Multisensory Bayesian Inference Depends on Synapse Maturation during Training: Theoretical Analysis and Neural Modeling Implementation

Mauro Ursino
mauro.ursino@unibo.it
Cristiano Cuppini
cristiano.cuppini@unibo.it
Elisa Magosso
elisa.magosso@unibo.it
Department of Electrical, Electronic and Information Engineering University of Bologna, I 40136 Bologna, Italy

Recent theoretical and experimental studies suggest that in multisensory conditions, the brain performs a near-optimal Bayesian estimate of external events, giving more weight to the more reliable stimuli. However, the neural mechanisms responsible for this behavior, and its progressive maturation in a multisensory environment, are still insufficiently understood. The aim of this letter is to analyze this problem with a neural network model of audiovisual integration, based on probabilistic population coding—the idea that a population of neurons can encode probability functions to perform Bayesian inference. The model consists of two chains of unisensory neurons (auditory and visual) topologically organized. They receive the corresponding input through a plastic receptive field and reciprocally exchange plastic cross-modal synapses, which encode the spatial co-occurrence of visual-auditory inputs. A third chain of multisensory neurons performs a simple sum of auditory and visual excitations.

The work includes a theoretical part and a computer simulation study. We show how a simple rule for synapse learning (consisting of Hebbian reinforcement and a decay term) can be used during training to shrink the receptive fields and encode the unisensory likelihood functions. Hence, after training, each unisensory area realizes a maximum likelihood estimate of stimulus position (auditory or visual). In cross-modal conditions, the same learning rule can encode information on prior probability into the cross-modal synapses. Computer simulations confirm the theoretical results and show that the proposed network can realize a maximum likelihood estimate of auditory (or visual) positions in unimodal conditions and a Bayesian estimate, with moderate deviations from optimality, in cross-modal conditions. Furthermore, the model explains the ventriloquism illusion and, looking at the activity in the

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multimodal neurons, explains the automatic reweighting of auditory and visual inputs on a trial-by-trial basis, according to the reliability of the individual cues.

1 Introduction

The problem of how the brain integrates inputs from different sensory modalities to achieve an optimal recognition of external events and produce accurate object reproduction is fundamental in cognitive neuroscience. Numerous recent behavioral work suggests that the brain combines cross-modal cues in a near-optimal statistical way by weighting cues of different modalities according to their reliability (as assumed in the classical Bayesian inference). This occurs when integration concerns visual and acoustic stimuli (Alais & Burr, 2004; Battaglia, Jacobs, & Aslin, 2003; Shams, Ma, & Beierholm, 2005; Wallace et al., 2004), texture and motion cues (Hillis, Watt, Landy, & Banks, 2004; Jacobs, 1999), visual and tactile inputs (Ernst & Banks, 2002), as well as trimodal cues (Wozny, Beierholm, & Shams, 2008). A typical effect of this near-optimal combination is the occurrence of illusory phenomena in the presence of a conflict between two stimuli of different sensory modality. In these cases, the observer favors the more reliable cue, producing a final estimate, which is more affected by the more reliable stimulus. By limiting our attention to visual-acoustic integration, common illusions include the ventriloquism effect in the spatial domain (Bertelson & Radeau, 1981; Hairston et al., 2003; Wallace et al., 2004), the fission and the fusion effects in the temporal domain (Andersen, Tiippana, & Sams, 2004; Shams, Kamitani, & Shimojo, 2000; Shams et al., 2005), and the McGurk effect concerning integration of phonemes with lip movements (McGurk & MacDonald, 1976).

A fundamental question that has brought increasing attention is how neural circuits can realize this near-optimal probabilistic inference. Some recent studies shed light on this issue (Ma, Beck, Latham, & Pouget, 2006; Ma & Rahamati, 2013; Pouget, Beck, Ma, & Latham, 2013; Pouget, Dayan, & Zemel, 2003). A basic idea, probabilistic population coding, is that the activity of a population of neurons can automatically encode a probability distribution. Then some form of metrics can extract the statistically optimal estimate from this distribution. In particular, Ma et al. (2006), and Ma and Rahamati (2013) have shown that a population of neurons having Poisson-like variability can codify the likelihood function of the attribute using the probabilistic population code. Moreover, they investigated how simple neural circuits can perform Bayesian inference. In particular, Ma et al. (2006) demonstrated that Bayesian inference can be realized by simply using a linear combination of population activity (Ma & Rahamati, 2013; Pouget et al., 2013). Subsequent experimental results in a multisensory task, involving visual and vestibular cues, confirmed this prediction in monkeys, showing
that multimodal neurons in the medial superior temporal area combine visual and vestibular inputs linearly with subadditive weights (Morgan, Deangelis, & Angelaki, 2008), and place more weight on the more reliable cue (Fetsch, Pouget, DeAngelis, & Angelaki, 2012). However, Fetsch et al. (2012) also observed that these weights should be readjusted rapidly, on a trial-by-trial basis, to follow the actual reliability of the stimuli. A form of divisive normalization that acts on the multisensory representation (Ohshiro, Angelaki, & DeAngelis, 2011) has been advocated to explain this weight readjustment with reliability.

Despite these important contributions, the problem of how a network of neurons can encode probabilities and exploit population activity to realize a near-optimal estimate in a rapidly varying environment is still far from being completely understood. In particular, several problems deserve attention. What kind of topological network (feedforward, feedback, or a combination of feedback and feedforward), trained by experience, is most suitable to realize a near-optimal cue combination? Which mechanisms for synapse learning can be used during training to incorporate prior information and mimic the developmental period in which a network encodes the statistics from the environment? How can likelihood probabilities and prior probabilities be combined in a near-optimal fashion to compute posterior distributions, as required by the Bayesian estimator? Finally, how can a network readjust weights for cue integration, on a trial-by-trial basis, using biologically inspired neural mechanisms?

In order to address the previous points, two experimental observations deserve attention. First, it is well known that the receptive fields (RFs) of sensory neurons are not fixed but develop during a maturation phase according to the spatial reliability of external inputs. This has been clearly observed in some subcortical areas (such as the cat’s superior colliculus; Wallace & Stein, 1997), but it is also evident in cortical auditory and visual neurons (Froemke & Jones, 2011; Pecka, Han, Sader, & Mrsic-Flogel, 2014). Such plasticity of the RFs may represent a suitable way to encode the likelihood probability of the inputs, based on experience.

Second, numerous recent experimental work emphasizes the idea that cortical areas, traditionally deemed as purely unisensory (such as the visual, auditory or somatosensory cortex), exhibit some kinds of cross-talk and exchange reciprocal information (Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006). For instance, many results show that the auditory neurons exhibit some multisensory behavior and are affected by concomitant visual inputs and somatosensory influences (Musacchia & Schroeder, 2009; Schroeder & Foxe, 2005). Similarly, studies on the visual cortex report that the activity of many visual neurons can be affected by auditory stimuli (Morrell, 1972) and that auditory inputs can activate part of the inferotemporal cortex (Ghazanfar & Schroeder, 2006). A few studies have also analyzed the effect of audiovisual stimuli on the somatosensory cortex (Zhou & Fuster, 2000, 2004).
A challenging hypothesis that we analyze in this letter is that these cross-modal synapses may mature under the pressure of the external inputs (e.g., to reflect the co-occurrence of cross-modal stimuli) and constitute an appropriate way to encode prior information on the statistics into network topology.

In recent years, we have developed neural network models of audio-visual integration that incorporate cross-modal synapses between unisensory areas (Cuppini, Magosso, Bolognini, Vallar, & Ursino, 2014; Magosso, Cona, & Ursino, 2013; Magosso, Cuppini, & Ursino, 2012; Ursino, Cuppini, & Magosso, 2014). Typical assumptions of these models were that neurons of the two modality have different receptive fields (the visual ones more accurate in the spatial domain, the auditory ones more accurate in the temporal domain), and that the cross-modal synapses mainly link neurons with proximal spatial preference. With these models, we were able to simulate some typical audiovisual illusions (such as the ventriloquism effect: Magosso et al., 2013, 2012) and the fusion and fission effects (Cuppini et al., 2014). In this previous work, however, both cross-modal synapses and receptive fields were assigned a priori, that is, they were not trained on the basis of the statistical input experience.

The aim of this letter is to introduce training mechanisms in a previous model to test whether the information necessary to realize a near-optimal Bayesian estimator (i.e., the likelihood probability of the individual stimuli and the prior probability) can be encoded in the synapses using biologically realistic learning rules. The trained model is subsequently exploited (using some population code metrics) to realize a near-optimal Bayesian estimate.

The network has two layers of unisensory neurons, which receive the external inputs (either auditory or visual) via a plastic receptive field and can connect reciprocally via initially latent cross-modal synapses. Moreover, competitive mechanisms are implemented within each layer. In the immature phase, the receptive fields are wide (equal for all neurons in both layers) and cross-modal synapses are null. Both kinds of synapses are subsequently shaped using a Hebbian mechanism of potentiation with a decay term.

The letter includes both a preliminary theoretical analysis of the network, based on some ideas from Ma et al. (2006) and from Patton and Anastasio (2003) and Sato, Toyoizumi, and Aihara (2007), to demonstrate which kinds of probabilities can be incorporated during training, and numerical computer simulations. In the first stage, the network is used to infer the positions of the auditory and the visual stimuli separately. Results are compared with those obtainable with the maximum likelihood estimate in the case of unimodal stimuli, and with the maximum posterior probability estimate (a kind of Bayesian estimator that exploits known prior probability) in the case of cross-modal stimuli. Simulations of the ventriloquism effect are also performed to compare model performance with behavioral results. In a second stage, the network is enriched with a further multisensory layer,
which receives input from the previous two layers (auditory and visual) to compute a single position for both stimuli. This is used to assess the single causal inference problem, where the observers are asked to envisage each presentation as a single event (Alais & Burr, 2004). In this condition, we analyze whether the proposed model can automatically reweight the cues according to their reliability.

Results demonstrate that the proposed network, with the implemented training rule, can realize a near-optimal Bayesian estimate (exploiting both likelihood and prior information) and can automatically combine cues, taking into account their reliability on a trial-by-trial basis.

2 Material and Methods

2.1 Theory

2.1.1 Bayesian Estimate: The General Problem. Let us assume that the brain processes two sensory inputs of different modalities (e.g., an acoustic and a visual one). In the following, a quantity belonging to a given sensory modality will be represented with the superscripts $A$ or $V$, respectively. Uppercase letters will be used to represent vectors or arrays, and lowercase letters (with a subscript) will be used to represent scalar component of vectors.

Each sensory input consists of a vector with $N$ component ($I^A$ and $I^V$, respectively) which describes the spatial distribution of the stimulus. For instance, the scalar quantity $i^A_j$ denotes the $j$th component of the acoustic input. We assume that each component $j$ ($j = 1, 2, \ldots, N$) codes for a particular spatial position, $\vartheta_j$. Hence, a vector ($N \times 1$) of spatial positions is defined:

$$\Theta = [\vartheta_1 \vartheta_2 \cdots \vartheta_j \cdots \vartheta_N]^T.$$ 

The two vectors $I^A$ and $I^V$ are the auditory and visual sensory representations of the external world reaching the brain. Both are affected by the spatial position of the input stimulus, the blurring properties of the sensory transduction, and noise.

Let us denote with $\vartheta^A$ and $\vartheta^V$ the positions of the acoustic and the visual stimuli, respectively, which generate the sensory representations. In terms of Bayesian estimates, the problem consists in inferring the positions $\vartheta^A$ and $\vartheta^V$ starting from the knowledge of the two sensory representations, $I^A$ and $I^V$, blurred and affected by noise. The problem is completely defined, from a statistical point of view, if one knows the likelihood probabilities of the two sensory representations and the prior probability of the positions.

We will assume that the sensory representation $I^A$ is only a function of the position of the acoustic stimulus, $\vartheta^A$, and $I^V$ is only a function of $\vartheta^V$. 

Moreover, they also depend on the strength of the stimulus and the presence of noise, both assumed independent for the two stimuli.

Hence, we can write the following expression for the likelihood probability of the overall sensory inputs:

\[ p(I^A, I^V | \vartheta^A, \vartheta^V) = p(I^A | \vartheta^A) p(I^V | \vartheta^V). \]  

(2.1)

Let us assume that the prior probability of the two positions \( p(\vartheta^A, \vartheta^V) \) is also known. It is worth noting that the two sensory representations are not independent (i.e., we generally have \( p(I^A, I^V) \neq p(I^A) p(I^V) \)) since the two positions \( \vartheta^A \) and \( \vartheta^V \) are not independent (generally \( p(\vartheta^A, \vartheta^V) \) is not uniform, and \( p(\vartheta^A, \vartheta^V) \neq p(\vartheta^A) p(\vartheta^V) \)).

