynchronies (SOAs) than their non-autistic peers. Autism has, however, been associated with decreased performance on both auditory (Kwakye et al., 2011) and audiovisual (De

Boer-Schellekens et al., 2013a) temporal-order judgement tasks, suggesting this may be due to impaired temporal precision, rather than a stronger causal prior. This usefully highlights the important point that changes in different parameters can have similar effects: a participant may integrate signals with a small intersensory conflict because they have a stronger causal prior (i.e. greater binding tendency), or instead because sensory noise means they are less able to estimate the signals' true causal structure. (See Brock, 2012, for a discussion of this prior/likelihood ratio problem as it relates more generally to sensory perception in autism, and Noel et al., 2020, for an example of similar priors but impaired likelihoods in autistic participants performing a visual navigation task.)

One study that does directly address this question, by applying Bayesian causal inference modelling to a multisensory perception task, also provides a specific example of how changes in different parameters can produce very similar behaviour. Noel et al. (2018) compared the ability of three age-matched groups of adolescents—some with ASD, some with schizophrenia, and a group of healthy controls—to judge the simultaneity of concurrently presented auditory and visual stimuli. The authors found that both the ASD and SZ groups integrated stimuli (i.e. judged them to be simultaneous) over a wider range of onset asynchronies than controls. However, BCI modelling revealed that this was due primarily to changed priors in the autistic group, and to a combination of both changed priors and likelihoods in participants with schizophrenia.

As with ASD, there is growing evidence that differences in priors may be responsible for some of the perceptual symptoms of schizophrenia, though in this case priors appear often to be *stronger* in SZ. A study of audiovisual speech perception showed that individuals with psychosis relied more heavily on cognitive and perceptual priors than healthy or at-risk controls (Haarsma et al., 2020). Similarly, Powers et al. (2017) conditioned participants who suffer from psychosis, and a group of healthy controls, to perceive an illusory sound when presented with a visual checkerboard stimulus. The psychosis group perceived significantly more illusory stimuli, and a hierarchical Gaussian filter model revealed that this was due to this group being more influenced by prior stimuli. This effect of stronger priors in SZ/psychosis may be limited to specific (perhaps higher-level) stimulus types, though: Kaliuzhna et al. (2019) and Valton et al. (2019) found no differences in the role of priors when perceiving low-level visual stimuli.

There is some suggestion that Parkinson's patients also differ in their use of priors for perceptual tasks. Perugini et al. (2016) applied a drift-diffusion model to assess the relative contribution of past experience and sensory information in responses to a visual orientation judgement task. It was found that participants from the PD group were less able to use prior information to inform their responses. However, to our knowledge, no study has yet specifically investigated whether causal priors for multisensory integration are affected by Parkinson's disease.

Neural mechanisms of Bayesian causal inference

Given the growing behavioural evidence that human observers integrate sensory signals in a way that is consistent with the principles of Bayesian causal inference, research has recently turned towards characterising the underlying neural mechanisms. Rohe and Noppeney (2015b, 2016) collected whole-brain functional magnetic resonance imaging (fMRI) images while presenting participants with auditory and visual stimuli at various degrees of spatial conflict and reliability (i.e. a ventriloquist paradigm). Multivariate decoding was combined with Bayesian modelling to demonstrate that the brain formed spatial representations according to different computational principles across the auditory and visual processing hierarchies. While primary sensory areas independently encoded the locations of the auditory and visual stimuli, the posterior intraparietal sulcus integrated auditory and visual signals into an integrated (i.e. forced-fusion) spatial representation. Finally, anterior intraparietal sulcus combined these into a final location estimate consistent with the predictions of Bayesian causal inference. Later work (Mihalik & Noppeney, 2020) has suggested that this final estimate was informed by causal inference estimates in dorsolateral prefrontal cortex.

An electroencephalography (EEG) study, using a similar ventriloquist behavioural paradigm, aimed to establish how these various representations arise dynamically over time (Aller & Noppeney, 2019). The results were highly consistent with the fMRI findings. In the early stages of processing (< 100 ms post stimulus), stimulus representations were most consistent with (segregated) unisensory estimates. These estimates then (100-200 ms) combined into a fully-integrated forced-fusion estimate, before resolving into a final estimate consistent with behavioural responses and the predictions of BCI (350-450ms). Interestingly, the neural processes underlying Bayesian causal inference in temporal signals have been found to evolve along a similar time course (Cao et al. 2019; Rohe et al., 2019). Collectively, these studies suggest that the brain integrates sensory signals into representations that take into account the signals' causal structure (i.e. common vs. independent sources) by dynamically encoding multiple perceptual estimates.

Conclusion

Growing evidence suggests that the human brain combines sensory signals in a way that is consistent with the principles of Bayesian causal inference. When signals come from common sources they are integrated, weighted by their relative reliabilities, into a more precise representation of the world. When they come from different source they are processed separately. This arbitration between sensory integration and segregation is determined by observers' causal inference, based on noisy correspondence cues such as spatial disparity or temporal asynchrony. These processes evolve throughout childhood, as children develop physiologically and build their sensory experience, and change again in later life as part of normal, healthy ageing.

Normative Bayesian models move beyond descriptive approaches, allowing us to characterise interindividual differences at the computational level. This brings the possibility of determining whether, for example, atypical populations (such as those with ASD, Parkinson's, or schizophrenia) experience multisensory illusions more (or less) frequently because of changes in sensory noise, causal priors, cost functions, or because they deviate from normative principles. Research to date suggests that individuals from some atypical populations may differ in their sensory noise and use of priors, but there is insufficient evidence to suggest that they deviate from the computational principles of Bayesian causal inference. Future research should thus aim to directly address this question, and to determine the neural and cognitive mechanisms (perhaps involving changes in selective attention and cognitive control) underlying any differences found.

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