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1 **Multisensory processes in birds: from single neurons to the influence of social interactions and**  
2 **sensory loss**

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9

10 Abstract: World experiences involve multisensory stimulation that arises simultaneously from multiple  
11 sources. Yet, we experience a coherent and unified world. Many studies have focused on how sensory  
12 information from distinct modalities are integrated and showed that numerous behavioural and  
13 cognitive benefits are provided by multisensory processes. Much work has been done with mammalian  
14 models but research on avian species also expands our knowledge on multisensory processes. Avian  
15 species exhibit a great diversity of behaviours and these species have provided evidence that  
16 multisensory processes benefit by the learning that occurs in natural situations. Cross-modal  
17 influences on the control of sensorimotor processes occur in circumstances of sensory loss. Also,  
18 studies suggest pervasive multisensory influences throughout the avian brain. This review summarizes  
19 research done on the imprinting behaviour of precocial bird species, on the ability of barn owls to  
20 detect prey and on the vocal communication of songbirds.

21

22 Keywords: Multisensory integration, cross-modality, imprinting, vocal communication, prey detection

23

## 24 **1. Introduction**

25 We experience a unified external world from a vast amount of information processed through multiple  
26 sensory systems. This leads us to assume convergence and integration of information from these  
27 different modalities to create this coherent world. Within this framework, studies on humans and non-  
28 human animals have emphasized numerous perceptual and behavioural benefits from experiencing  
29 multiple sensory inputs (Stein et al., 2020). This includes a reduction in ambiguity, especially in noisy  
30 environments, lower sensory thresholds, enhancement of the speed and/or accuracy of stimulus  
31 detection, as well as facilitating the acquisition of higher cognitive functions and sensorimotor skills  
32 such as those involved in language and speech (Frassinetti et al., 2002; Frens et al., 1995; Lovelace et  
33 al., 2003; McDonald et al., 2000; Ross et al., 2007; Stein et al., 1989; Sumby and Pollack, 1954). The  
34 mechanism by which multisensory information is combined by neural circuits has been studied for  
35 many years. The number of identified multisensory anatomical circuits is continuously increasing and  
36 suggests that the perceptual benefit of multisensory integration is supported by functional interaction  
37 between sensory areas of different modalities from the early stages of sensory processing to more  
38 integrative levels (Cappe et al., 2009; Choi et al., 2018; Ghazanfar and Schroeder, 2006; Lohse et al.,  
39 2021a; Stein and Stanford, 2008a). Our understanding of neurophysiological mechanisms underlying  
40 multisensory processes has also increased (see Box 1 and Figure 1) and has revealed a set of empirical  
41 principles by which two sensory inputs interact to modify their neural responses (Stein and Stanford,  
42 2008a; van Atteveldt et al., 2014).

43 Much of our knowledge of how multisensory processes are mediated, and at what level of hierarchy  
44 processing they occur, has been achieved by mammal studies. Surveys on bird species have also been  
45 useful in multisensory integration-related research. One of the main advantages of birds has been the  
46 opportunity to exploit their naturally occurring behaviour and the species-specific abilities they use in  
47 natural contexts. Bird groups exhibit a great diversity of behaviour, especially in their learning  
48 behaviour and/or specific abilities. As some of the abilities that bird groups can exhibit are not shared  
49 by mammalian species used as experimental animal models, birds enlarge the perspective on  
50 multisensory processing function. They also allow highlighting shared computations and neural

51 mechanisms with mammals, including humans. This report aims to summarize the current knowledge  
52 of multisensory processes based on behavioural, neuroanatomical and electrophysiological studies  
53 made on different avian species. Multisensory processes embrace various forms of complexity, from  
54 the “simple” cross-modal cue integration to top-down modulations by high-level cognitive functions  
55 (see box 1) (Meijer et al., 2019). We thus emphasized the synergistic effects of multisensory and  
56 learning processes in birds. We summarized the detection performance in barn owls because of their  
57 remarkable abilities to perform cue integration of auditory and visual information to detect a prey. We  
58 then described the neuronal mechanisms underlying cross-modal cue integration in the learning  
59 context of conspecific (parent) recognition by focusing on the imprinting behaviour exhibited by  
60 precocial avian species. Finally, we focus on the vocal communication in songbirds that has striking  
61 parallels with human speech. In songbirds, considered as auditory specialists, recent studies have  
62 opened up a new line of research. They have revealed the potential control of sensory inputs, other  
63 than auditory, on song behaviour, even in deaf songbirds. They have also extended our current  
64 knowledge on multisensory processes. They have provided evidence that cross-modal integration can  
65 serve not only sensory perception but also motor control of vocal production, making possible to  
66 finely adjust vocal acoustic features. Finally, we discuss how avian research can be informative on  
67 corresponding processes in the mammal brain.

## 68 **2. Interconnected sensory pathways. Multisensory anatomical pathways in birds**

69 The main limitation of using birds as a model organism system was once thought to be the large  
70 differences in brain organization between avian and mammalian species, including a lack of a  
71 neuroarchitecture comparable to that of the cerebral cortex. However, studies have now revealed many  
72 analogies or homologies in both brain structures and networks between birds and mammalian species.  
73 A cortex-like organization based on connectivity patterns has demonstrated that the avian brain  
74 organization is more similar to that of mammals than previously thought (Medina and Reiner, 2000a;  
75 Reiner et al., 2004; Stacho et al., 2020).

76 Multisensory processes in mammalian brains have been thought to result from the convergence of the  
77 different sensory streams in interconnected high-order cortical areas. The idea that multisensory

78 interaction is limited to high stages of brain processing has been challenged by studies demonstrating  
79 such interactions in the midbrain, particularly in superior colliculus, to cortical brain regions including  
80 primary sensory areas, classically considered as unisensory brain regions (Cappe et al., 2009; Stein  
81 and Stanford, 2008a).

82 In the avian brain, heteromodal connections at the different stages of sensory processing have also  
83 been described (Figure 2). Connections between the auditory and the visual pathways already occur in  
84 the midbrain: the auditory nucleus mesencephalic lateralis, pars dorsalis (MLd), also known as inferior  
85 colliculus and the optic tectum (OT), a midbrain visual area considered to be the avian homolog of the  
86 superior colliculus (Gutfreund et al., 2002; Hyde and Knudsen, 2000; Knudsen and Knudsen, 1983;  
87 Luksch et al., 2000). In many mammalian species, the generation and control of eye and head  
88 movement involves the superior colliculus, characterized by aligned maps of space for auditory, visual  
89 and tactile modalities (King and Hutchings, 1987; Sterbing et al., 2002; Wallace et al., 1996; Wallace  
90 and Stein, 1996). As in the superior colliculus of mammals, multisensory neurons that respond both to  
91 visual and auditory stimuli are common in the avian OT. In barn owls, auditory maps are located in the  
92 OT. This shows a remarkable topographic resolution that is aligned to the visual one (Wagner et al.,  
93 2013). Auditory or visual stimuli that originate from a single location in space activate the same set of  
94 neurons in the avian superior colliculus (Knudsen, 1982) suggesting that neurons in the TeO nucleus  
95 exhibit multisensory properties.

96 Importantly, multisensory convergence is not limited to the midbrain, similarly to mammals.  
97 Connections between the auditory and visual pathways have been identified in the avian pallium,  
98 where a cortex-like canonical circuitry exists. The analogue of the primary auditory cortex, so called  
99 Field L, connects with the homologue of the primary visual cortex, the visual part of the Wulst,  
100 (Medina and Reiner, 2000b; Stacho et al., 2020; Wild and Williams, 1999). At a higher stage, the non-  
101 sensory associative area, the nidopallium caudolaterale (NCL), considered as the avian analogue of the  
102 mammalian prefrontal cortex, receives inputs from both auditory and visual areas, as does its  
103 mammalian counterpart (Güntürkün, 2005; Kröner and Güntürkün, 1999). Also, tangential projections  
104 connect distant somatosensory, visual and auditory territories (Stacho et al., 2020). Thus, the

105 connectivity pattern of the avian brain can mediate multisensory processing at different stages of the  
106 brain organization.