According to the Bayesian rule and using equation 2.1, we can write the following expression for the a posteriori probability

\[ p(\vartheta^A, \vartheta^V | I^A, I^V) = \frac{p(\vartheta^A, \vartheta^V) p(I^A, I^V | \vartheta^A, \vartheta^V)}{p(I^A, I^V)} = \frac{p(\vartheta^A, \vartheta^V) p(I^A | \vartheta^A) p(I^V | \vartheta^V)}{p(I^A, I^V)}. \]  

(2.2)

In order to have the best estimate, we have to maximize the numerator of equation 2.2, starting from knowledge of the sensory representations \( I^A \) and \( I^V \). In other words, the estimates (say, \( \hat{\vartheta}^A \) and \( \hat{\vartheta}^V \), respectively) must satisfy the following rule:

\[ \left[ \hat{\vartheta}^A, \hat{\vartheta}^V \right] = \arg \max \left\{ p(I^A, I^V | \vartheta^A, \vartheta^V) \right\} \]

\[ = \arg \max \left\{ p(\vartheta^A, \vartheta^V) p(I^A | \vartheta^A) p(I^V | \vartheta^V) \right\}. \]  

(2.3)

In order to maximize equation 2.2, we need the knowledge of the likelihood probabilities and the prior probability.

2.1.2 The Likelihood Probabilities. Let us now assume that we know a given realization of the sensory input (in the following, we will consider a generic sensory input \( S \), with either \( S = A \) or \( S = V \)). Hence, we know

\[ I^S = [i_1^S i_2^S \cdots i_j^S \cdots i_N^S]^T, \]

which represents an \( N \times 1 \) array. This is the input stimulus reaching the brain. Moreover, let us assume that the prior distribution is uniform (or we simply do not know the prior). In this case, equation 2.3 simplifies to

\[ \hat{\vartheta}^S = \arg \max \left\{ p(I^S | \vartheta^S) \right\}. \]  

(2.4)
that is, one needs to maximize the likelihood probability of the sensory representation to obtain the sensory estimate $\hat{\vartheta}_S$.

In the following, we assume that the sensory input consists of a deterministic term (say, $M^S(\vartheta^S)$) on which some gaussian white noise with zero mean value is superimposed (say, $N^S$). Hence, we can write the following expression for the random vector $I^S$,

$$I^S = M^S + N^S.$$  

(2.5)

or, in scalar form,

$$i^S_j = m^S_j + n^S_j, \quad j = 1, 2, \ldots, N,$$  

(2.5')

where the underline signifies that the corresponding quantity is random. If the noise terms are independently generated, then $i^S_j$ are also independent variables, and so the following expression holds for the likelihood probability:

$$p(I^S | \vartheta^S) = \prod_{j=1}^{N} p(i^S_j | \vartheta^S).$$  

(2.6)

The deterministic term in equation 2.5 is a function of the strength of the stimulus (indeed, the higher the strength, the higher $m^S_j$) and the stimulus position. In particular, this term is maximal when $\vartheta_j = \vartheta^S$ and progressively decreases with distance. We used a gaussian function to represent the deterministic spatial properties of the input. We can write

$$m^S_j(\vartheta^S) = i^S_{\text{Max}} \exp \left\{-d(\vartheta^S, \vartheta_j)^2/(2\sigma^2)\right\} \quad j = 1, 2, \ldots, N,$$  

(2.7)

where $d(\vartheta^S, \vartheta_j)$ represents the distance between the position of the stimulus $\vartheta^S$ and the actual position $\vartheta_j$; $\sigma^S$ is the standard deviation of the gaussian function, here representing the spatial accuracy of the input (i.e., the greater $\sigma^S$, the more blurred the stimulus); and $i^S_{\text{Max}}$ accounts for the strength of the external stimulus. According to equation 2.7, when $d(\vartheta^S, \vartheta_j) = 0$, the sensory input is maximal (apart from the effect of noise), while the sensory input progressively decreases with distance.

In this work, the distance has been computed through a circular structure, so every sensory input receives similar excitation, independent of being close to the center or to the border. Hence, the following equation has been used to compute the distance:

$$d(\vartheta^S, \vartheta_j) = 0,$$  

(2.8)
where $D$ represents the overall spatial distance (i.e., $0 < \theta_j < D$). By way of example, assuming $D = 180^\circ$, the position $\theta^S = 1^\circ$ is equally distant from position $\theta_j = 180^\circ$ and from position $2^\circ$; moreover, it is equally distant from position $179^\circ$ and from position $3^\circ$, and so on.

Since we assumed that noise has a gaussian distribution with zero mean value, the likelihood probability $p(i^S_j | \theta^S)$ assumes the following expression:

$$p(i^S_j | \theta^S) = \frac{1}{\sqrt{2\pi \upsilon^S}} \exp \left\{ -\left[ i^S_j - m^S_j(\theta^S) \right]^2 / (2\upsilon^S) \right\} = \frac{1}{\sqrt{2\pi \upsilon^S}} \times \exp \left\{ -\left[ i^S_j - i^S_{\text{Max}} \exp \left( -\left( d(\theta^S, \theta_j) \right)^2 / (2\sigma^S) \right) \right] \right\}^2$$

for $j = 1, 2, \ldots, N$, (2.9)

where $\upsilon^S$ represents the standard deviation of the noise (hence, the greater $\upsilon^S$, the greater the effect of noise).

Finally, using equations 2.6 and 2.9 together, we can write the overall expression of the likelihood probability for the sensory input as a function of the stimulus position:

$$p(I^S | \theta^S) = \prod_{j=1}^{N} p(i^S_j | \theta^S) = \prod_{j=1}^{N} \frac{1}{\sqrt{2\pi \upsilon^S}} \times \exp \left\{ -\left[ i^S_j - i^S_{\text{Max}} \exp \left( -\left( d(\theta^S, \theta_j) \right)^2 / (2\sigma^S) \right) \right] \right\}^2$$

for $j = 1, 2, \ldots, N$, (2.10)

It is worth noting that equations 2.7 and 2.10 are not only a function of the stimulus position, $\theta^S$, but also of the input strength (i.e., parameter $i^S_{\text{Max}}$). However, for simplicity, the latter dependence has not been explicitly shown in the left-hand member.
The likelihood function is given by expression 2.10 in which a specific value of \( I^S \) (a single realization of the random vector) is used. Hence,

\[
    l(\vartheta^S) = p(I^S | \vartheta^S) \quad \text{with } I^S \text{ known.} \tag{2.11}
\]

Let us compute the natural logarithm of the likelihood function. From equation 2.11, we have

\[
    \ln(l(\vartheta^S)) = -\sum_{j=1}^{N} \ln(\sqrt{2\pi \upsilon^S}) - \frac{1}{2\upsilon^S} \sum_{j=1}^{N} \left\{ i^S_j - i^S_{\text{Max}} \exp \left[ -\frac{(d(\vartheta^S, \vartheta_j))^2}{2\sigma^S} \right] \right\}^2. \tag{2.12}
\]

The maximum likelihood estimate (MLE) is obtained by computing the value (say, \( \hat{\vartheta}^S \)) that maximizes equation 2.12. Similar equations hold for the visual (\( S = V \)) and the auditory (\( S = A \)) likelihood functions.

2.1.3 A Neural Network Model for Maximum Likelihood Estimate. Our problem is now to find a simple neural network, consisting of \( N \) neurons, which can be trained with a realistic rule to automatically find the maximum of equation 2.12, from knowledge of the input vector \( I^S \).

In the following, each neuron will be represented through the subscript \( k \). Let us consider that each neuron in the chain is more sensitive to a specific position, \( \vartheta_k (k = 1, 2, \ldots, N) \), that is, we use the same positions previously used for the sensory vector; this can be obtained using a receptive field, for each neuron, centered at the preferred position. We will denote each receptive field as \( R^S_k \) \((k = 1, 2, \ldots, N)\); this is a vector with dimension \( N \times 1 \). The input to the \( k \)th neuron with a preferred position \( \vartheta_k \) in the sensory modality \( S \) (say, \( u^S_k \)) is then computed as the scalar product between the sensory input and its receptive field. We can write

\[
    u^S_k = \sum_{j=1}^{N} r^S_{kj} i^S_j, \tag{2.13}
\]

where \( r^S_{kj} \) is the \( j \)th component of vector \( R^S_k \).

Each neuron then computes its output activity (say, \( y^S_k \)) by passing the input through a monotonically increasing nonlinear function (which
mimics the presence of a lower threshold and upper saturation for neuron’s activity). By denoting this monotonic function with \( \varphi(u) \), we can write

\[
y^S_k = \varphi(u^S_k) = \varphi\left(\sum_{j=1}^{N} r^S_{kj} i^S_j \right).
\]

(2.14)

During numerical simulations, we will use a sigmoidal function, as done in neural network modeling. However, for our considerations, we just need that \( \varphi(u) \) is monotonically increasing.

We can now demonstrate that in order to compute the maximum likelihood estimate, we need that

1. All neurons have an identical receptive field, which differs just for the preferred position.
2. After training, the receptive field reproduces the spatial distribution of the sensory input:

\[
r^S_{kj} = r^{S \text{ max}} \exp \left[-\frac{(d(\vartheta_k, \vartheta_j))^2}{2\sigma^2} \right] \quad j = 1, 2, \ldots, N.
\]

(2.15)

We now analyze how equation 2.15 can be approximately realized using a physiological training rule (i.e., a Hebbian rule with a decay term). If we make use of equation 2.15 within equation 2.12, we obtain the following general expression for the logarithmic likelihood function at the position \( \vartheta_k \) \((k = 1, 2, \ldots, N)\):

\[
\ln(l(\vartheta_k)) = -\sum_{j=1}^{N} \ln \left(\sqrt{2\pi u^{S^2}}\right)
- \frac{1}{2u^{S^2}} \sum_{j=1}^{N} \left( i^S_j - i^{S \text{ max}} \exp \left[-\frac{(d(\vartheta_k, \vartheta_j))^2}{2\sigma^2} \right] \right)^2 =

= -\sum_{j=1}^{N} \ln \left(\sqrt{2\pi u^{S^2}}\right) - \frac{1}{2u^{S^2}} \sum_{j=1}^{N} \left( i^S_j - i^{S \text{ max}} \frac{r^{S \text{ max}}}{r^S_{kj}} \right)^2 =

= -\sum_{j=1}^{N} \ln \left(\sqrt{2\pi u^{S^2}}\right) - \frac{1}{2u^{S^2}} \sum_{j=1}^{N} i^S_j

\[
- \frac{1}{2u^{S^2}} \left( i^{S \text{ max}} \frac{r^{S \text{ max}}}{r^S_{kj}} \right)^2 \sum_{j=1}^{N} r^S_{kj} + \frac{1}{u^{S^2}} i^{S \text{ max}} \sum_{j=1}^{N} i^S_j r^S_{kj}.
\]

(2.16)
Of course, the first two terms in the right-hand member of equation 2.16 are independent of $k$. However, in virtue of the assumption 1, we can claim that the quantity $\sum_{j=1}^{N} r_{kj}^S$ is also independent of $k$ (in particular, we use a circular distance in writing the expression of the receptive fields in order to avoid any border effect). Therefore, we can write

$$\ln(l(\vartheta_k)) = \alpha + \frac{1}{u^S_{\text{Max}}} \sum_{j=1}^{N} r_{kj}^S i_j^S,$$ \hspace{0.5cm} (2.17)

where $\alpha$ represents the sum of the first three terms in the right-hand member of equation 2.16, which does not depend on the particular value of $\vartheta_k$. Therefore, in order to maximize the logarithmic likelihood function, one simply needs to maximize the quantity $u_k^S = \sum_{j=1}^{N} r_{kj}^S i_j^S$ (see equation 2.13). Finally, by remembering that $\varphi(u)$ is an increasing monotonic function, we have

$$\hat{\vartheta}_k^S = \arg \max \{ \ln(l(\vartheta_k)) \} = \arg \max \{ u_k^S \} = \arg \max \{ y_k^S \}.$$ \hspace{0.5cm} (2.18)

Equation 2.18 says that the neuron with maximal activity signals the stimulus position, according to a maximum likelihood estimate (of course, with a resolution provided by the distance between two consecutive $\vartheta_k$). For this reason, in the following we will assume that the stimulus position is coded by the neuron with maximal activity. Alternatively, in order to improve the resolution, we will also use a barycenter metric (which, due to the network circular symmetry, provides a value quite close to the maximum).

In order for equation 2.18 to be verified, assumptions 1 and 2, concerning the receptive fields, must be true. These require a few comments. Assumption 1 implies that the preferred position of the neurons has a uniform distribution (i.e., positions are equally represented in the network) and that, during training, all positions are stimulated from the external input in the same way (i.e., no position receives a stronger input than another or a more frequent input). Assumption 2 implies that the receptive field, after training, reproduces the average spatial distribution of the input at the given preferred position (i.e., $r_{kj}^S \propto m_j^S(\vartheta_k)$). The latter requirement can be attained using the following training rule, which in vectorial form can be written as

$$\Delta R_{kj}^S = \gamma y_k^S (I^S - R_k^S),$$ \hspace{0.5cm} (2.19)

where $\Delta R_{kj}^S$ represents the variation in the receptive field entering a neuron in the sensory modality $S$ with preferred position $\vartheta_k$. In scalar form,
\[
\Delta r^{S}_{k,j} = \gamma y^{S}_{k} \left( \hat{r}^{S}_{j} - r^{S}_{kj} \right),
\]

(2.19')

which is substantially a Hebb rule with a decay term (see neural network textbooks for more details on this rule, for instance Hertz, Krogh, & Palmer, 1991).

According to equation 2.19, a neuron with high-output activity modifies its receptive field, shaping it based on the actual input and pruning the distal portion of its previous configuration. Conversely, silent neurons with poor output activity do not appreciably modify their receptive field. As demonstrated in neural network textbooks (Hertz et al., 1991), after a long training, the receptive field vector \( R^{S}_{k} \) will be positioned close to the mean value of the inputs, which significantly activated that neuron. In our case, this value is proportional to \( M^{S}(\vartheta^{k}) \): in scalar form, this is equation 2.7 with \( \vartheta^{S} = \vartheta^{k} \). Hence, we have

\[
R^{S}_{k} \propto M^{S}(\vartheta^{k}),
\]

(2.20)

which is the vector form of equation 2.15.

It is worth noting that to improve the effect of the adopted training rule, so that equation 2.20 is actually satisfied, one can benefit from a winner-takes-all dynamics for the neurons, so that in response to an external input, just a few neurons win the competition, while most neurons are silent. In this way, a neuron modifies its synapses only when the input is close to its preferred spatial position. For this reason, as usually done when working with this kind of network, we introduced lateral synapses implementing a competition between neurons (see section 2.2.1).

2.1.4 A Cross-Modal Network for the Posterior Probability (Bayesian) Estimate. Let us now consider the case in which the two sensory inputs (\( I^{A} \) and \( I^{V} \)) are not independent, as in the previous case, but are linked through the prior probability \( p(\vartheta^{A}, \vartheta^{V}) \). In this case, one has to maximize the numerator of equation 2.2, which can be rewritten in logarithmic form. We have

\[
\left[ \widehat{\vartheta}^{A}, \widehat{\vartheta}^{V} \right] = \arg \max \left\{ p(\vartheta^{A}, \vartheta^{V}) \left( p(I^{A} | \vartheta^{A}) p(I^{V} | \vartheta^{V}) \right) \right\} = \\
= \arg \max \left\{ \ln \left( p(\vartheta^{A}, \vartheta^{V}) \right) + \ln \left( p(I^{A} | \vartheta^{A}) \right) + \ln \left( p(I^{V} | \vartheta^{V}) \right) \right\}. 
\]

(2.21)

Of course, in case of uniform prior probability, equation 2.21 is the same as the likelihood estimate, performed separately on \( \vartheta^{A} \) and \( \vartheta^{V} \).
In the following, we will denote with \( \psi (\theta^A, \theta^V) \) the function to be maximized,

\[
\psi (\theta^A, \theta^V) = \ln (p(\theta^A, \theta^V)) + \ln (p(I^A | \theta^A)) + \ln (p(I^V | \theta^V)) = \ln (p(\theta^A, \theta^V)) + \ln (l(\theta^A)) + \ln (l(\theta^V)),
\]

with \( I^A \) and \( I^V \) known.

Let us now consider that each of the log likelihood function \( \ln(l(\theta^S)) \) in equation 2.21' has expression 2.12, but with different parameters in the two modalities (\( S = A, S = V \)); in particular, we assume that \( \sigma^A \) is different from \( \sigma^V \): the two stimuli have different spatial accuracy and \( i^A_{\text{Max}} \neq i^V_{\text{Max}} \) (i.e., the two stimuli may have a different strength). Hence, equation 2.21' can be written as

\[
\psi (\theta^A, \theta^V) = - \sum_{j=1}^{N} \ln \left( \sqrt{2\pi \sigma^A} \right) - \frac{1}{2\sigma^A} \sum_{j=1}^{N} \left( i^A_j - i^A_{\text{Max}} \right)^2 \exp \left[ \frac{- (d(\theta^A, \theta_j))^2}{2\sigma^A} \right] - \sum_{j=1}^{N} \ln \left( \sqrt{2\pi \sigma^V} \right) - \frac{1}{2\sigma^V} \sum_{j=1}^{N} \left( i^V_j - i^V_{\text{Max}} \right)^2 \exp \left[ \frac{- (d(\theta^V, \theta_j))^2}{2\sigma^V} \right] + \ln (p(\theta^A, \theta^V)),
\]

where \( \nu^V \) and \( \nu^A \) represent the standard deviation of the noise in the visual and auditory sensory representation. The maximum posterior probability Bayesian estimator (BE) is obtained by computing the values \( (\hat{\theta}^A, \hat{\theta}^V) \) that maximize equation 2.22 using a known prior probability.

Let us now consider a network of \( N \) neurons for each modality implementing the corresponding likelihood function according to expression 2.16. By using equation 2.16 within equation 2.22, we can compute the following expression for the function \( \psi (\theta^A, \theta^V) \), evaluated at two different positions (position \( \theta^A_k \) for the \( k \)th auditory neuron and position \( \theta^V_h \) for the
Let us now consider that all neurons in a given modality have identical receptive fields. In this condition, the third and seventh terms in equation 2.23 are independent of the particular values of \( k \) and \( h \). Hence, the maximization of equation 2.23 corresponds to the maximization of the following new function (by also neglecting all other terms that do not depend on \( k \) and \( h \)):

\[
\tilde{\psi} (\vartheta^A_k, \vartheta^V_h) = \frac{1}{u^A} \iota^A_{\text{Max}} \sum_{j=1}^N i^A_j r^A_{kj} + \frac{1}{u^V} \iota^V_{\text{Max}} \sum_{j=1}^N i^V_j r^V_{kj} + \ln \left( p (\vartheta^A_k, \vartheta^V_h) \right).
\]

(2.24)

It is worth noting that the first two terms in the right-hand member of equation 2.24 are proportional to the external inputs to the auditory and visual neurons, respectively \((u^A_k\), equation 2.13\), and implement the likelihood functions in the two modalities. Hence, if we assume that the neuron output depends only on the term \( u^S_k = \sum_{j=1}^N r^S_{kj} u^S_j \) with \( S = A \) or \( V \), we cannot account for the prior probability (i.e., the third term in equation 2.24). As is clear from equation 2.24, estimating the optimal values of \( \vartheta^A_k, \vartheta^V_h \) requires that the inputs to the auditory and visual neurons are modified to account for the prior probability. In other words, both the auditory and visual neurons must receive a cross-modal term from the other modality, reflecting the prior knowledge.
A typical condition occurs when the two stimuli (the auditory and visual one) frequently originate from the same spatial event; hence, the two positions are correlated. We can assume that the prior probability is given by the weighted sum of a uniform distribution, \( p' (\vartheta^A, \vartheta^V) \), reflecting the possibility that a visual and an auditory stimulus are produced by different events, and a second term, \( p'' (\vartheta^A, \vartheta^V) \), reflecting the (higher) probability that the auditory and visual events are originated from the same source:

\[
p (\vartheta^A, \vartheta^V) = \beta_1 p' (\vartheta^A, \vartheta^V) + \beta_2 p'' (\vartheta^A, \vartheta^V).
\] (2.25)

We can write

\[
p' (\vartheta^A, \vartheta^V) = \frac{1}{D^2}, \quad \text{uniform distribution.} \] (2.26)

Moreover,

\[
p'' (\vartheta^A, \vartheta^V) = p (\vartheta^A) p'' (\vartheta^V | \vartheta^A)
= \frac{1}{D} \frac{1}{\sqrt{2\pi \sigma^{AV^2}}} \exp \left( -\frac{d (\vartheta^A, \vartheta^V)^2}{2\sigma^{AV^2}} \right). \] (2.27)

Equation 2.27 has been written assuming that a single position (e.g., the auditory one) has a uniform distribution (i.e., \( p (\vartheta^A) = 1/D \)); the probability of the second position, in case of a single source, dramatically decreases with the distance. The parameter \( \sigma^{AV} \) reflects the spatial accuracy for the superimposition of the two stimuli, when they originate from the same source. Of course, equation 2.27 integrated on the entire space of possible positions (i.e., between 0 and \( D \)), must satisfy the fundamental axiom of probability. To this end, the following constraint must be used: \( \beta_1 + \beta_2 = 1 \), hence \( \beta_2 = 1 - \beta_1 \).

We thus obtain

\[
p (\vartheta^A, \vartheta^V) = \beta_1 \frac{1}{D^2} + (1 - \beta_1) \frac{1}{D} \frac{1}{\sqrt{2\pi \sigma^{AV^2}}} \exp \left( -\frac{d (\vartheta^A, \vartheta^V)^2}{2\sigma^{AV^2}} \right). \] (2.28)

Parameter \( \beta_1 \) represents the fraction of cross-modal stimuli coming from independent sources. Conversely, \( 1 - \beta_1 \) represents the fraction of cross-modal stimuli coming from a single source.

It is worth noting that equation 2.28 can also be used to implement the causal inference problem: \( \beta_1 = 1 \) signifies that the subject considers the two sources as completely independent, while \( \beta_1 = 0 \) considers the two sources as coming from the same event.
Finally, let us consider the inclusion of equation 2.28 into equation 2.24 in the two extreme cases. If $\beta_1 = 1$, maximization of equation 2.24 simply returns the maximum likelihood estimate, separately performed on the auditory and the visual network (to separately maximize the first and second terms in the right hand member). Conversely, if $\beta_1 \neq 1$, the prior probability must be taken into account. Let us consider the typical case where $\beta_1 \ll 1$, and so the first term in equation 2.28 is negligible. Then equation 2.24 furnishes

$$
\tilde{\psi} (\vartheta^A_k, \vartheta^V_h) = \frac{1}{\nu^A} \sum_{j=1}^{N} i^A_j r^A_{kj} + \frac{1}{\nu^V} \sum_{j=1}^{N} i^V_j r^V_{hj}
$$

$$
- \ln \left( D \sqrt{2\pi \sigma^{AV^2}} \right) - \frac{d (\vartheta^A_k, \vartheta^V_h)^2}{2\sigma^{AV^2}}.
$$

(2.29)

Since the third term is constant, the quantity to be maximized now becomes

$$
\tilde{\psi} (\vartheta^A_k, \vartheta^V_h) = \frac{1}{\nu^A} \sum_{j=1}^{N} i^A_j r^A_{kj} + \frac{1}{\nu^V} \sum_{j=1}^{N} i^V_j r^V_{hj} - \frac{d (\vartheta^A_k, \vartheta^V_h)^2}{2\sigma^{AV^2}}.
$$

(2.32)

This signifies that we need a cross-modal term, which reduces the function to be maximized, the greater the distance between the two positions, $\vartheta^A_k$ and $\vartheta^V_h$.

Let us now assume that the last term in equation 2.30 is equally divided into two equal contributions. We can write

$$
\tilde{\psi} (\vartheta^A_k, \vartheta^V_h) = \frac{1}{\nu^A} \sum_{j=1}^{N} i^A_j r^A_{kj} - \frac{U^A}{4\sigma^{AV^2}} r^A_{max} \frac{d (\vartheta^A_k, \vartheta^V_h)^2}{r^A_{max}}
$$

$$
+ \frac{1}{\nu^V} \sum_{j=1}^{N} i^V_j r^V_{hj} - \frac{U^V}{4\sigma^{AV^2}} r^V_{max} \frac{d (\vartheta^A_k, \vartheta^V_h)^2}{r^V_{max}}
$$

(2.31)

We can interpret the term inside the first bracket as the input to the auditory neuron at position $k$ and the term in the second bracket as the input to the visual neuron at position $h$. Both are then transformed into neuron output through a monotonic function. If this assumption holds, maximization of equation 2.31 is the same as maximization of the activity in the two neural chains (the auditory one, to obtain $\vartheta^A_k$, and the visual one, to obtain $\vartheta^V_h$). We can conclude that each neuron must receive an additional
Figure 1: Neural network model. (a) The neural network used in this letter to address the problem of two separate estimates for the positions of the auditory and visual stimuli. Each neuron accomplishes the scalar product of the external stimulus and its receptive field \((r_{kj})\), but also receives lateral synapses \((\lambda_{kj})\) from other neurons of the same modality and cross-modal synapses \((w_{kj})\) from neurons of the other modality. Synapses \(r_{kj}\) and \(w_{kj}\) are trained with the adopted learning rule. After training, they acquire a campanular shape (see Figure 4). (b) Modification of the previous network to address the single causal inference problem, when the observer is envisaged as treating the two stimuli as a single event (see section 2.2.3). Neurons in the downstream multimodal network receive excitatory inputs from the two unisensory (auditory and visual) neurons located at the same position, with identical weights.

input, besides that coming from its receptive field, signaling the distance from the winner in the other modality. We claim this can be easily realized with cross-modal synapses.