### 107 **3. Multisensory cue integration in an auditory specialist bird species: the barn owl**

108 Cross-modal cue integration, which benefits stimulus detection or discrimination, is considered as a  
109 form of multisensory processing which mostly relies on bottom-up neural mechanisms. In this section,  
110 we focus on one bird species, the barn owl (*Tyto alba*), who uses cross-modal cue integration to detect  
111 preys. Neuronal mechanisms underlying this behaviour are in described in the light of mechanisms  
112 observed in mammals, including humans.

#### 113 **3.1 The prey detection behaviour**

114 The barn owl (*Tyto alba*) provides an appropriate model system for investigating interactions between  
115 visual and auditory information in the context of natural behaviour. This nocturnal bird species is  
116 characterized by its high and precise efficiency to detect small prey by hearing (Konishi, 1973;  
117 Hausmann *et al.*, 2008; Singheiser *et al.*, 2010). The barn owl is clearly a species specialized in  
118 auditory processing. Yet, barn owls use cross-modal cue integration of auditory and visual signals  
119 when light conditions are suitable (Knudsen *et al.*, 1979; Konishi, 1973; Wagner *et al.*, 2013). When  
120 barn owls hear or see a potentially salient signal, their head turns in a quick saccadic movement to face  
121 that signal. Barn owls can use auditory or visual cues alone to detect their prey (Hausmann *et al.*,  
122 2008; Konishi, 1973; Singheiser *et al.*, 2010). They are also able to exploit this signal combination  
123 when it occurs simultaneously. In such a case, they use the fastest sensory signal, the auditory one, to  
124 initiate their behaviour, *i.e.*, the saccadic movement and the most precise signal, the visual one, to  
125 refine the location of the emitter. Consequently, this results in similar short response latency and high  
126 spatial precision than when auditory and visual cues are presented alone, respectively (see more details  
127 in a review Wagner *et al.*, 2013; Whitchurch and Takahashi, 2006). Beyond this potential benefit from  
128 an audio-visual stimulus, the audio-visual combination can impact the target selection. Barn owls can  
129 adjust their visual search behaviour by shifting their gaze, according to the location of the sound  
130 source. They select the visual target closest to the sound source, suggesting that auditory and visual

131 information, when combined, are used for selecting the most relevant target rather than for simply  
132 localizing stimuli (Hazan et al., 2015).

### 133 **3.2 Multisensory neuronal processes at play for detecting prey**

134 In barn owls, cross-modal interactions influence spiking activity of TeO neurons (Knudsen and  
135 Brainard, 1991). Visual information occurring at a given location in the visual field enhances neuronal  
136 responses to sound originating from the same location while no such modulation is observed when  
137 visual stimuli originate elsewhere (Zahar et al., 2009). Also, bimodal responses of multisensory  
138 neurons exceed responses to unimodal stimuli (Zahar et al., 2009). However, this bimodal  
139 enhancement of neuronal responsiveness cannot be predicted by responses to unimodal stimuli since  
140 the number of spikes driven by the audio-visual compound is not higher than the sum of spikes driven  
141 by each unimodal stimulus (Zahar et al., 2009). In terms of the temporal pattern of spikes, bimodal  
142 compounds evoke responses that are better phase locked to stimuli presentation than responses based  
143 on the summation of unimodal responses. This suggests that multisensory tectal neurons exhibit a non-  
144 linear integration of auditory and visual information which is a property shared with neurons of the  
145 mammalian superior colliculus (Meredith and Stein, 1986). This might allow neurons to better detect  
146 events (Zahar et al., 2009). Cross-modal interactions also influence auditory maps in barn owls  
147 (Knudsen and Brainard, 1991). During development, manipulation of visual information, based on a  
148 prismatic effect, induces an experience-dependent shift in the auditory space map (Knudsen and  
149 Brainard, 1995, 1991). A similar effect has been reported in the mammalian superior colliculus:  
150 visually depriving ferrets during development leads to an abnormal auditory space map in this brain  
151 region (King, 1993; King and Carlile, 1993). This refinement of the auditory space map according to  
152 visual inputs in these two evolutionary distant animal species illustrates a crucial role of interactions  
153 between auditory and visual spatial information in the shaping of neurons. It also suggests a required  
154 matching of the representation of both auditory and visual space that depends on the experience. The  
155 adaptive alignment of the auditory space map sheds light on the importance of multisensory  
156 processes in coherent perception of the space.

157 The TeO, where many neurons are multisensory, is part of the tectofugal pathway, one of the two main  
158 avian visual pathways in addition to the thalamofugal pathway (Fig 1; Knudsen, 1982; Knudsen and  
159 Brainard, 1991; Reches and Gutfreund, 2009; Zahar et al., 2009). It sends its efferents to the thalamic  
160 nucleus rotundus which, in turn, projects to the telencephalic entopallium. This region is considered to  
161 be an analogue of the extrastriate cortex (Jarvis et al., 2005; Karten and Shimizu, 1989). The TeO  
162 receives inputs from the retinae but also from the external nucleus of the inferior colliculus, where an  
163 auditory space map has been described (Knudsen et al., 1987; Wagner et al., 1987). The external  
164 nucleus of the inferior colliculus projects to the main auditory nucleus of the thalamus of the  
165 ascending auditory system (the nucleus ovoïdalis). Given the hypothetical convergence of auditory  
166 and visual inputs, studies have examined multisensory properties of neurons along the tectofugal  
167 pathway. Neurons in both entopallium and nucleus rotundus respond to both auditory and visual  
168 stimuli (Reches and Gutfreund, 2009). In the entopallium, neurons show enhanced and earlier peaked  
169 responses to spatiotemporally congruent multisensory stimuli in comparison to responses to unimodal  
170 or incongruent stimuli. Responses of entopallium neurons to bimodal stimuli exceed the simple linear  
171 summation of unimodal responses, reflecting a non-linear integration of visual and auditory stimuli  
172 (Reches and Gutfreund, 2009). Therefore, the entopallium appears to be a brain region where  
173 multisensory properties exhibit some of the principles that characterize multisensory integration and  
174 that were reported in mammals (Stein and Stanford, 2008b; Wallace et al., 1996). Auditory responses  
175 in the entopallium were examined, after pharmacological inactivation of the TeO, to determine their  
176 origin (Reches and Gutfreund, 2009). A complete loss of auditory responses in the entopallium  
177 supports the hypothesis that auditory information ascends through the tectofugal pathway, which is a  
178 visual pathway in other species. In the context of this information *i.e.* bimodal responses in areas  
179 whose homolog regions in mammals are known to be visual, these areas might also be multisensory in  
180 other species but with a contribution of the auditory modality varying among species (Reches and  
181 Gutfreund, 2009). This view is consistent with the possibility that cortical brain areas are multisensory  
182 rather than sensory specific (Ghazanfar and Schroeder, 2006). In the chicken, a species not considered  
183 to be an auditory specialist, spatial auditory information is conveyed to the TeO. Therefore, the barn  
184 owl, as a species considered as specialized in auditory processing, led researchers to reconsider how



185 sensory information is processed throughout the brain (Reches and Gutfreund, 2009). Interestingly, the  
186 stimulation of a premotor area involved in the control of gaze direction induces changes in the  
187 auditory space map of the TeO (Winkowski and Knudsen, 2006), thus illustrating a top-down  
188 modulation that is reminiscent of the modulation of visual responses by stimulation of the frontal  
189 cortex in non-human primates (Moore and Armstrong, 2003).

190 In a framework for examining the importance of multimodalities on perception and detection of  
191 stimuli, another neural phenomenon is worth consideration. The stimulus-specific adaptation (SSA)  
192 phenomenon occurs in neurons that show a decrease in their responsiveness to frequent stimuli while  
193 rare stimuli reinstate strong responses. This neuronal adaptation has been proposed to allow deviance  
194 detection or surprise saliency by emphasizing unexpected stimuli relative to expected ones. The  
195 finding that neurons in the entopallium exhibit a SSA effect for visual stimuli suggests that SSA may  
196 be enhanced by pairing visual with auditory stimuli. One study addressed this issue and reported that  
197 rare bimodal stimuli evoke stronger responses than rare visual stimuli. However, no such difference  
198 was observed in responses to frequent stimuli (Reches et al., 2010). In addition, responses were  
199 enhanced when the visual stimulus was presented with an auditory stimulus that matched spatially but  
200 not when the bimodal stimuli were spatially incongruent. In a study based on a simple adaptation  
201 paradigm where the same stimulus was repeated several times, the first unexpected bimodal stimulus  
202 triggered a multisensory enhancement in the TeO while responses to subsequent stimuli did not show  
203 clear multisensory enhancement (Zahar et al., 2009). These findings provide evidence that the  
204 integration of visual and auditory information can benefit detection of unexpected or salient events and  
205 is achieved, as in mammals, by a network including midbrain and cortical areas, most probably in a  
206 bottom-up manner (Choi et al., 2018).