These ideas are implemented via the neural network described below.

### 2.2 Calculation: Implementation of the Neural Network

#### 2.2.1 Basal Structure of the Network

The neural network model consists of two chains of \(N\) unisensory neurons (see Figure 1, upper panel). Each neuron codes for a particular spatial position in its modality. Moreover,
each chain is topologically organized: proximal neurons code for proximal positions. In the following, we will denote with a superscript the particular area (auditory or visual) and with a subscript the neuron position within the area.

Each neuron receives three different kinds of inputs: a sensory input from the environment (say, \( u \)), a lateral input from neurons of the same modality (say, \( l \)), and a cross-modal input from neurons of the other modality (say, \( c \)). The global input (equal to the sum of the previous three contributions) is then passed through a sigmoidal relationship, \( \phi() \), which accounts for the presence of a lower threshold and upper saturation in neuron activity, and a first-order low-pass filter with time constant \( \tau \), which accounts for the neuron’s integrative capacity.

Hence, for the generic \( k \)th neuron in the modality \( S \) (\( S = A \) or \( V \) for the auditory and visual modalities, respectively), we can write

\[
\tau \frac{dy^S_k}{dt} = -y^S_k + \phi \left( u^S_k + l^S_k + c^S_k \right),
\]

where \( y^S_k \) represents the neuron output and the sigmoidal relationship is described by the following equation,

\[
\phi(x) = \frac{1}{1 + \exp\left(-s(x - x_0)\right)}.
\]

\( s \) and \( x_0 \) are parameters, which set the slope and the position of the sigmoidal relationship. According to equation 2.33, the neuron output activity is normalized between zero and one (zero means a silent neuron, one a maximally activated neuron).

It is worth noting that for simplicity, we used the same parameters (\( \tau \), \( s \), and \( x_0 \)) for all neurons independent of their modality. This choice was adopted to minimize the number of model assumptions.

The expression for the sensory input is computed as the scalar product of the sensory representation of the stimulus \( (I^S_k = [i^S_{1k} i^S_{2k} \ldots i^S_{Nk}]^T) \) and the neuron receptive field \( (R^S_k = [r^S_{1k} r^S_{2k} \ldots r^S_{Nk}]^T) \):

\[
u^S_k = \sum_{j=1}^{N} r^S_{kj} i^S_j,
\]

which is the same as equation 2.13.

We assumed that the neuron receptive field, \( R^S_k \), initially has a large extension, described with a gaussian function, and then progressively shrinks during training to fit the width of the external input (see section 2.2.2).
The lateral input is computed as
\[ I_k^S = \sum_{j=1}^{N} \lambda_{kj} y_j^S, \]  
(2.35)
where \( \lambda_{kj} \) represents a lateral intra-area synapse connecting the presynaptic neuron \( j \) to the postsynaptic neuron \( k \) in the same area. Here, we used the classical Mexican hat arrangement: a neuron is excited by proximal neurons in the same area and inhibited by more distal ones,
\[ \lambda_{kj} = \lambda_{ex} \exp \left( -\frac{d(\vartheta_j, \vartheta_k)^2}{2\sigma_{ex}^2} \right) - \lambda_{in} \exp \left( -\frac{d(\vartheta_j, \vartheta_k)^2}{2\sigma_{in}^2} \right), \]  
(2.36)
where \( \lambda_{ex}, \lambda_{in}, \sigma_{ex}, \sigma_{in} \) are parameters that set the strength and width of the excitatory and inhibitory portions of the Mexican hat. In particular, we have \( \lambda_{ex} > \lambda_{in} \) and \( \sigma_{ex} < \sigma_{in} \). Moreover, \( d(\vartheta_j, \vartheta_k) \) represents the distance between neurons’ preferred positions:
\[ d(\vartheta_j, \vartheta_k) = \begin{cases} |\vartheta_j - \vartheta_k| & \text{if } |\vartheta_j - \vartheta_k| \leq D/2 \\ D - |\vartheta_j - \vartheta_k| & \text{if } |\vartheta_j - \vartheta_k| > D/2 \end{cases}. \]

It is worth noting that we used the same expression of lateral synapses (see equation 2.36) in both the auditory and visual areas to limit the number of model assumptions.

Finally, the cross-modal term in equation 2.32 is computed as the convolution of the vector of cross-modal synapses and the activity in the other unisensory area:
\[ c_k^S = \sum_{j=1}^{N} w_{kj}^{SQ} y_j^Q \] \text{ with } S = A \text{ or } V \quad Q = A \text{ or } V \text{ with } S \neq Q, \]  
(2.37)
where \( w_{kj}^{SQ} \) represents a cross-modal synapse from the presynaptic neuron \( j \) in area \( Q \) to the postsynaptic neuron \( k \) in area \( S \). We assumed that the cross-modal synapses are initially ineffective and are progressively reinforced during the training phase.

### 2.2.2 Training the Network
Starting from the initial basal value of synapses, the network has been trained during a period in which the sensory input representations (i.e., \( I^A \) and \( I^V \)) have been given with a random distribution. In particular, we assumed that the sensory inputs are composed of a deterministic term, which represents the spatial distribution of
the input, centered on the stimulus spatial position, and a gaussian white noise term (zero mean value and assigned standard deviation). Hence,

\[ i^S_k = i^S_{\text{Max}} \exp \left( -\frac{(\vartheta^S - \vartheta_k)^2}{2\sigma^S} \right) + n^S_k \]  

with \( S = A, V \), \( (2.38) \)

where \( \vartheta^S \) represents the spatial position of the stimulus, \( i^S_{\text{Max}} \) is the stimulus strength (equal to the value of the stimulus at the central position in the absence of noise), and \( \sigma^S \) is the standard deviation of the spatial representation. According to physiology, we assumed that the visual inputs are spatially more accurate than the auditory ones; hence, we set \( \sigma^V < \sigma^A \). Conversely, we assumed that the standard deviation of noise (say, \( \nu^S \)) is a given fraction of the input strength. In the subsequent simulations, we assumed \( \nu^S = i^S_{\text{Max}}/3 \).

The positions of the two stimuli (\( \vartheta^A \) and \( \vartheta^V \) in equation 2.38) have been randomly generated from the prior probability distribution in equation 2.28, using a very small value for parameter \( \beta_1 \) (see section 3)—we assumed that the two stimuli, when simultaneously present (cross-modal condition), are always generated from the same source.

The synapses describing the receptive field, \( r^S_{kj} \) and those describing the cross-modal link between the two areas, \( w^{SQ}_{kj} \) have been trained using a learning rule with a classical Hebbian potentiation factor and a decay term. We can write, in scalar form,

\[ \Delta r^S_{kj} = \gamma y^S_k \left( i^S_j, -r^S_{kj} \right) \]  

with \( S = A, V \), \( (2.39) \)

\[ \Delta w^{SQ}_{kj} = \gamma y^S_k \left( y^Q_j - w^{SQ}_{kj} \right) \]  

with \( S = A, V \) \( Q = A, V \) \( Q \neq S \). \( (2.40) \)

Equations 2.39 and 2.40 have been applied, at each step, using the final steady-state values of the neuron output (i.e., when transient phenomena are exhausted).

At the beginning of training, all cross-modal synapses are assumed equal to zero. Conversely, the receptive field synapses have a broad spatial extension and moderate amplitude, identical for the two modalities:

\[ r^S_{kj} = r_0 \exp \left( -\frac{(d_j - d_k)^2}{2\sigma^2_R} \right) \]  

with \( S = A, V \), \( (2.41) \)

where \( r_0 \) sets the initial strength of the receptive field and \( \sigma_R \) establishes its initial spatial extension (we assume \( \sigma_R > \sigma_A \) and \( \sigma_R > \sigma_V \), a wide initial
Table 1: Parameters Values.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma^A$</td>
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</tr>
<tr>
<td>$\sigma^V$</td>
<td>$4^\circ$</td>
</tr>
<tr>
<td>$i^A_{\text{Max}}$</td>
<td>$36$</td>
</tr>
<tr>
<td>$i^V_{\text{Max}}$ (moderately blurred)</td>
<td>$47$</td>
</tr>
<tr>
<td>$i^V_{\text{Max}}$ (strongly blurred)</td>
<td>$86$</td>
</tr>
<tr>
<td>$\nu^A = i^A_{\text{Max}}/3$</td>
<td>$\nu^V = i^V_{\text{Max}}/3$</td>
</tr>
<tr>
<td>$\tau$</td>
<td>$5$ ms</td>
</tr>
<tr>
<td>$\lambda_{\text{ex}}$</td>
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</tr>
<tr>
<td>$\lambda_{\text{in}}$</td>
<td>$1.85$</td>
</tr>
<tr>
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</tr>
<tr>
<td>$\sigma^V_{\text{in}}$</td>
<td>$24^\circ$</td>
</tr>
<tr>
<td>$\sigma^A_{\text{av}}$</td>
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</tr>
<tr>
<td>$\beta_1$</td>
<td>$10^{-14}$</td>
</tr>
<tr>
<td>$N$</td>
<td>$180$</td>
</tr>
<tr>
<td>$D$</td>
<td>$180$</td>
</tr>
<tr>
<td>$x_0$</td>
<td>$0.7$</td>
</tr>
<tr>
<td>$s$</td>
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<td>$r_0$</td>
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<tr>
<td>$w^V_{\text{MV}}$</td>
<td>$16$</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>$0.04$</td>
</tr>
</tbody>
</table>

receptive field). Of course, equation 2.41 holds only at the first step of training.

2.2.3 Inference of a Single Position. The previous network can provide a separate estimation for the auditory and visual positions, using the maximum activity or the barycenter in each layer separately. However, in a complex environment, the observer is asked to infer a single position for a multisensory event. To assess this problem, we included a further downstream layer of multimodal neurons (see Figure 1, bottom panel). The single position is then computed using the maximum activity (or the barycenter) in this layer.

For simplicity, we assumed that each neuron in the multimodal layer receives excitation just from the two unisensory neurons (auditory and visual), located at the same spatial position, via identical weights. This network arrangement agrees with the assumption by others (see Ma et al., 2006 and Fetsch et al., 2012) that the sum of population codes can be used to realize an optimal Bayesian inference. The output of the multimodal neurons is then computed using the same sigmoidal characteristic, $\phi(x)$ (see equation 2.33, used for unisensory neurons. Hence, we can write:

$$y^M_k = \varphi \left( u^M_k \right) = \varphi \left( w^{MA} y^A_k + w^{MV} y^V_k \right),$$

where $y^M_k$ is the activity of the multimodal neuron at position $k$, and $w^{MA} = w^{MV}$ are the two synapse weights from the unisensory neurons to the multimodal neuron (see table 2 and the appendix for the parameter choice). Temporal dynamics has not been used in equation 2.42, since this is superfluous in a feedforward schema.

All model parameters are shown in Table 1. Parameter assignment is discussed in the appendix.

3 Results

In order to test the concepts developed in section 2, we simulated the neural network behavior and compared the results with those obtainable with the
Figure 2: The receptive fields shrink during training. Examples of the progressive shrinking of the receptive fields (RFs) during training with the adopted rule. The figures illustrate the RFs of two exemplary neurons (one auditory, left panel; the other visual, right panel) with preferred position at 90°. The behavior of the other RFs is similar, with small statistical differences due to noise and random input presentations. The dashed green lines are the RFs at different steps during training. The continuous red lines are the final RFs. It is worth noting that at the end of training, the visual RFs are more tuned than the auditory ones, reflecting the more precise spatial localization of the inputs.

3.1 Receptive Fields. First, we analyzed how the RFs are progressively affected by training. To this end, Figure 2 shows how the RFs of two representative auditory and visual neurons change: they are initially large and progressively shrink until they reach a final stable configuration. Worth noting, the RFs of auditory neurons remain quite large, whereas the visual

Theoretical estimators (the MLE in unimodal conditions and the Bayesian maximum posterior probability estimator in cross-modal conditions).