#### 207 **4. An example of cue integration learning: the imprinting behaviour**

208 The bottom-up transfer of information in the sensory cortex can be modulated by top-down signals  
209 from higher-order areas involved in various cognitive functions. Studies in mammals, including  
210 humans (Robinson and Sloutsky, 2004), have shown that learning induces changes in the perception of  
211 sensory stimuli and that top-down signals contribute to modulate the neuronal responses of sensory

212 cortex (Polley et al., 2006; Poort et al., 2015). In birds, the imprinting behaviour is a remarkable  
213 paradigm used for the study of neural mechanisms underlying learning processes. It has provided  
214 evidence that multisensory experience promotes learning, which might rely on the modulation of low-  
215 level areas by high-level areas through changes in neuronal responses to sensory stimuli.

216 Imprinting has been described in precocial bird species such as chickens, ducks, and quail where  
217 neonate individuals are relatively mature and capable of locomotion in the immediate postnatal period  
218 (Lorenz, 1937). It involves the young bird approaching and following a stimulus, *i.e.* an animated  
219 object such as a moving red dot, or an individual such as a sibling (or mother, father), learning the  
220 characteristics of this stimulus, and consequently expressing a preference for that stimulus compared  
221 to a novel stimulus. Filial imprinting has been interpreted as being adaptive as it presumably increases  
222 survival of the young birds.

223 Initial surveys mainly investigated the imprinting of young birds to a unimodal stimulus such as a  
224 visual stimulus (Bateson, 1978; Kovach and Hickox, 1971). The observation that mothers emit calls  
225 after egg hatching led researchers to expose neonate birds to either an audio-visual compound  
226 stimulus, *i.e.* a visual stimulus presented simultaneously with the maternal call or a visual stimulus  
227 alone (Bolhuis and Honey, 1994; Honey and Bolhuis, 1997). In domestic chicks, the presentation of  
228 the maternal call during training selectively enhanced subsequent chick preference for the visual  
229 training stimulus over a new one in comparison to conditions where the visual stimuli were presented  
230 alone (Kampen and Bolhuis, 1991; Van Kampen and Bolhuis, 1993). Reciprocally, simultaneous  
231 exposure to bimodal stimuli of the training compound affected the approach behaviour toward the  
232 training auditory stimulus (Kampen and Bolhuis, 1991). An enhanced preference for the visual  
233 stimulus was not observed when stimuli were presented sequentially or when the visual stimulus  
234 preceded the audio-visual compound (Honey and Bolhuis, 1997). This indicated the importance of the  
235 temporal congruency in the exposure to multisensory stimuli (Bolhuis, 1999). Altogether, these studies  
236 have provided evidence that learning in early life can benefit from multisensory information.

237 A recent study that focused on recognition and generalization abilities also provided evidence that  
238 multisensory information benefits learning and perceptual abilities (Versace et al., 2017).

239 Generalization through imprinting behaviour enables chicks to recognize familiar individuals in spite  
240 of changes in their appearance (e.g., mother hen and siblings seen from different angles). In this case,  
241 the natural imprinting stimulus was a single object such as a particular individual. Yet, an object can  
242 also consist in a temporal series of multiple elements characterized by their sequential organization,  
243 e.g., a series of multiple distinct sounds as, for example, words or sentences in human speech. Thus,  
244 the question was whether chicks are able to learn to recognize stimuli organized according to either an  
245 XX or XY pattern and to generalize to novel stimuli where X and Y are novel items. Multisensory  
246 information helps to identify and recognize objects or scenes (Shams and Seitz, 2008), enhancing the  
247 perceptual representation of sensory features of stimuli used. For example, a visual stimulus can  
248 enhance the representation of a temporally paired sound stimulus in the auditory cortex (Atilgan et al.,  
249 2018). This study demonstrated that multisensory information also helps to extract sequential patterns  
250 available for further generalization and categorization processes. The presentations of XX and XY  
251 patterns, where both X and Y consisted of audio-visual stimuli, was more effective than patterns in the  
252 visual or auditory modality for discriminating between novel stimuli according to their sequential  
253 pattern. This study provided evidence that multisensory information promotes the capacity to extract  
254 the sequential structure of stimuli (Versace et al., 2017).

255 This study raises the question of how multisensory association benefits learning. It is unclear whether,  
256 and to what extent, multimodal learning differs from unisensory learning. In imprinting studies, a  
257 significant behavioural approach to the training stimuli was observed in tests where presentations of  
258 only one sensory stimulus of the audiovisual compound, either the auditory stimulus or the visual  
259 stimulus, was presented (Kampen and Bolhuis, 1991; Van Kampen and Bolhuis, 1993). This  
260 suggested imprinting-induced changes in the representation of each unisensory information. Thus, it is  
261 unclear if these changes in the representation of each unisensory information stimulus are  
262 accompanied by the emergence of a representation of the multisensory compound that could form a  
263 unitary object. Some studies have addressed this issue by examining the neural mechanisms  
264 underlying imprinting. Recordings of neuronal responses were performed in birds trained with a visual  
265 stimulus associated with a taped maternal call (Brown and Horn, 1994; Horn et al., 2001; Nicol et al.,

266 1995). In chicks, the intermediate and medial mesopallium (IMM), a multisensory region that receives  
267 afferents from all sensory systems and projects to motor areas (Brown and Horn, 1994; Horn, 1985;  
268 Town and McCabe, 2011), is a critical area for the imprinting behaviour (McCabe et al., 1992, 1981).  
269 Strong evidence implicates the IMM in recognition memory that underpins imprinting (Horn, 2004).  
270 Neuronal recordings showed that imprinting using a bimodal stimulus affected both the number of  
271 IMM neurons responsive to the visual or auditory component when presented alone, in comparison to  
272 a novel stimulus of the same modality. This provided evidence for alterations in unisensory  
273 representations of stimuli areas (Brown and Horn, 1994; Town and McCabe, 2011). Town and  
274 McCabe (2011) also compared neuronal responses using different types of audiovisual stimuli,  
275 including the training ones, novel or incongruent stimuli, the latter combining the training stimulus of  
276 one sensory with a novel stimulus in the other modality. In this case, the training visual stimulus was  
277 coupled with an auditory stimulus. Neuronal activity did not show any effect of training on responses  
278 driven by the audiovisual training stimulus. Responses to the training compound stimulus were similar  
279 to that of a novel one, although chicks were able to behaviourally discriminate between the imprinted  
280 and novel audiovisual stimuli (Town and McCabe, 2011). Yet, results also indicated that the  
281 incongruent audiovisual stimulus drove more responses from IMM neurons in imprinted than in naïve  
282 chicks (Town and McCabe, 2011) suggesting that IMM could detect mismatching between the  
283 auditory and the visual components of the imprinted stimuli. This suggests an encoding of the  
284 multisensory training stimuli, but elsewhere in the avian brain than in IMM. It does not rule out the  
285 possibility of a multisensory representation of the compound. These differences between imprinted  
286 and naïve birds also illustrate that learning yields to changes in response properties of sensory neurons,  
287 suggesting a local effect of learning and/or a top-down modulation exerted by IMM neurons on  
288 sensory neurons.

289 In conclusion, precocial avian species through their imprinting behaviour have provided support for  
290 the possibility that multimodal information promotes learning and also offered the opportunity to  
291 study how multisensory inputs may lead to a unified representation of the multimodal object.

292 **5. Multisensory influences in a model system for studying vocal communication: the**  
293 **songbirds.**

294 Songbird research supports the idea that being an auditory specialist does not exclude the influence of  
295 other modalities, especially visual information. As an animal model system, songbirds have also  
296 provided unique evidence that cues from multisensory modalities can act in concert to promote the  
297 perceptual and sensorimotor skill learning required in vocal communication.