The network was subjected to 18,000 epochs of training. Each epoch consisted of five trials: two unisensory auditory stimuli, two unisensory visual stimuli and one cross-modal stimulus. At the end of each individual trial (duration 120 ms), when the neurons are in steady-state conditions, the synapses were trained using the learning rules described in section 2 (i.e., a Hebb rule with a decay factor). Hence, the total number of trials was 90,000. The position of the stimuli was randomly chosen between 1 and 180 (uniform distribution). In the case of cross-modal stimuli, the visual stimulus was always almost coincident with the auditory one: we used equation 2.28, with $\sigma_{AV} = 1.5°$ and $\beta_1 \equiv 0$ (hence, the two positions differ less than 3°, with 90% probability). This choice reproduces a situation in which the two stimuli originate from the same source and so have almost identical location. The same cross-modal probability was used, as a prior probability, in implementing the theoretical Bayesian estimator.

All parameters characterizing the training phase (e.g., learning rate, superimposed noise) are reported in section 2.
An important consequence of the adopted training rule is that after training, the RF of each neuron reflects the average input exciting that neuron. In our model, this is provided by equation 2.7 a gaussian function with assigned standard deviation ($\sigma^A = 20^{\circ}$ for the auditory inputs and $\sigma^V = 4^{\circ}$ for the visual ones). To check this prediction, Figure 3 compares the final RFs of the two exemplary neurons with the gaussian functions representing the average inputs used during training. The agreement is very good for what concerns the auditory RF; the visual RF also shows good agreement as to the spatial SD but with a small difference in the amplitude. We ascribe this small difference to the effect of lateral synapses.

In conclusion, we can say that after training with the specific adopted rule, the SD of the RFs carefully reflects the average SD of the input stimuli, with the visual neurons more spatially focused than the auditory ones.

3.2 Cross Modal Synapses. If all input stimuli were unimodal, no cross-modal synapses would be generated and the two networks would behave as purely unisensory. In this condition, changes in the RFs would be the unique effect of training, and the network would implement a maximum likelihood estimate of the individual unisensory inputs (see section 2 for a demonstration). However, thanks to the presence of a certain amount of cross-modal stimuli, cross-modal synapses are also created between the two networks. By way of example, Figure 4 shows the synapses entering into one exemplary auditory and one exemplary visual neuron from all neurons in the other modality. The cross-modal synapses initially are ineffective and progressively are reinforced on the basis of the sensory experience perceived during the training. At the end of this phase, a neuron in one

Figure 3: The final receptive fields match the average inputs. Comparison between the final values of the RFs (for the two same exemplary neurons as in Figure 2) and the average inputs used during training at the given location (see equation 2.7). The RFs (continuous red lines) are very close to the average inputs (dashed blue lines), an essential property of the adopted learning rule.
Figure 4: Cross-modal synapses’ development during training. Examples of the progressive development of cross-modal synapses during training with the adopted rule. The figure illustrates the synapses entering into two exemplary neurons (one auditory, left panel; the other visual, right panel) with preferred position at 90°, from all other neurons in the other modality (these are synapses $w_{90}^{AV}$ and $w_{90}^{VA}$ with $j = 1, 2, \ldots, 180$). The dashed green lines are the synapse patterns at different steps during training. The continuous red lines are the final synapses. The synapses start from zero and then progressively rise up to a final steady-state level, reflecting the statistics of cross-modal stimuli.

modality receives synapses from neurons in the other modality, which code for approximately the same position. This incorporates the multisensory experience in the cross-modal synapses and thus reflects a prior knowledge on the frequent co-occurrence of stimuli at the same position.

After training, we tested network behavior with a variety of input stimuli. First, we analyzed how the network provides separate estimates for the visual and auditory modality (in both unimodal and cross-modal conditions), computed as a metric (the maximum or the barycenter) in the corresponding visual and auditory layers. We also tested a third metrics (the vector population decoder described in Fischer & Peña, 2011). However, it provides results almost indistinguishable from those of the barycenter metrics. Then we examined how the network, in the case of cross-modal stimuli presentation, can infer a single position by envisaging the bimodal presentation as a single event by computing the metrics in the downstream multisensory layer.

3.3 Model Response to Unimodal Inputs. First, we simulated the response of the trained network to unimodal inputs. In this condition, due to the low values of cross-modal synapses, only the network in one modality is excited; the other layer remains silent (we verified that a single unimodal stimulus does not produce any phantom effect in the other modality).

As described in the section 2.1.3, in unimodal conditions, the external input to neurons (i.e., the inner product between the stimulus and the
Figure 5: The external input in a unimodal layer matches the likelihood function in unimodal conditions. Comparison between the external input (inner product between the stimulus and receptive field) reaching the 180 neurons in a unisensory layer during a unimodal stimulation (dashed red line) and the logarithm of the likelihood function (dot-dash blue line). All figures refer to a single unimodal stimulation (left panel, auditory; right panel, visual), with the noisy external stimulus placed at 90 degree. Per each neuron, the external input was computed as the scalar product of the external stimulus and the receptive field. The continuous green lines represent the overall input to the neurons, including the contributions of lateral synapses from other neurons of the same modality. The curves are normalized to sum one. Worth noting, the log-likelihood function is very close to the external input. The contribution of the lateral synapses moderately sharpens this curve, but does not appreciably modify the maximum or the barycenter.

Moreover, we can observe that the network auditory likelihood is larger than the visual one, reflecting the poorer spatial accuracy of the auditory stimuli. This signifies that a visual stimulus placed at a certain distance may
Figure 6: The errors in the network estimates match the maximum likelihood errors. Comparison between the errors in the perceived positions of the auditory (upper panel) and visual (bottom panel) stimuli, obtained in unimodal trials with the maximum likelihood estimator (black asterisks) and the network metrics (position of the neuron with maximal activity, green circles; barycenter of the activity, continuous line). For each modality, 180 unimodal trials were performed with stimuli at all positions. The figure displays the position of the stimulus in the $x$-axis, and the perceived error (estimated position minus true position) in the $y$-axis. Worth noting, the estimates obtained with the network are close to the MLE estimates. Moreover, visual estimates are more precise than the auditory ones. Mean values and SD are reported in Table 2.

affect the auditory response (due to the broader neural input of auditory neurons) but not vice versa. As shown later, this phenomenon is at the origin of ventriloquism, that is, the capacity of the more accurate stimulus to affect perception of the less accurate one.

Finally, we compared the positions estimated with the network (in unimodal conditions) with those of the MLE. To this end, we performed 180 trials for each modality by providing a noisy unimodal stimulus at each position. Results are shown in Figure 6, where the predictions obtained with the MLE (by maximizing equation 2.12) are compared with the predictions obtained with the network using the position of the maximally active neuron. For completeness, we also show the results obtained using the barycenter of neuron activity in the layer. The results underline the strong similarities between the MLE and the network estimate in the case of both maximum activity or barycenter metrics. As expected, the estimate of the visual position is more accurate compared with the auditory position estimate.

A final comparison between the different estimates (in terms of mean value and SD) is given in the upper panel of Table 2. In this table we present
Table 2: Comparison between the Performance of the Maximum Likelihood Estimator, the Network Barycenter Estimator, and the Maximal Network Activity Estimator, Computed in Unimodal Conditions (Upper Panel), and Comparison with the Bayesian Estimator in Cross-Modal Conditions (Bottom Panel).

<table>
<thead>
<tr>
<th>Unisensory</th>
<th>Maximum Likelihood</th>
<th>Barycenter</th>
<th>Maximum Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean (auditory)</td>
<td>−0.21</td>
<td>−0.24</td>
<td>−0.23</td>
</tr>
<tr>
<td>SD (auditory)</td>
<td>1.55</td>
<td>1.51</td>
<td>1.58</td>
</tr>
<tr>
<td>Mean (visual)</td>
<td>−0.1</td>
<td>−0.21</td>
<td>−0.22</td>
</tr>
<tr>
<td>SD (visual)</td>
<td>0.81</td>
<td>0.98</td>
<td>0.97</td>
</tr>
<tr>
<td>Cross-Modal</td>
<td>Bayesian Estimate</td>
<td>Barycenter</td>
<td>Maximum Activity</td>
</tr>
<tr>
<td>Mean (auditory)</td>
<td>−0.18</td>
<td>−0.15</td>
<td>−0.12</td>
</tr>
<tr>
<td>SD (auditory)</td>
<td>0.98</td>
<td>1.00</td>
<td>0.99</td>
</tr>
<tr>
<td>Mean (visual)</td>
<td>−0.1</td>
<td>−0.22</td>
<td>−0.22</td>
</tr>
<tr>
<td>SD (visual)</td>
<td>0.78</td>
<td>1.00</td>
<td>0.95</td>
</tr>
<tr>
<td>Mean (multisensory)</td>
<td>-</td>
<td>−0.20</td>
<td>−0.11</td>
</tr>
<tr>
<td>SD (multisensory)</td>
<td>-</td>
<td>0.93</td>
<td>0.95</td>
</tr>
</tbody>
</table>

Notes: The input strengths and noise levels were the same as in Table 1. Results have been obtained within 180 independent trials for each modality at all network positions. We report the mean values of the estimates, to show that all estimators are almost unbiased, and the SD of the estimates, as an index of their variability (hence, accuracy of the single estimate). The same estimations were performed in cross-modal conditions, with coincident visual and auditory stimuli. In this case, we compared network results with those of the Bayesian estimator to infer the position of the auditory and visual stimuli. Finally, the last lines represent the estimate of a single common position inferred by the network model in the downstream multisensory layer.

the mean value of the estimates, evaluated on 180 trials, to show that all estimates are almost unbiased, and the SD, as an indicator of their accuracy.

In conclusion, we can say that in unimodal conditions, each trained network approaches an MLE of the stimulus position quite well. In particular, it is worth noting that the SDs in Table 2 depend on two factors: the noise level added to the inputs (the higher the noise, the higher the SD) and the way noise affects the maximum in the curves of Figure 5 (the wider the curves, the higher the noise effect). The latter effect is related to the inverse of the second derivative of the log probability (according to the Cramer-Rao limit). Hence, SDs are not identical to the width of the likelihood functions but are influenced by it.

A reason that the SD in the model is close to the SD of the MLE (despite a sharper activation curve) is that the true external input to the network, without lateral mechanisms, is the same as the log likelihood. The network instantaneously uses this input (the dashed red line in Figure 5) to activate
the corresponding layer, from which a maximum can be extrapolated. This maximum (the neuron with higher activation) then governs the subsequent lateral competition mechanism: a winner-takes-all dynamics that reinforces the maximum without changing its position. In other words, the accuracy in our model is substantially the same as in the MLE, since the lateral synapses just sharpen the activation curve around a preestablished maximum.

3.4 Model Response to Cross-Modal Inputs. Subsequently we simulated network behavior in response to cross-modal stimuli. First, we repeated the estimates in Table 2 using two cross-modal stimuli at the same position. The results are presented in the bottom panel of Table 2 and compared with the predictions of the maximum posterior probability Bayesian estimator (see equation 2.22). To this end, we used the same prior probability (see equation 2.28) adopted during training in the case of cross-modal stimuli (i.e., a uniform distribution of one stimulus and a gaussian density with 1.5° standard deviation, to represent the distance between the two stimuli). Parameter $\beta_1$ was chosen close to zero, to admit the remote possibility that the two cross-modal inputs originate independently (see section 2 for more details). The choice of the prior probability is discussed in the section 4. Finally, in cross-modal conditions, we also evaluated the accuracy of a single position estimate for both stimuli, performed in the multisensory layer (see section 3.5).

Several conclusions can be drawn by comparing results in cross-modal conditions with those in the unisensory cases:

- The accuracy of the auditory estimate improves compared with the unisensory case, thanks to the presence of a spatially coincident input of the other modality.
- The accuracy of the visual estimate in the multisensory condition is almost the same as in the unisensory case.
- The accuracy of the position inferred in the multisensory layer is just a little better than position estimates in each of the unisensory layers.
- There is good agreement between model estimates in multisensory conditions and the Bayesian estimates, although the latter have a smaller SD for the visual case.

However, the results were obtained using rather strong inputs, able to evoke a significant activity in the unisensory layers (more than two-thirds the maximum). Since the benefits of multisensory integration are especially evident in the presence of weak stimuli (inverse effectiveness), we repeated the previous estimates using weaker inputs (able to evoke an activity in unisensory conditions as low as 30% of the maximum) and greater percentage noise. Now (see Table 3) one can observe that the SDs in unisensory conditions are higher than in the previous case due to the greater influence of noise. In multisensory conditions, we can observe a moderate improvement in both auditory and visual estimates, especially evident looking at
the maximum activity estimator. However, the performance of the network is less accurate compared with the Bayesian estimator. A significant improvement of the estimate can be achieved looking at the position in the multisensory layer (it computes a single position for both stimuli); in particular, the barycenter metrics exhibits very high performance. This is the consequence of inverse effectiveness; activity in the multisensory layer reveals a strong enhancement compared with the unisensory case.