298 Songbirds are a group of more than 4000 species with complex vocalization behaviour and high  
299 listening sensitivity. Birdsong is an acoustically complex communication signal that provides rich  
300 information about the singer and plays a crucial role in social interactions, especially in the contexts of  
301 mate attraction and territorial defence. Songbirds are one of the few non-human animal groups that  
302 learn their singing behaviour. During a critical period of at least several weeks, immatures need to hear  
303 an adult vocal model, called the tutor song, to learn to copy that song. They use auditory feedback to  
304 drive and maintain what they vocally produce. Eliminating or disrupting auditory feedback during  
305 song development results in abnormal songs (Iyengar and Bottjer, 2002; Konishi, 1965, 1964; Marler  
306 and Sherman, 1983). Deprivation of normal auditory feedback in adult songbirds also results in  
307 gradual changes in song structure (Brainard and Doupe, 2001, 2000; Horita et al., 2008; Lombardino  
308 and Nottebohm, 2000; Nordeen and Nordeen, 1992). Song behaviour has remarkable parallels to  
309 human speech given the strong dependence of hearing one's own vocal signals in both infants and  
310 adults (Doupe and Kuhl, 1999). However, human speech perception can be affected by visual  
311 information, as in the famous McGurk effect (McGurk and Macdonald, 1976) and ventriloquism effect  
312 (Slutsky and Recanzone, 2001): visual information provided by movements of the mouth and face  
313 strongly influences what is perceived (Kuhl, 2010, 2007). Also, human speech learning critically relies  
314 on auditory information perception although multisensory integration through information given by  
315 caregivers participates to learning progress (Mason et al., 2019). While literature from studies  
316 performed in mammalian models is rich on data providing evidence for multisensory processing in  
317 audiovisual perception and learning, knowledge remains sparse on how multimodal integration can  
318 shape motor production, *i.e.* lead to changes in acoustic features of vocalizations. Songbird vocal

319 behaviour offers the great opportunity to shed light on this role that remains to be explored. Songbird  
320 research has mostly focused on the role of auditory signals on vocal learning, perception and  
321 production. However, the influence of other sensory signals, including visual ones, has long been  
322 assumed (Hultsch et al., 1999; Todt et al., 1979).

### 323 **5.1 Multisensory perception in songbirds**

324 In songbirds, the auditory processing of vocal communicative signals involves a substantial number of  
325 brain regions including auditory areas as well as the interconnected neural networks specialized in  
326 song production and song learning, known as the song system (Fig. 3) in which neurons respond to  
327 song playbacks (e.g. Dave and Margoliash, 2000; Giret et al., 2014; Prather et al., 2008). Little is  
328 known about the neural pathways and mechanisms underlying multisensory processes in song  
329 behaviour. Some studies have reported anatomical evidence that nuclei of the song system receive  
330 inputs from the visual system (Paterson and Bottjer, 2017; Wild, 1994). Physiological studies showed  
331 that neurons in the song nucleus, at the departure of both the motor and the learning pathways, known  
332 as the HVC (proper name), respond to light flashes (Bischof and Engelage, 1985; Seki and Okanoya,  
333 2006). Indirect evidence comes from investigations focused on the impact of social conditions at the  
334 neuronal level (Cousillas et al., 2006; George et al., 2011, 2012; Hessler and Doupe, 1999a; Menardy  
335 et al., 2014). Some of these investigations attempted to examine the respective contribution of visual  
336 and auditory components in neuronal responses (Avey et al., 2005; Cousillas et al., 2006). Social  
337 conditions may affect neuronal responsiveness in auditory areas (Menardy et al., 2014; Woolley and  
338 Doupe, 2008) including the auditory area considered as a homologue to the primary auditory cortex of  
339 mammals and consequently as a unisensory area, known as the Field L complex (Cousillas et al.,  
340 2006; George et al., 2012). In European starlings (*Sturnus vulgaris*), exposure to an audio-visual  
341 combination consisting of playback of conspecific songs and a picture of an individual evoked  
342 neuronal responses that differed from those evoked by the song playback alone (Cousillas et al., 2006;  
343 George et al., 2012). Therefore, even in a species known as a powerful model system for exploring the  
344 auditory processing of complex signals, visual stimuli may tune the primary auditory cortex.  
345 Furthermore, the modulation of auditory responses of single neurons in the Field L by visual stimuli

346 depends on the degree of familiarity of the stimuli: seeing a familiar or an unfamiliar conspecific  
347 yields to a suppression or an enhancement of auditory responses, respectively (George et al., 2011).  
348 Factors of social cognition may thus have an impact on the integration of multisensory signals and this  
349 impact may occur in primary sensory areas.

350 The avian primary auditory cortex, along with other sensory areas, projects to the NCL (Fig. 1),  
351 considered to be analogous to the mammalian prefrontal cortex (Güntürkün, 2005). As such, the NCL  
352 is a good candidate to investigate the neurophysiological mechanisms of multisensory integration at  
353 the single cell scale. Electrophysiological recordings of NCL neurons were performed in carrion crows  
354 (*Corvus corone*) previously trained to form arbitrary associations between a sound and a colour.  
355 During the learning, a set of NCL neurons was tuned to one or the other association between the  
356 auditory and visual stimuli (Moll and Nieder, 2015), independently of the ordering of the stimuli (first  
357 visual or auditory) (Moll and Nieder, 2017), such that the bird response could be predicted based on  
358 the neuronal activity (Moll and Nieder, 2015). Corvids are songbirds who exhibit impressive cognitive  
359 abilities related to interindividual competition and cooperation that depend on the processing of both  
360 vocal and visual signals (Bugnyar, 2021). They live in complex fission-fusion societies in which  
361 interindividual recognition is critical for group maintenance. This recognition involves discrimination  
362 among conspecifics which can rely on multisensory signals, as in large-billed crows (*Corvus*  
363 *macrorhynchos*) who use both the calls and the appearance of conspecifics to discriminate group  
364 members from non-group members (Kondo et al., 2012). The integration of multisensory signals is  
365 thus essential for social cognition, and the NCL may be a core area for this process (Brecht and  
366 Nieder, 2020). The question remains open on how individual neurons, either in unisensory (Field L) or  
367 high-order (NCL) areas acquire their multisensory properties. One possibility is that multisensory  
368 properties actually arise in the NCL and contribute to modulate neuronal activity within sensory areas  
369 in a top-down manner. Another hypothesis is that unisensory areas (e.g. Field L) acquire their  
370 multisensory properties that eventually converge through bottom-up processes to higher-order areas,  
371 such as in the NCL. Further experiments are required to assess more precisely these processes.

372 Multisensory processes also play a role in female behaviour, particularly in their courtship behaviour  
373 that they display as receiver of songs (Amy et al., 2015). Receiver behaviour has been described as  
374 influenced by signals from different modalities in various avian species (Candolin, 2003; Mitoyen et  
375 al., 2019; Partan and Marler, 2005). In the non-songbird pigeon (*Columba livia*), an audio-videotape  
376 was more effective in triggering courtship displays from females than auditory or visual signals alone  
377 (Partan et al., 2005). In the brown-headed cowbird, the preference of females was assessed through  
378 their courtship displays to compound stimuli made from videos of a male paired with song playbacks.  
379 Manipulation of visual or acoustic parameters of the compound stimulus indicated that changing the  
380 intensity of the video affected the attractiveness of the song playback and provided additional evidence  
381 for how visual signals influence song processing (Ronald et al., 2018, 2017). Female zebra finches  
382 elicit strong preference for the courtship songs compared to non-courtship songs, although the acoustic  
383 differences between these two song types are very subtle (Chen et al., 2017; Clayton, 1988; Miller,  
384 1979; Woolley and Doupe, 2008). While singing for a female, male zebra finches also perform a  
385 stereotyped dance including head and body movements (Ullrich et al., 2016). Zebra finch songs may  
386 thus convey information on the social context in which they were produced (the male singing while  
387 alone or while socially interacting with a female). Interestingly, an fMRI study revealed that courtship  
388 and non-courtship songs induce different levels of activation of the caudocentral nidopallium (NCC), a  
389 sensory area outside of the classic avian auditory pathway, suggesting that this area plays a key role in  
390 the assessment of social, putatively multisensory, signals (Van Ruijssevelt et al., 2018). In canaries,  
391 females produce multimodal signals, a copulation solicitation display and calls, in response to  
392 conspecific songs (Amy et al., 2015). Lesions of the HVC nucleus in females change their behavioural  
393 responses to conspecific and heterospecific songs, suggesting that the HVC belongs to a neural  
394 network involved in the control of courtship cues (Del Negro et al., 1998). Anatomical surveys suggest  
395 that this neural network extend to downstream areas including premotor nuclei (RA and the respiratory  
396 premotor nucleus retroambigualis (RAm), Wild and Botelho, 2015). This overview suggests that  
397 feedforward mechanisms from sensory areas to premotor nuclei drive the multimodal courtship cues  
398 provided by females in response to male courtship songs.



## 399 **5.2 A multisensory approach of vocal learning**

400 Humans are not the only species in which vocal learning and perception are affected by social  
401 interactions. Song learning is also shaped by social interactions that rely on sensory inputs from  
402 several modalities. This suggests that information from multiple sources may be integrated or may  
403 interact to influence the perceiver. Surveys focused on birdsong learning often compare the learning  
404 performances of juveniles that experienced social interaction to those of juveniles that did not. For  
405 example, auditory information through tape tutoring is as efficient as live tutoring in song sparrows  
406 (*Melospiza melodia*) and swamp sparrows (*Melospiza georgiana*), but this is not true for other species  
407 (Catchpole and Slater, 2003). For highly social birds like zebra finches (*Taeniopygia guttata*), song is  
408 better learned from live tutors than from song playback (Eales, 1989; Slater, 1988). This raises the  
409 question of whether visual and acoustic information provided by the adult tutor during interactions can  
410 promote the song learning process. Such a question must then consider that other aspects can influence  
411 vocal learning processes. The motivation to learn or the attention to the stimuli source (e.g. a talking  
412 parent or a singing bird) are involved in vocal learning (Chen et al., 2016). In an attempt to control for  
413 these factors, a focus on basic perceptual mechanisms indicated that, in nightingales (*Luscinia*  
414 *megarhynchos* L.), juveniles can be tutored with a tape but their vocal learning performance is  
415 improved when strobe flashes are tuned to be synchronous with song notes (Hultsch et al., 1999).  
416 Other studies have addressed the issue by examining song acquisition in young birds that are allowed  
417 either to visually and acoustically interact with a live tutor, or to other conditions that include  
418 interacting only acoustically with a tutor or passively hearing the adult model (Chen et al., 2016;  
419 Derégnaucourt et al., 2013; Varkevisser et al., 2022). Tutoring for as little as one day in zebra finches  
420 is sufficient to highlight the benefit of multimodal information on song learning: interacting both  
421 acoustically and visually with tutors made songs more similar to the tutor's songs than interacting only  
422 acoustically or passively hearing the adult models (Chen et al., 2016). Also, young zebra finches that  
423 are either housed with, could see and hear, or only hear the same tutor showed that having access only  
424 to auditory information delays the timing of, and reduces, the vocal learning (Varkevisser et al., 2022).  
425 Song learning is consistently enhanced when the juvenile's own songs are contingently paired with a  
426 video playback of a female exhibiting a special behaviour, *i.e.* a wing stroke, that is considered as a

427 non-vocal feedback since it is commonly observed in response to attractive songs (Miller et al., 2008;  
428 Smith et al., 2000; West and King, 1988). Interestingly, young birds who received non contingent  
429 visual displays of a female feedback sang less accurate songs (Carouso-Peck and Goldstein, 2019).  
430 Another interesting approach is to use a stuffed model, or even better, robotic models that can be  
431 controlled by the experimenter (Araguas et al., 2022; Bolhuis et al., 1999). A robot can for example  
432 provide vocal responses (songs or calls) to the vocalization produced by the juvenile either in a  
433 contingent or non-contingent way, allowing to control for social interactions (Araguas et al., 2022). In  
434 humans, visual and acoustic information provided by adults during social interactions with infants  
435 enhanced acquisition of speech sounds (Goldstein et al., 2003; Kuhl, 2010). Babbling infants who  
436 received contingent feedback rapidly restructured their vocalizations (Goldstein and Schwade, 2008).  
437 Therefore, evidence that visual cues act in concert with auditory cues or influence the auditory  
438 processing to promote vocal learning in songbirds as well as in humans suggest that multimodal  
439 information plays a key role in vocal communication (Goldstein et al., 2003).

440 Birdsong learning has received attention from neuroscientists (e.g. Gobes et al., 2010; Okubo et al.,  
441 2015; Ölveczky et al., 2011; Shank and Margoliash, 2009). However, it still remains to investigate  
442 mechanisms underlying the impact of multisensory integration during development at the neuronal or  
443 network level. A network of brain areas has been proposed to mediate multimodal integration  
444 processes during song ontogeny, based on anatomical data (Paterson and Bottjer, 2017). Now,  
445 functional characterization remains to be carried out to better understand how multimodal integration  
446 maps onto the network.

### 447 **5.3 A multisensory approach on the neuronal bases of birdsong production**

448 Beside vocal perception and learning, vocal production in adults is another cognitive function in which  
449 multisensory processes likely play a role (Tremblay et al., 2003). In human speech, the monitoring of  
450 what is said does not exclusively rely on auditory information (Ito and Ostry, 2010; Lametti et al.,  
451 2012; Tremblay et al., 2003). Songbirds as an animal model system provide insights into this issue. In  
452 adult songbirds, social interactions based on multiple sensory modalities may shape singing behaviour.  
453 For example, male brown-headed cowbirds (*Molothrus ater*) rapidly adjust their song according to a

454 visual display, such as a wing stroke, provided by females (West and King, 1988). However, no study  
455 has investigated the extent to which socially-induced variations in song production depend on the  
456 visual component. In songbirds, the social environment is not the sole condition in which changes in  
457 vocal outputs may occur. Plastic changes in song features may be induced in a reinforcement learning  
458 paradigm. This paradigm commonly consists in providing auditory feedback, e.g. a loud white noise  
459 contingent to the fundamental frequency and the pitch of one song element (called a syllable)  
460 (Andalman and Fee, 2009; Canopoli et al., 2014; Tumer and Brainard, 2007; Warren et al., 2011).  
461 Singing birds alter the pitch of the target syllable allowing them to avoid the white noise delivery.  
462 Investigations based on this pitch-shifting learning paradigm have primarily investigated the role of  
463 auditory information in the monitoring of vocal signals. Recent studies have examined whether non-  
464 auditory feedback can substitute for the white noise. They provided the first evidence that a visual (a  
465 light-off or a light-on) as well as a tactile stimulus (applied to the scalp), respectively, can guide  
466 changes in the pitch value (McGregor et al., 2021; Zai et al., 2020). These results support the idea that  
467 the ability to carefully adjust one's own vocalizations, shared by humans and songbirds, can efficiently  
468 rely on information from several different modalities. These experiments have opened a new line of  
469 perspective supporting the idea that vocal production relies on multimodal processes.

470 Support for this hypothesis is provided by other studies. Multisensory processes are commonly  
471 considered to be susceptible to circumstances producing sensory loss. Zai and coll. (2020) showed that  
472 exposure of adult birds to visual stimuli in the pitch-shifting learning paradigm could drive vocal  
473 changes in hearing birds, as previously mentioned, but also in deafened birds. Male deafened zebra  
474 finches after bilateral cochlea removal are able to shift the pitch of one target syllable in the paradigm  
475 in which a light was switched off every time the pitch produced was lower (or higher) than a threshold  
476 value (Zai et al., 2020). These results demonstrate that visual signals in songbirds may exert an  
477 efficient control on vocal production when the auditory feedback is lacking. Importantly, birds with  
478 normal hearing and deafened birds exhibit differences in their behaviour adaptation. Deafened birds  
479 shifted the syllable pitch to increase the rate of visual stimuli delivery while hearing birds did the  
480 opposite. In both cases, somatosensory signals were available to control how to sing (Suthers et al.,