These results point out the advantage of having multisensory integration versus unisensory inputs.

Subsequently, we investigated the ventriloquism effect (Bertelson & Radeau, 1981; Hairston et al., 2003; Wallace et al., 2004). To this end, we provided two cross-modal inputs at different positions: the auditory stimulus was placed from position 1° to 180°, and at each auditory position, we added a second visual stimulus with a distance from −40° to +40° from the auditory one. A fundamental aspect of these trials is that both networks are simultaneously excited and, due to the presence of cross-modal synapses, the activity in one network is affected by the activity in the other. Hence, the perceived position of the stimuli (both computed with the maximum activity or the barycenter metrics) is shifted compared with the real one.

A first summary of the results is presented in the upper panels of Figure 7, where we show the shift between the true position of the stimulus and the perceived position (in the corresponding unimodal layers), plotted versus the distance between the auditory and the visual stimuli. Each point in the figure is the average over 180 trials (we averaged all trials with the same distance between the two stimuli) computed with both the maximum and barycenter metrics. As it is clear from the figure, the perceived position of the auditory stimulus is significantly shifted in the direction of the visual one (positive distances signify that the visual stimulus is at the right of the auditory one and vice versa); hence, we can observe a sort of ventriloquism effect. The perception error is maximal (about 8°) when the audiovisual distance is at about 20°. The perceived position of the visual stimulus is also shifted in the direction of the auditory one, but the error is much smaller (maximum error less than 1.0°). The results are in good agreement with the behavioral ones (Bertelson & Radeau, 1981; Hairston et al., 2003; Wallace et al., 2004) (see the bottom panel in Figure 7). The only significant difference is that in the model, the perception error decreases at a distance greater than 20°, where the behavioral data still exhibit a large error. Possible reasons for these differences are discussed in section 4.

In order to clarify the nature of the ventriloquism effect, Figure 8 shows some snapshots obtained during a single trial (the activity in the two layers frozen at different instants during an exemplary simulation). This figure shows how the activity in the auditory layer, initially positioned around the true auditory stimulus (85°), progressively shifts in the direction of the visual one, as a consequence of the cross-modal inputs, to reach a final position at about 92°.
Figure 7: The network simulates the ventriloquism effect. Ventriloquism effect simulated with the network during cross-modal trials and compared with data from the literature. Cross-modal trials were performed by moving the auditory stimulus from position $1^\circ$ to position $180^\circ$ and, at each auditory position, adding a second visual stimulus with a distance from $-40^\circ$ to $+40^\circ$ from the auditory one. Results are averaged over the 180 trials per each shift. The x-axis represents the audiovisual distance (where positive values indicate that the visual stimulus is placed on the right), and the y-axis is the perceived error (estimated position minus true position). The upper panels show the results with the barycenter metrics (left) and the maximum activity metrics (right) (auditory perception: continuous red line; visual perception: dotted blue line). The bottom panel compares model results (continuous line) with data from the literature. Behavioral data are from (Bertelson & Radeau, 1981; Hairston et al., 2003; Wallace et al., 2004). The auditory perception exhibits a significant shift toward the visual one (ventriloquism). The visual perception exhibits just a minor shift toward the auditory location.

Finally, we compared the predictions of the model, in case of cross-modal inputs, with those obtained with the maximum posterior probability Bayesian estimator (see equation 2.22) in the same cross-modal conditions. The results, illustrated in Figure 9, show satisfactory agreement between the position errors, obtained with the model, and those provided by the
Figure 8: The temporal development of ventriloquism effect. Snapshots of the network activity during the initial 50 ms of a cross-modal stimulation. The figures represent the activities of some central neurons (between position 60 and 120) in the auditory layer (continuous red lines) and the visual network (dash-dotted blue lines) at successive instants, in response to a cross-modal stimulation. The auditory stimulus was placed at $85^\circ$ and the visual stimulus at $100^\circ$ (the true positions are displayed through vertical dashed lines). The progressive shift of the auditory activity toward the visual position is evident. At the end, the auditory shift is about $7^\circ$.

Bayesian estimator. However, we can observe a certain discrepancy between model and Bayesian estimates, especially in the range $20^\circ$ to $30^\circ$ for the auditory position and $15^\circ$ to $20^\circ$ for the visual one. In these ranges, in fact, the Bayesian estimator predicts a smaller ventriloquism for the auditory position and a greater visual shift than the model prediction. To understand these differences, recall that during training, we used not independent cross-modal inputs but inputs at strongly correlated positions. Accordingly, in order to realize the Bayesian estimator, we assumed a prior probability with a very low value of parameter $\beta_1$ (close to zero) in equation 2.28. However, even very small changes in the value of $\beta_1$ are reflected in significant changes in the Bayesian estimate. Moreover, when realizing the Bayesian estimator, we assumed that the standard deviation of correlated inputs in the prior probability (i.e., parameter $\sigma^{AV} = 1.5^\circ$) is perfectly known. This is not the case of a true estimator, which should also perform an estimation of this parameter on real data. For instance, with a value $\sigma^{AV} = 1.0^\circ$, the results of the Bayesian estimator exhibit a smaller ventriloquism range for the auditory perception (up to about $15^\circ$) while the ventriloquism range increases if one uses $\sigma^{AV} = 2.0^\circ$. Conversely, the model behavior is only
Figure 9: The network produces a near-optimal Bayesian estimate in cross-modal conditions. Comparison between the errors in the perceived positions of the auditory (left panel) and visual (right panel) stimuli, obtained in cross-modal trials with the maximum posterior probability (Bayesian) estimator (black asterisks) and the network metrics (position of the neuron with maximal activity, green circles; barycenter of the activity, continuous red line). Cross-modal trials were performed with the auditory stimulus varying from position 1° to position 180° and, at each auditory position, adding a second visual stimulus with a distance from −40° to +40° from the auditory one. The figures display the audiovisual distance on the x-axis and the perceived error (estimated position minus true position) on the y-axis. Worth noting, the estimates of the auditory shift obtained with the network are close to the Bayesian estimates in the range 20° and above 30°.

marginally affected by moderate changes in the parameter $\sigma_{AV}$ (indeed, we repeated the training procedure with $\sigma_{AV}$ in the range 1° to 2°, and observed that the network results are only moderately affected).

In conclusion, we can say that the Bayesian estimates are strongly affected by the values of parameters in the prior probability, while model predictions are less sensitive to a change in these parameters in the training phase.

3.5 Inference of a Single Cause. In all previous simulations, the network provided two separate estimates for the visual and the auditory positions (computed as the barycenter or maximum activity in the corresponding layer); we mimicked trials where subjects are asked to infer the two positions distinctly. Conversely, in the last portion of this work we simulated behavioral experiments in which subjects are asked to infer a unique position, from the combination of the stimuli, treated as a single multisensory event. To perform this behavioral task, we exploited the third layer of multimodal neurons downstream from the unisensory layers, as illustrated in Figure 1b.
Table 3: Comparison between the Performance of the Maximum Likelihood (or Bayesian) Estimator, the Maximal Network Activity Estimator, and the Network Barycenter Estimator, Computed in Unimodal Conditions and Cross-Modal Conditions with Spatially Coincident Auditory and Visual Stimuli.

<table>
<thead>
<tr>
<th></th>
<th>Unimodal Maximum Likelihood</th>
<th>Unimodal Barycenter</th>
<th>Unimodal Maximum Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean (auditory)</strong></td>
<td>0.17</td>
<td>0.19</td>
<td>0.16</td>
</tr>
<tr>
<td><strong>SD (auditory)</strong></td>
<td>2.49</td>
<td>2.57</td>
<td>2.57</td>
</tr>
<tr>
<td><strong>Mean (visual)</strong></td>
<td>−0.39</td>
<td>−0.68</td>
<td>−0.56</td>
</tr>
<tr>
<td><strong>SD (visual)</strong></td>
<td>3.44</td>
<td>2.72</td>
<td>3.42</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Cross-Modal Bayesian Estimate</th>
<th>Cross-Modal Barycenter</th>
<th>Cross-Modal Maximum Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean (auditory)</strong></td>
<td>−0.02</td>
<td>0.12</td>
<td>0.08</td>
</tr>
<tr>
<td><strong>SD (auditory)</strong></td>
<td>1.17</td>
<td>2.09</td>
<td>1.84</td>
</tr>
<tr>
<td><strong>Mean (visual)</strong></td>
<td>−0.07</td>
<td>−0.63</td>
<td>−0.33</td>
</tr>
<tr>
<td><strong>SD (visual)</strong></td>
<td>1.01</td>
<td>2.48</td>
<td>1.41</td>
</tr>
<tr>
<td><strong>Mean (multisensory)</strong></td>
<td>-</td>
<td>−0.13</td>
<td>−0.17</td>
</tr>
<tr>
<td><strong>SD (multisensory)</strong></td>
<td>-</td>
<td>0.95</td>
<td>1.36</td>
</tr>
</tbody>
</table>

Notes: The meaning of the results is the same as in Table 2. However, these simulations have been performed with weaker inputs ($\sigma_A^{\text{max}} = 26$, $\sigma_V^{\text{max}} = 11$ and greater absolute noise $\nu_A = \sigma_A^{\text{max}}$, $\nu_V = \sigma_V^{\text{max}}/2$) to emphasize the benefit of multisensory integration.

The single position estimates, in the case of spatially coincident cross-modal stimuli, are shown in Tables 2 and 3. In particular, Table 3 emphasizes the strong benefit of a multisensory estimate in the case of poor signal-to-noise ratio.

Subsequently, we repeated the cross-modal spatial localization tasks by Alais and Burr (2004). In this case, each trial consists of a cross-modal presentation, with the visual and auditory stimuli in conflict: the visual input was shifted $\Delta^\circ$ rightward and the auditory stimulus $\Delta^\circ$ leftward of the central target position. These trials were repeated at all 180 target positions by varying the shift in the range ($-6^\circ$ $+6^\circ$); in each trial, the barycenter of the multimodal network (or, alternatively, the maximum) in the final steady-state condition was computed as a metrics for the estimated position. The results were then averaged on all 180 positions for each shift. The trials were repeated in three different conditions: (1) basal parameter values, where the visual input is much more spatially accurate than the auditory one ($\sigma_V = 4^\circ$; $\sigma_A = 20^\circ$); (2) the two inputs with the same spatial accuracy ($\sigma_V = 20^\circ$; $\sigma_A = 20^\circ$); and (3) blurred conditions, where the visual stimulus is less accurate than the auditory one ($\sigma_V = 40^\circ$; $\sigma_A = 20^\circ$).
Figure 10: The multimodal layer provides more weights to the more reliable stimulus. Model simulations of the experiments by Alais and Burr (2004) where the observer is asked to treat the two cross-modal stimuli as a single perception. The position was estimated using the barycenter of the activity in the multimodal network of Figure 1b. Cross-modal trials were performed by varying a target position from $1^\circ$ to $180^\circ$ and, at each target position, using a visual stimulus shifted by $+\Delta^\circ$ from the center and an auditory stimulus shifted by $-\Delta^\circ$ from the center (hence, a positive value of $\Delta$ means that the visual stimulus is shifted rightward). At each target position, the “conflict” parameter $\Delta$ was varied from $-6^\circ$ to $+6^\circ$. Results show the distance between the perceived position and the target position (i.e., the position error), averaged over the 180 cases, plotted versus the audiovisual conflict. Three cases are presented: (a) basal parameter values, with the visual stimulus much more spatially accurate than the auditory one ($\sigma_V = 4^\circ; \sigma_A = 20^\circ$, black line and squares); (2) the two inputs with the same spatial accuracy ($\sigma_V = 20^\circ; \sigma_A = 20^\circ$, red line and closed circles); and (3) blurred condition, where the visual stimulus is less accurate than the auditory one ($\sigma_V = 40^\circ; \sigma_A = 20^\circ$, blue line and triangles). Results by Alais and Burr (2004) are reported in the right panel for comparison. In basal conditions, the visual stimulus dominates the response. In blurred conditions, the response follows the auditory shift.

The results are summarized in Figure 10 and compared to the results of Alais and Burr (2004). The network automatically accounts for the different reliability of the stimuli. In basal conditions, the estimated position follows the visual shift. Conversely, in blurred conditions, the estimated position is mainly affected by the position of the auditory input.