481 2002). Bird behaviour varied depending on the number of sensory modalities that conveyed  
482 information. Visual and somatosensory information was perceived in deafened birds while auditory  
483 information was also available to hearing birds. The magnitude of pitch changes induced by visual  
484 information also differed between hearing and deaf birds, being lower in hearing than in deafened  
485 birds (Zai et al., 2020). This lower magnitude of song changes in hearing bird could reflect a form of  
486 auditory dominance which minimizes the influence of visual signals. Similar sensory dominance was  
487 reported in an audio-visual fear conditioning paradigm in which the conditioned fear-response of  
488 rodents was weakened when a loud noise was simultaneously presented (Iurilli et al., 2012). In this  
489 experiment, the very high amplitude of the auditory stimulus provides more salient or reliable  
490 information than the visual stimulus. The auditory stimulus is thus prioritized over the visual stimulus,  
491 resulting in a segregation of sensory modalities in a bottom-up manner (Meijer et al., 2019). In the  
492 experiment performed in birds, hearing birds had access to both auditory and visual feedback while  
493 deafened birds only had access to visual feedback (Zai et al., 2020). The loss of auditory feedback may  
494 thus reveal the salience or the relevance of the visual feedback, that is constantly overshadowed by  
495 auditory feedback in hearing birds. Since hearing birds are able to adjust their song less efficiently  
496 than deafened birds, it suggests a dominance of one sensory (here auditory) modality in hearing birds  
497 and so a partial segregation of sensory modalities in a bottom-up manner. Given the fine motor control  
498 that the pitch shifting learning task requires, it might also be hypothesized that top-down processes  
499 from high order brain areas do occur to adjust the behavioural strategy (changing the song to get more  
500 or less visual stimuli). Further experiments will be necessary to understand how the respective  
501 influences of the different sensory modalities interact and control vocal production.

502 A specialized neural pathway is required for auditory-guided song learning during development and  
503 song maintenance in adults and is analogous to the basal ganglia-thalamo-cortical circuit of mammals.  
504 This pathway is involved in the drive of vocal plasticity induced either by visual or tactile stimuli in  
505 the pitch-shifting learning paradigm (McGregor et al., 2022; Zai et al., 2020). Lesioning Area X or  
506 LMAN, two nuclei of the avian basal ganglia-thalamo-cortical circuit, prevent the non-auditory-  
507 induced vocal plasticity (McGregor et al., 2022; Zai et al., 2020) demonstrating that this circuit is not

508 solely involved in the processing of auditory feedback in songbirds. Other evidence comes from  
509 assessment of the impact of social context focusing on this pathway (Kao and Brainard, 2006). In  
510 zebra finches, adult males produce a highly stereotyped song with slight variations between renditions.  
511 In the presence of a female, males produce courtship songs that becomes even more stereotyped  
512 (Sossinka and Bohner, 1980; Dunn & Zann, 1996; Hessler & Doupe, 1999a; Kao et al, 2005). The  
513 basal ganglia-thalamo-cortical pathway is strongly affected by social cues (Hessler and Doupe, 1999a;  
514 Jarvis et al., 1998; Kao et al., 2008). Neural recordings showed that the pattern of singing-related  
515 neural activity in two regions, the Area X and the LMAN, is dependent on whether the bird is singing  
516 in isolation or to a female (Hessler and Doupe, 1999a, 1999b; Kao et al., 2008). Therefore, as  
517 information from different modalities may guide learning-induced changes in song structure, the avian  
518 basal ganglia-thalamo-cortical pathway could be viewed as mediating vocal changes from different  
519 sensory information and not exclusively from auditory information. Multisensory neurons in the basal  
520 ganglia of mammals exhibit the ability to integrate multisensory information (Nagy et al., 2006; Reig  
521 and Silberberg, 2014). Multisensory integration may help in the effective processing of sensory events  
522 and the changes in the environment during motor actions controlled by the basal ganglia. Interestingly,  
523 an early survey reported a positive correlation between the volume of the area X and of the visual  
524 nucleus rotundus and the rate of courtship songs, but not with the rate of non-courtship songs in male  
525 brown-headed cowbirds. This result thus highlights that the female-directed singing is a multimodal  
526 courtship behaviour not only recruiting a song-related nucleus (Area X), but also a visual area (nucleus  
527 rotundus).

528 In summary, research findings highlight the powerful influence of multisensory conditions on  
529 behaviour, in juveniles as well as in adult males and females. Birdsong, as human speech, plays a  
530 critical role in the social life of individuals. The findings demonstrate that social interactions, through  
531 multisensory signals, also strongly influence vocal behaviour. Neurophysiological studies have  
532 identified many brain areas where signals from multiple sensory sources may potentially converge.  
533 Yet, it is unclear how the neural mechanisms by which information from different sensory modalities  
534 interact or are integrated to influence songbird behaviour. There is currently great interest in the basal-

535 ganglia forebrain circuits for deciphering neural mechanisms underlying the learning and generation of  
536 song behaviour. Recent evidence indicates that these circuits are required for non-auditory information  
537 to drive changes in the song features of adult songbirds (McGregor et al., 2022; Zai et al., 2020).  
538 Future research will help resolve the neural mechanisms by which non-auditory information exerts its  
539 influence.

## 540 **Conclusion and Perspectives**

541 This review focused on various avian taxa, behaviours and brain networks and highlighted fields of  
542 research that deserve more investigations to better understand the processing and control of  
543 multisensory signals (Figure 4). Our main goal was to highlight the current state of the art on  
544 multisensory processing in birds. Recent reviews have been focused on the neuronal substrates  
545 underlying multisensory processes but they were essentially restricted to research in mammalian  
546 models (Meijer et al., 2019; Stein et al., 2020). Yet, a clear strength of the research on multisensory  
547 processing in birds is, to our view, related to the type of behaviours being investigated. Prey detection  
548 as well as imprinting or vocal communication are behaviours observed in natural conditions. Although  
549 controlling all factors is a tremendous task when studying natural behaviours, they shed light on  
550 specific processes that could not be revealed by simpler behavioural paradigms (Khastkhodaei et al.,  
551 2016; Meijer et al., 2019). The research findings for example support the idea that facing a given  
552 object through more than one sensory modality, as is often the case in the natural world, makes  
553 cognitive abilities, including the evaluation of the object salience as well as acquisition of  
554 sensorimotor skills, more effective.

555 This review aimed at highlighting the relevance of studying multisensory processing in another group  
556 of animals than mammals. To this end, we have attempted to present multisensory processes in the  
557 light of what is known from mammalian models, when data were available. This comparative  
558 approach has allowed us to establish that some of the neuronal mechanisms identified in mammalian  
559 models are also implemented in birds, thus arguing for evolutionary conserved strategies within brain  
560 networks to achieve multisensory integration. Several examples indeed argue for bottom-up or top-  
561 down modulation various forms of multisensory processing. In birds as well as in mammalian species,

562 multisensory processes affect numerous brain areas and pathways, ranging from the midbrain to  
563 primary sensory or high-order sensory cortical areas including brain regions of the basal ganglia-  
564 thalamo-cortical pathways. The availability of the range of techniques (e.g. large scale  
565 electrophysiological recordings, optogenetic methods) used in birds now allows to investigate not only  
566 neuronal dynamics but also to assess causal relationships between neuronal activity and behaviours  
567 that may depend on multisensory integration (Guitchounts et al., 2013; Roberts et al., 2012).

568 Beyond similarities between birds and mammals highlighted in this review, birds have allowed to raise  
569 original questions that mammalian species used as animal models left unresolved. The importance of  
570 multisensory signals in the fine motor control required by birdsong production to adjust acoustic  
571 features of vocalizations (McGregor et al., 2022; Zai et al., 2020), or in the case of a sensory loss, has  
572 opened a new line of research. This new field of research leads to assume that multisensory  
573 information may guide changes in vocal production in species that learn to vocalize such as humans.  
574 Studies of multisensory processing in birds should provide new insights on mechanisms underlying  
575 speech acquisition and production in the human brain.

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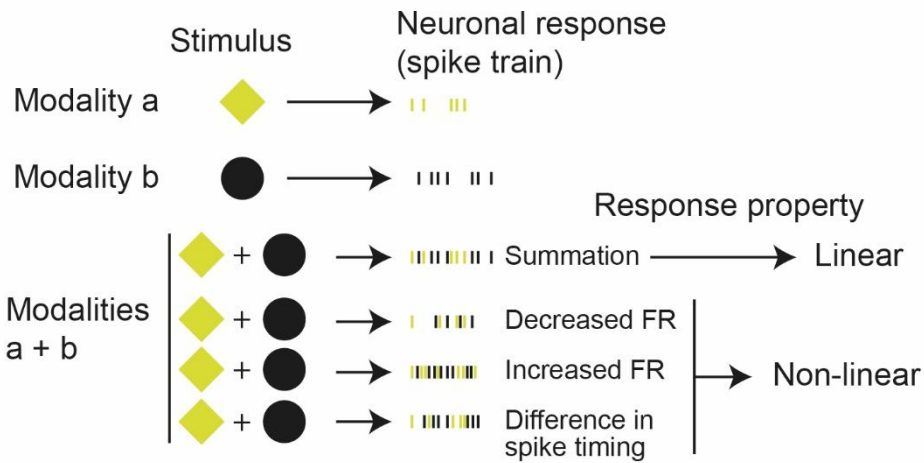
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1062 **Figure captions**

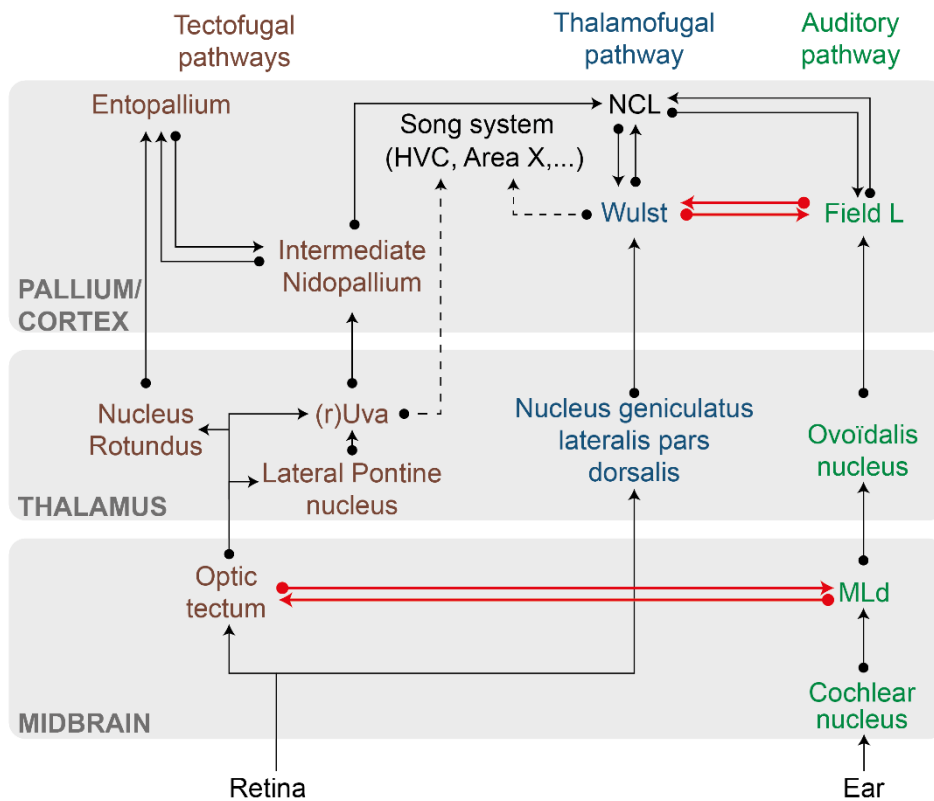


1063

1064 **Figure 1: Expected neuronal responses to unisensory and multisensory stimuli**

1065 In response to a multisensory stimulus (modalities a – green diamond - and b – black circle), neuronal  
 1066 responses may result from linear properties (summation of the firing rate, FR) or non-linear properties  
 1067 (FR decrease, FR increase, and/or different temporal spike patterns).

1068



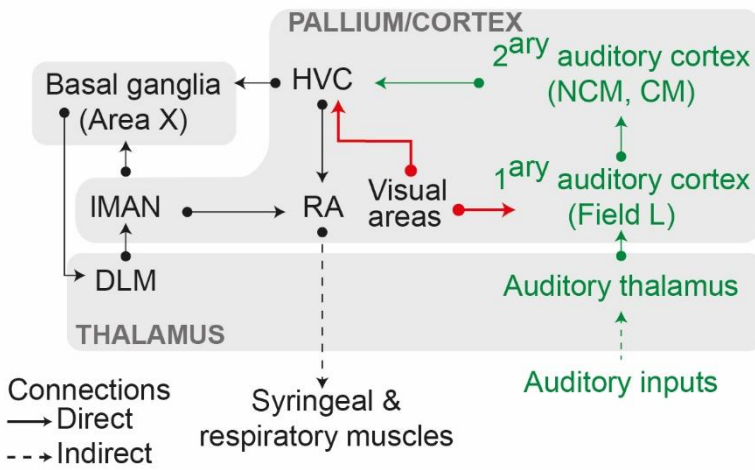
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1070 **Figure 2: Interconnections between visual and auditory pathways in the bird brain.**

1071 Birds have one auditory pathway (green) and two main visual pathways: the tectofugal (left, brown)  
 1072 and the thalamofugal (middle, blue) pathways. Interconnections between visual and auditory areas are  
 1073 reported in the midbrain (optic tectum – MLd, red arrows). In the pallium, direct connections have  
 1074 been identified between visual and auditory centres (Wulst – Field L, red arrows). The Wulst is  
 1075 considered as analogous to the mammalian primary visual cortex (V1). Visual and auditory  
 1076 information converge in the NCL (nidopallium caudolaterale, considered as analogous to the  
 1077 mammalian prefrontal cortex). In songbirds, there are indirect projections to the song system (dashed  
 1078 line) originating from visual relay (auditory areas projections to the song system are not shown). MLd:  
 1079 nucleus mesencephalic lateralis, pars dorsalis (indirect connections between the cochlear nucleus and  
 1080 MLd are not shown); (r)UVA: (rostral) nucleus Uvaeformis. For more details on the Wulst and  
 1081 (r)UVA circuits, see (Stacho et al., 2020; Wild and Gaede, 2016, respectively).

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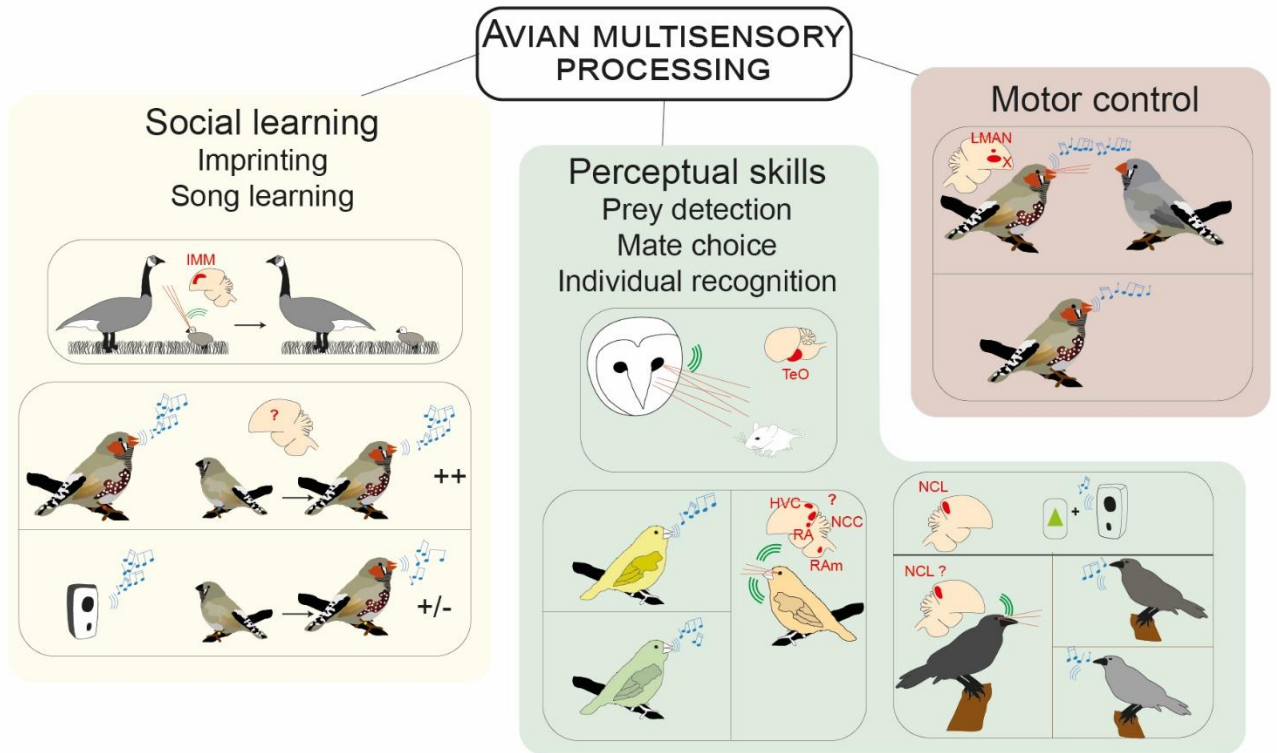