Finally, in order to better understand the previous results, Figure 11 shows an example of the global activity in the multimodal layer at three different positions of the auditory and visual stimuli (in the basal case, moderately blurred and strongly blurred), and Figure 12 summarizes the activity of two exemplary neurons in the multimodal layer. This has been computed by using a central position at $90^\circ$ for the multisensory combination (hence, the visual stimulus shifts to the right from $84^\circ$ to $96^\circ$, and, simultaneously, the auditory stimulus shifts to the left from $96^\circ$ to $84^\circ$). The
Figure 11: The activity in the multimodal layer shifts with the stimulus reliability. Activity in the multimodal layer during the trials described in Figure 10 when the target (the central) position for the stimuli was at 90°. In these simulations, in order to improve the aspect of the tuning curves with less saturation, we slightly reduced the inputs (auditory input: $i_A^{\text{Max}} = 35$; visual input $i_V^{\text{Max}} = 14$ (normal), 35 (moderately blurred), 70 (blurred). The dot-dashed blue lines are the responses when the visual stimulus is at position 84° and the auditory stimulus at position 96°. The dashed red lines are the responses when both stimuli are at position 90° (note the significant multisensory enhancement). The continuous black lines are the responses when the visual stimulus is at 96° and the auditory stimulus at 84°. Upper panel: normal conditions: the activity is dominated by the visual input. Bottom panel: blurred condition: the activity is dominated by the auditory input.

First neuron has the preferred position at 84° (i.e., to the left compared with the central position) and the second the preferred position at 95° (to the right).

Figure 11 shows that the activity in the multimodal layer follows the more reliable input. Figure 12 displays the same behavior at the level of the individual neuron. In basal conditions, both neurons respond maximally when the visual stimulus is close to their preferred position and reduce their response when the visual stimulus moves away from the preferred position despite the simultaneous proximity of an auditory stimulus. This signifies that these neurons give more relevance to the visual input than to the auditory one and their tuning curves are prevalently visual. Conversely, in blurred conditions, the same neurons maximally respond to the presence of an auditory stimulus at their preferred position and reduce their response when the auditory inputs leave the position despite the presence of a visual stimulus; that is, the neurons gave more emphasis to the auditory modality.
The responses of two exemplary neurons in the multimodal network, during the trials described in Figure 11, when the target (the central) position for the stimuli was at $90^\circ$. The left panel refers to the neuron with preferred position $84^\circ$; the right panel to the neuron with preferred position $95^\circ$. The $x$-axis reports the audiovisual conflict, and the $y$-axis displays the neuron activity in the three experimental conditions (black line and asterisks: basal, i.e., visual more accurate; red line and open circles: same accuracy for the audio and visual stimuli; blue line and diamonds: blurred visual stimulus). In the basal condition, each neuron gives more weight to the visual input (i.e., it maximally responds when the visual input is close to its preferred position); in blurred conditions, each neuron provides more weight to the auditory input (i.e., it maximally responds when the auditory input is close to its preferred position).

Hence, the appearance is that of a shift of the tuning curves and of an automatic readjustment of the corresponding weights.

4 Discussion

The aim of this work was to analyze whether a simple neural network, consisting of two layers of unimodal neurons, connected via plastic cross-modal synapses, can be trained to realize a near-optimal Bayesian estimator. This approach is inspired by some pivotal ideas recently developed by Ma et al. (2006), Ma and Rahamati (2013), and Pouget et al. (2013, 2003), usually referred to using the term probabilistic population coding. In particular, we exploit the idea that a chain of neurons can encode the probability functions. However, our approach also introduces some original elements within this framework.

4.1 Innovative Aspects and Significance of the Results. First, the synapses are not assigned a priori but learned during a training period, in order to encode the statistics of the environment; that is, the network learns the likelihood probabilities and the prior probability functions from a repetition of random stimuli. To this end, we used a biologically plausible rule consisting of the classic Hebb potentiation, based on the correlation of the presynaptic and postsynaptic activities, joined with a forgetting factor,
to avoid an unbounded synapse increase. The significant achievement of this rule is that after sufficient training, it can encode the average input vector that excites the neuron (Hertz et al., 1991).

As it is well known, in order to realize a Bayesian estimator with maximal posterior probability, two kinds of complementary pieces of information must be encoded: the likelihood probability and the prior probability. The first summarizes the process of data formation—how the input data statistically depend on the unknown parameters (in our case, the unknown parameters are the positions of the auditory and the visual stimuli). The second encodes information on the statistics of the parameter themselves.

Our theoretical analysis (see section 2.1) and the subsequent simulation trials demonstrate that under the assumption of gaussian white noise, the likelihood probabilities can be encoded in the neuron receptive fields, while the prior knowledge on the co-occurrence of the stimuli can be encoded in the cross-modal synapses. The possibility of encoding other forms of prior probability will be discussed in section 4.2.

Perhaps the most innovative aspect of this work is the role assigned to cross-modal synapses to represent the prior. An indirect validation (or rejection) of this aspect may consist in comparing the strength of these synapses after training with results taken from physiology. Although many data in the literature support the existence of cross-modal links between the auditory and visual areas (Driver & Noesselt, 2008; Falchier, Clavagnier, Barone, & Kennedy, 2002; Ghazanfar & Schroeder, 2006; Rockland & Ojima, 2003; Schroeder & Foxe, 2005), it is quite difficult to infer numerical values for the synapse strength. However, a few considerations can be made. These synapses must be weak enough to avoid a phantom effect (i.e., a unisensory stimulus in one modality does not produce activation of neurons in the other unisensory area). Moreover, they must be strong enough to significantly reduce the response time in one part of the cortex (auditory or visual) in cross-modal conditions compared with the unisensory case. We verified that the present values of cross-modal synapses satisfy both conditions (unpublished simulations).

As evident from Figure 9, some differences can be observed between the Bayesian estimates and those provided by the network. A reason is that the Bayesian estimator is significantly affected by small changes in the prior, whereas the model exhibits lesser variability. It is worth noting, however, that with our network, we do not aspire to simulate a Bayesian estimator perfectly but rather to simulate behavioral data and provide a tentative explanation on how these can be reproduced via neural mechanisms.

Although the realization of a near-optimal Bayesian estimator works satisfactorily, as shown in Figure 9, the posterior probability estimator can also be realized with a feedforward neural network in which three layers of neurons (two encoding the likelihood functions for each modality, the other the prior probability) converge toward a superior layer (see Ma et al, 2006; Pouget et al., 2013). This idea exploits the property of the logarithmic
function (Pouget et al., 2013); that is, the product of probabilities can be converted into the sum of their logarithms, and so computed in a downstream network, which realizes this sum. A problem with this feedforward schema, however, is how a chain of neurons can learn the prior probability and, moreover, where this is realized in the brain.

Orhan and Ma (2016) recently used feedforward networks with hidden units, trained with an error-based learning rule as a model of probabilistic inference (however, this training algorithm is not biologically plausible). Ohshiro et al. (2011) used a model consisting of two layers of primary neurons, each sensitive to a different sensory modality, which send feedforward synapses to a layer of integrative multisensory neurons. Hence, their schema resembles our network in Figure 1b but without cross-modal synapses. The main dissimilarity with our model is that they use divisive normalization instead of lateral inhibition to simulate suppression and assume different weights for the feedforward synapses in order to account for a different reliability of multisensory cues. Conversely, the different reliability of the stimuli in our model derives not from a difference in feedforward synapses but from the different likelihood, encoded in the neuron input, and from the cross-modal interaction (so that the more reliable input affects the less reliable one). This was achieved with a biologically realistic rule for synapse reinforcement. In particular, it is worth noting that we used exactly the same rule for adjusting both the receptive fields and the cross-modal terms. In our opinion, a limitation of the Oshiro model is that the feedforward synapses must be modified ad hoc to provide a different dominance of one cue on the other, whereas in our model, this reweighting occurs automatically as a consequence of input changes, as demonstrated in the simulations of Figures 10 to 12 (see below for further comments on this automatic reweight).

The cross-modal synapses developed during training can account for the presence of some well-known illusory phenomena of multisensory integration. In the work reported in this letter, we simulated the ventriloquism effect, where a flash attracts a spatially neighboring beep. In previous work (Cuppini et al., 2014), using a more sophisticated temporal dynamics for synapses, we demonstrated that cross-modal terms are able to account for the fusion and fission effects too, where beeps cause illusions on the number and time of perceived flashes (Andersen et al., 2004; Shams et al., 2000). Recently we also analyzed the emergence of the well-known McGurk effect as a result of a cross-modal training, and, conversely, whether a delayed maturation of cross-modal synapses can account for the poor integration of phonemes and lip movements observed in children with autism spectrum disorders (Cuppini et al., 2015).

Various authors recently underlined the strict relationship that exists between Bayesian inference (exploiting prior probabilities) and illusory phenomena in a variety of multisensory tasks (Kilteni, Maselli, Kording, & Slater, 2015; O’Reilly, Jbabdi, & Behrens, 2012; Samad, Chung, & Shams,
2015). Moreover, the same Bayesian inference principles that govern the perception of objects in the environment can govern the perception of one’s own body (Kilteni et al., 2015; Samad et al., 2015). Hence, we expect that encoding prior knowledge via maturation of cross-modal synapses may represent a diffuse mechanism able to unify many different illusory phenomena (concerning both the external world and the self) and Bayesian inference into a single neural network topology.

Finally, in the last part of this study, using a further layer of multimodal neurons, we investigated the single causal inference problem, in which the observer must provide a single inference (in our case, a single spatial position) for conflicting stimuli. This problem can be encountered in many practical cases (let us consider, for instance, a classic multisensory structure, the superior colliculus, whose final inference is a single spatial position to drive a saccadic movement). It is worth noting that while the problem of inferring separate positions for the two (auditory and visual) stimuli is dealt by the two unisensory networks separately (which, however, exhibit a cross-modal talk and, hence, acquire a kind of multisensory behavior), the problem of computing just one position to drive behavior requires a chain of multisensory neurons receiving stimuli previously elaborated by the respective unisensory regions. Hence, according to our schema in Figure 1b, we can distinguish between two kinds of multisensoriality. First, the neurons in the auditory and visual layers do not respond to a unisensory stimulus of the other modality (indeed, we verified that after learning, a single unisensory stimulus does not induce a phantom activity in the other modality). Here, the multisensory behavior emerges only in cross-modal conditions, in the form of a modification in the activity of one network induced by the activity in the other. Second, conversely, the neurons in the downstream layer are intrinsically multimodal; they actually respond to unisensory stimuli in each modality.

Our network suggests that both kinds of multisensoriality are useful in practice but with different aims. The first kind of “weak” multimodal behavior may be typical of perceptual areas traditionally deemed as unisensory; indeed, in these areas, some cross-modal links with regions of other modalities have been demonstrated anatomically and functionally (Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006; Morrell, 1972; Musacchia & Schroeder, 2009; Schroeder & Foxe, 2005). We hypothesize that the aim is to implement prior knowledge on the co-occurrence of the stimuli. The second “strong” multisensoriality is typical of downstream associative areas (such as superior temporal sulcus, ventral intraparietal area, and ventral premotor cortex; Ghazanfar & Schroeder, 2006), where multimodal neurons have been known for a long time. Their aim is to identify a single response, common to both stimuli, to drive behavior.

An interesting result of our model is that the downstream multimodal neurons apparently reweight the individual inputs according to their reliability: the more reliable the input, the stronger is its influence on multimodal
neurons. This kind of behavior agrees with the predictions of Bayesian inference models (Pouget et al., 2013) and has been confirmed in behavioral tasks (Alais & Burr, 2004) and neurophysiological recordings on multimodal neurons (Fetsch et al., 2012; Morgan et al., 2008). However, the true neural mechanisms through which neurons can reweight the cues on a trial-by-trial basis were still unclear (Fetsch et al., 2012).

In our model, this result is obtained without modifying the real synaptic weights from the unimodal to the multimodal layers (which have been taken equal for both modalities) but is simply the consequence of the automatic remodulation of neuron activities in the two unimodal layers. The latter, in turn, depends on two concurrent biological mechanisms. First is the external input to the neuron, which is the inner product of the stimulus and the neuron receptive field. Although the receptive fields are trained on the basis of the experience, to encode the past reliability of the stimuli (and so the likelihood probability), they do not change significantly from one trial to the next; this inner product changes on a trial-by-trial basis, reflecting the characteristic of the present input (i.e., more precise or more blurred). Second are the cross-modal connections, which move the barycenter from the position of the less reliable stimulus toward the position of the more reliable one. The mechanism can be understood looking at Figure 8. In the location of the more reliable stimulus (position $\vartheta^V = 100^\circ$ in Figure 8), the neurons in the other modality (the auditory ones) still exhibit a not-negligible activity (or their activity is just subthreshold); hence, these neurons can be significantly excited by the cross-modal inputs coming from the other modality. The positive loop occurring between the two activities (visual and auditory) then produces even a stronger excitation at the given position, which is detected by the downstream multimodal layer as a reinforcement of the more precise modality influence. Conversely, in the position where the less reliable stimulus is centered (position $\vartheta^A = 85^\circ$ in Figure 8), the activity of the neurons in the other modality (the visual ones) is significantly below threshold; hence, these neurons cannot be appreciably excited by the cross-modal connections. This effect may be emphasized by the competitive mechanisms, implemented via lateral Mexican hat synapses, that further modulate the activity in the unimodal networks to favor the stronger and depress the weaker.