1084

1085 **Figure 3: The auditory pathway and the songbird song system**

1086 The song system includes the song motor pathway (HVC: proper name; RA: Robust nucleus of the  
1087 arcopallium, analogous to the human laryngeal motor cortex) and the anterior forebrain pathway  
1088 (IMAN: lateral magnocellular nucleus of the anterior nidopallium; Area X, analogous to mammalian  
1089 basal ganglia; DLM: dorsolateral nucleus of the anterior thalamus). It receives inputs from the  
1090 auditory pathway (green), visual areas (red line, see Figure 1 for more details) and the ventral  
1091 tegmental area (not shown). CM: Caudal mesopallium; NCM: Nucleus of the caudal mesopallium.

1092



1093

1094 **Figure 4: Knowns and unknowns in the field of avian multisensory processing**

1095 Avian multisensory processing has been mostly studied in the context of social learning, perception,  
 1096 and motor control. In precocial birds (left, top), filial imprinting highlighted the involvement of the  
 1097 IMM, a multisensory region that receives afferents from all sensory systems and projects to motor  
 1098 areas. In songbirds (left, bottom), it remains to identify which brain network yield young songbirds to  
 1099 learn better copies of their tutor songs when they can directly socially interact. In barn owls (middle,  
 1100 top), the multisensory based detection of preys requires the TeO, a visual area. In songbirds, female  
 1101 preferences for certain song types involve song nuclei (HVC, RA) and nuclei outside of the song  
 1102 system (NCC, RAm). In corvids (right, bottom), songbird species used to assess their higher cognitive  
 1103 abilities, learning of arbitrary audio-visual associations recruits neurons of the NCL, avian analogue of  
 1104 the mammalian prefrontal cortex, which might also be at play for multimodal recognition of  
 1105 conspecifics. In male songbirds (right, top), the cortico-basal ganglia network (LMAN and Area X) is  
 1106 involved in the socially-dependent modulation of the song motor control. See main text for references.

1107

1108 **Box 1: What is multisensory integration at the neuronal level?**

1109 Multisensory integration generally refers to the set of processes by which redundant and/or  
1110 complementary information arriving from different sensory modalities (e.g., vision, audition, touch)  
1111 are combined to yield an enriched perceptual experience of multimodal events. This form of  
1112 multisensory processing reflects what is commonly reported as cue integration. Yet, multisensory  
1113 processing includes other forms of integration such as sensory selection, multisensory based object  
1114 recognition and segregation of cross-modal stimuli (Meijer et al., 2019). Sensory selection reflects the  
1115 ability to neglect the information from one modality. Multisensory based object recognition involves a  
1116 transfer of information from one modality to another during a discrimination task: animals are trained  
1117 to identify an object based on a single modality (e.g. touch) and are then tested to identify the same  
1118 object using another modality (e.g. sight). Modality segregation occurs when information from one  
1119 modality overshadows information from another modality.

1120 While multisensory cue integration relies mostly on bottom-up neuronal processes with a feedforward  
1121 transmission from low-level to associative areas, learning and cognitive skills might also modulate  
1122 multisensory integration through top-down modulations exerted by higher-level areas. In the present  
1123 review, multisensory processes refer not only to multisensory cue integration but also to the whole set  
1124 of processes by which information of one modality influences or interacts with the processing of the  
1125 specific information of another modality.

1126 Multisensory processes and integration have been quantified using a wide range of experimental  
1127 approaches (Stevenson et al., 2014). At the neuronal level, the most commonly implemented method  
1128 focuses on single- or multiunit responses, driven by multimodal signals consisting of two or more  
1129 modality-specific components presented in a spatiotemporally congruent manner (for more details and  
1130 metrics used, see Stevenson et al., 2014). These neuronal responses are often evaluated using spike  
1131 counts (sometimes in combination with a spike train analysis) and are compared to responses evoked  
1132 by a modality-specific component presented in a temporally and/or spatially incongruent way or to  
1133 components presented separately. This comparison presumes a convergence of inputs from multiple  
1134 sensory sources onto individual neurons in the brain region of interest. Neuronal responses to

1135 multimodal signals can rely on linear response properties, in which case the responses approximatively  
1136 correspond to the sum of all responses to unimodal signals (Figure 1). When these responses cannot be  
1137 explained by responses to unimodal signals because they are higher or lower than expected based on  
1138 their summation, then this non-linearity is commonly considered as reflecting a multisensory  
1139 integration. Using spike train analyses, one typically estimates of the mutual information between  
1140 unimodal or multimodal stimuli and uses the temporal spike patterns to examine whether neurons  
1141 transmit more information from multisensory stimuli than from a unisensory stimulus (Bizley et al.,  
1142 2007). Yet, the benefit provided by multisensory integration at the behavioural level may be due to  
1143 linear properties (Angelaki et al., 2009). Also, certain computational models suggest that both linear  
1144 and non-linear operations could be achieved by multisensory neurons (Morgan et al., 2008; Ohshiro et  
1145 al., 2011).

1146 Neurons exhibiting multisensory integration have been studied in the superior colliculus, a midbrain  
1147 structure that contains multisensory convergence zones (Stein and Stanford, 2008a; Wallace et al.,  
1148 1998). These neurons guide orienting behavior towards salient stimuli, a form of cue integration that  
1149 relies on bottom-up processes. Experimental evidences also suggest that these neurons can drive  
1150 attention through an interplay between bottom-up and top-down mechanisms (Talsma et al., 2010). In  
1151 this brain structure, responses of multisensory neurons to bimodal congruent stimuli consisting of  
1152 unimodal stimuli that are aligned in space and temporally synchronized are typically stronger than  
1153 responses to the unimodal components. Interestingly, bimodal incongruent stimuli that are misaligned  
1154 in space do not induce this enhancement in responses when compared with the unimodal responses. A  
1155 depression was also observed in some responses evoked by bimodal incongruent stimuli. This  
1156 differential effect suggests that congruent bimodal stimuli arise from the same object while  
1157 incongruent information arise from competing objects. The multisensory integration could thus help  
1158 bind the different unisensory components into a single unified object.

1159 Enhanced responses to bimodal stimuli that are suitable for target detection have been described in  
1160 other regions than the superior colliculus, including primary sensory cortices (e.g. Bizley et al., 2007;  
1161 Kayser et al., 2008; Knöpfel et al., 2019). However, combining stimuli from two different modalities

1162 can manifest differently in different brain regions, including a suppression of responses in primary  
1163 sensory cortices (Angelaki et al., 2009; Dehner et al., 2004; Garner and Keller, 2022; Ibrahim et al.,  
1164 2016; Iurilli et al., 2012; Lohse et al., 2021b). This effect may allow a sharpening of functional  
1165 properties, such as orientation selectivity in V1 or reducing the impact of information from other  
1166 modalities, including distracting or self-generated signals, to increase the salience of information from  
1167 one specific modality (Ibrahim et al., 2016; Iurilli et al., 2012; Lohse et al., 2021b). It has also been  
1168 observed in the context of task learning (Garner and Keller, 2022).

1169 Another methodological approach, measuring local field potentials, is also based on  
1170 electrophysiological recordings in the brain region of interest. This has provided complementary  
1171 information to the information obtained through single- and multiunit recordings, from subthreshold  
1172 mechanisms at the synaptic level and provided insight into how neural populations may encode  
1173 multisensory signals. A resetting of ongoing oscillations has been proposed as the possible mechanism  
1174 used to amplify sensory signals by optimizing neuronal excitability (Lakatos et al., 2007; van  
1175 Atteveldt et al., 2014).