4.2 Limitations and Future Studies. Of course, our study exhibits some limitations, which should be clearly recognized and may be investigated subsequently. First, in our theoretical analysis and in the following training procedure, we assumed that the receptive fields of all neurons in the same modality are equal (or almost equal, apart from minor statistical fluctuations). Accordingly, during training, we used a uniform distribution to generate the unimodal inputs and shrink the RFs. Indeed, in these conditions, each single unisensory network realizes the likelihood function of the stimulus, and a metrics extracts the MLE, which is the best estimator.
in case of uniform prior. The only nonuniform prior information exploited in this work is on the co-occurrence of cross-modal stimuli, encoded in the reciprocal cross-modal synapses.

Hence, in our study, we did not consider the possibility of having a distribution of unimodal stimuli that is not uniform (e.g., some positions in space are more frequently stimulated than others or the reliability of the stimuli depends on position). Of course, in the latter case, the MLE would not be optimal even in unimodal trials, and prior information should be incorporated directly within the unisensory nets.

As Fisher and Peña (2011) demonstrated, a way to account for a nonuniform prior for the unisensory stimuli is using a population code where the prior is encoded in the density of the preferred directions (i.e., using more neurons in the more probable spatial zones). In our model, this may be realized using a greater number of neurons and modulating the receptive fields, which can be automatically trained to emphasize the non-uniform distribution of the inputs.

In our model, we used just 180 neurons (resolution one per degree) just to reduce the computational effort. However, the number of neurons is not constrained and can be increased, thus improving both resolution and robustness for instance, we performed some trials using 500 neurons, as in Cazettes, Fischer, and Pena (2016) and Fischer and Peña (2011); the results, not shown for briefness, are quite similar as to the ones presented in this letter.

Furthermore, in this study, we did not train lateral synapses. This is a common choice when dealing with self-organized networks, where lateral connections are usually assigned before training (let us consider, for instance, the classic Kohonen algorithm for topological maps; Kohonen, 1995). Actually, training lateral synapses poses serious problems for network stability (our unpublished simulations), and so we decided not to train them in order to reduce model complexity. However, we can consider this aspect in future model extensions. Indeed, as shown in Figure 5, by modulating lateral synapses, one can modify the unisensory likelihood, thus providing more or less accuracy to the input stimulus. We argue that training lateral synapses may be important in conditions where the prior distribution of the unisensory stimuli is not uniform, to increase excitation in the more likely spatial zones and decrease excitation in the less probable ones. This may be an alternative or complementary to a spatial modulation of the receptive fields (as described in the previous paragraph).

Another limitation concerns the way we simulated cross-modal conditions. During training, we always assumed that two cross-modal stimuli originate in the same position (with a possible difference of just a few degrees). This is also reflected in the value of parameter $\beta_1$ in equation 2.28, that was chosen very close to zero. It will be of great interest to train the network with different cross-modal paradigms: for instance, assuming a consistent probability also for independent cross-modal inputs (i.e.,
a higher value of $\beta_1$) and/or using a different ratio of cross-modal versus unimodal stimuli (fixed at one-third per each neuron in this study). In particular, according to the adopted training rule, the strength of cross-modal synapses is affected by the mean value of the inputs, and so by the ratio of cross-modal versus unimodal stimuli: the higher this ratio is, the higher are the cross-modal terms, which may be reflected in a stronger ventriloquism effect (our unpublished simulations).

Another kind of prior information that may be taken into account in future work is a different frequency of auditory and visual stimuli (e.g., in speech recognition tasks, the auditory input may occur more frequently and acquire a greater value than lip movement information). We claim that the last case may be treated using different values for the feedforward synapses from the unisensory areas to the downstream multisensory area, reflecting a different prior value of the two modalities. Actually, these synapses were not trained in the trials presented here but assigned with identical values for the two modalities.

Furthermore, during training we used a given spatial reliability for the auditory input ($\sigma^A = 20^\circ$) compared with visual reliability ($\sigma^V = 4^\circ$). This is the only difference between the two unisensory layers. The use of auditory inputs with even smaller reliability (e.g., $\sigma^A = 32^\circ$ as used by Magosso et al., 2013) may extend the ventriloquism effect at even larger distances, thus explaining some experimental data showing cross-modal influences even at $30^\circ$ to $40^\circ$. Finally, the width and strength of lateral synapses, which control the tuning curves of individual neurons and so the excitation region in each network, may have a role in modulating cross-modal synapses, and so the extension of the ventriloquism effect.

A sensitivity analysis of all these aspects is certainly worthwhile in future studies, leading to the generation of testable predictions on how the manipulation of model parameters may be reflected in changes in learning and behavior.

A limitation of our model, which may be the focus of future studies, concerns the description of the auditory net. In fact, while the visual net can be considered a good replication of the primary visual areas, where a spatial topological organization is already present, the auditory net possibly mimics higher stages of the auditory pathway. In fact, the primary auditory cortex is not spatially organized, and spatial information on the auditory stimuli is extracted only later, from interaural time difference or interaural phase difference (Recanzone & Sutter, 2008; Saberi et al., 1998). A problem here may be the assumed independence of noise, since at higher stages, noise may exhibit a certain correlation due to feedforward convergence. Nevertheless, neural noise is not only due to convergence from previous stages, but may also arise from intrinsic stochasticity within neurons (i.e., neural variability at the present stage). Hence, we expect that noise in the auditory net should exhibit both a correlated component and an independent one. The effect of correlated noise can be tested in future work in the
simulation setup and in theoretical equations (i.e., with the use of a proper autocorrelation matrix).

Finally, an important problem deserving future study concerns the judgment on the number of independent causes, a problem often referred to as causal inference. Readers can consult some pivotal papers by Kording et al. (2007), Shams and Beierholm (2010), and Ma and Rahmati (2013) on the main theoretical aspects of this problem. In this study we always used a single cause during training (either unimodal or cross-modal); that is, we voluntarily decided to ignore the possibility of two simultaneous causes to reduce problem complexity. Hence, the two unisensory networks are used to assess the auditory and visual positions separately, and the multimodal network tries to fuse them into a single event to drive behavior. A more complex scenario occurs when the observer first infers whether the inputs are produced by two independent causes or by a single cause and then, based on this preliminary decision, infers the acoustic and visual positions. This can be reformulated by saying that the estimator should use the first term in the right-hand member of equation 2.28 ($\beta_1 = 1$) when two separate causes were previously recognized and the second term ($\beta_1 = 0$) when a single cause is inferred. Looking at the simulations of the ventriloquism effect, we can say that the network partially incorporates this distinction: when the audiovisual distance is less than $20^\circ$, the auditory stimulus is shifted toward the visual one in an effort to treat the two stimuli as a single event. This is indeed what is occurring in the Bayesian estimator when using a single cause for the prior ($\beta_1 = 0$). When the distance is greater than $20^\circ$, the audiovisual interaction disappears, as in the case of two independent causes.

We think that the causal inference problem may be better addressed by the downstream multimodal network. The latter should discriminate between two causes or a single cause, for instance, on the basis of the peaks in its activity, and then provide feedback to the individual unisensory areas. This more complex network structure may be an ambitious future target in an effort to find a network implementation for causal inference.

5 Conclusion

This study represents an effort to implement Bayesian inference via biologically inspired neural networks. Taking inspiration from the probabilistic population coding theory proposed by Ma et al. (2006), Ma and Rahmati (2013), and Pouget et al. (2003, 2013), we exploit the idea that populations of neurons can encode probability. However, we also suggest that cross-modal synapses may represent a straightforward way to incorporate prior knowledge and that the adopted learning rule is a powerful mechanism to encode the statistical information on the environment (in both the RFs and cross-modal connections). A further downstream multimodal network may finally compute a single position if required to drive behavior.
Further studies should examine cases where the stimuli do not have a uniform distribution, the effect of parameter manipulations on network performance and behavior, to formulate testable predictions, and the possibility or discriminating between one and two causes to automatically deal with the causal inference problem.

Appendix: Parameter Assignment

The value of all model parameters (see Table 1), has been assigned from data present in the literature according to the main criteria summarized below.

A.1 External Inputs. A fundamental point in the model is that the visual inputs exhibit better spatial resolution compared with the auditory ones (Recanzone, 2009; Recanzone, Guard, & Phan, 2000). This is mimicked in the network by setting $\sigma^A > \sigma^V$ in equation 2.7. It is worth noting that these are the only differences between the two areas; all other parameters were assumed equal for the two areas to reduce the number of assumptions.

The strength of the external visual and auditory stimuli (parameters $I_{\text{Max}}^A$ and $I_{\text{Max}}^V$ in equation 2.7) was chosen so that the overall input elicits a response in the upper portion of the linear part of the sigmoidal static characteristic (i.e., a little below saturation). However, the values of $I_{\text{Max}}^V$ were suitably increased in blurred conditions, to counteract the presence of a wider lateral inhibition (this is also the reason why $I_{\text{Max}}^A > I_{\text{Max}}^V$; see Table 1).

The standard deviation of noise was chosen as great as one-third of the maximum input (i.e., $\nu^A = I_{\text{Max}}^A/3$ and $\nu^V = I_{\text{Max}}^V/3$). This is the maximal noise that can be tolerated without inducing spurious activation bubbles in the network (which should be erroneously interpreted as a phantom input).

A.2 Parameters of Individual Neurons. The total number of neurons, $N$, was 180; their total spatial distance, $D$, was $180^\circ$, assuming a spatial resolution of $1^\circ$ between one neuron and the next. The central abscissa for the sigmoidal relationship $x_0$ in equation 2.33 has been assigned to have negligible neuron activity in basal condition (i.e., when the input is zero). The slope of the sigmoidal relationship, $s$, has been assigned to have a smooth transition from silence to saturation in response to external stimuli. The time constant, $\tau$, in equation 2.32 agrees with values (a few milliseconds) normally used in deterministic mean-field equations (Treves, 1993).

A.3 Parameters of Synaptic Connections. Parameters that establish the width and the strength of lateral synapses in both areas ($\lambda_{\text{ex}}, \lambda_{\text{in}}, \sigma_{\text{ex}},$ and $\sigma_{\text{in}}$ in equation 2.36) have been assigned to simultaneously satisfy several criteria: (1) the excitation is locally greater than inhibition, to have a Mexican hat arrangement; (2) excitation is small enough to avoid unstable phenomena
(e.g., the spread of a large activation bubble or the excessive amplification of local noise); and (3) inhibition must be strong enough to warrant competition between two stimuli in the same area.

Parameters $r_0$ and $\sigma_R$ in equation 2.41 were given so that the initial receptive fields of all neurons are wider than the auditory and visual inputs, but with a smaller amplitude. This causes an initial wide activity in the networks, but avoiding instability (i.e., not all neurons become simultaneously active).

The strength of cross-modal synapses, $w^\text{SQ}_{kj}$ in equation 2.37, was initially set at zero, assuming ineffective cross-modal link before maturation.

The synapses from the unisensory areas to the downstream multimodal area ($w^\text{MA}$ and $w^\text{MV}$ in equation 2.42) were given so that a unimodal stimulus close to saturation causes half-maximal activation in the multimodal area (hence, two congruent cross-modal activations in the unisensory areas, both quite close to saturation, lead the multimodal area to saturation too).

**A.4 Training Parameters.** The learning factor, $\gamma$ in equations 2.39 and 2.40, was given small enough to avoid excessive oscillations from one learning trial to the next (so that the new value of the synapses is not excessively affected by the last input) but large enough to ensure good convergence within the 100 training epochs.

The ratio between cross-modal inputs versus unimodal inputs was one-fifth (one cross-modal, two visual unimodal, two auditory unimodal per epoch). Different ratios may be tried in future work.

Parameter $\sigma^{AV}$ in the expression of the prior probability, equation 2.28, which establishes the possible distance between two cross-modal inputs coming from the same source, was taken as low as $1.5^\circ$. This signifies that two inputs from the same source have $90\%$ probability of differing by less than $3^\circ$. The effect of a different parameter choice has been commented on in the main text. Parameter $\beta_1$ in equation 2.28, which establishes the percentage occurrence of independent cross-modal inputs, was set very close to zero (during training, we never use independent cross-modal inputs). This value cannot be set exactly equal to zero so that incongruent stimuli, during the ventriloquism trials can be separated. This problem requires a deeper analysis, using the causal inference problem assessment (see section 4).

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