

The sensory substrate of multimodal communication in brown-headed cowbirds: are females sensory ‘specialists’ or ‘generalists’?

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Abstract Many animals communicate with multimodal signals. While we have an understanding of multimodal signal production, we know relatively less about receiver filtering of multimodal signals and whether filtering capacity in one modality influences filtering in a second modality. Most multimodal signals contain a temporal element, such as change in frequency over time or a dynamic visual display. We examined the relationship in temporal resolution across two modalities to test whether females are (1) sensory ‘specialists’, where a trade-off exists between the sensory modalities, (2) sensory ‘generalists’, where a positive relationship exists between the modalities, or (3) whether no relationship exists between modalities. We used female brown-headed cowbirds (*Molothrus ater*) to investigate this question as males court females with an audiovisual display. We found a significant positive relationship between female visual and auditory temporal resolution, suggesting that females are sensory ‘generalists’. Females appear to resolve information well across multiple modalities, which may select for males that signal their quality similarly across modalities.

Keywords Multimodal sensory processing · Temporal resolution · Individual variation · Brown-headed cowbirds · Sensory filtering

Abbreviations

ABR	Auditory brain-stem response
AEP	Auditory evoked potential
AIC	Akaike information criterion
ERB	Equivalent rectangular bandwidth
FFF	Flicker fusion frequency
TDT	Tucker Davis Technologies
SAS	Statistical analysis software

Introduction

Many courtship signals combine information across several sensory modalities (Partan and Marler 1999, 2005; Candolin 2003; Heberts and Papaj 2005). The receiver sensory system detects and filters the signal in the peripheral sensory system, allowing only certain signal information to be processed in the central nervous system. Therefore, sensory filtering (i.e., sensory processing capacity) is the first step to determine which signal content is used for mate-choice decisions. Nevertheless, we know relatively little about how receivers filter signal content across sensory modalities (Ronald et al. 2012). This gap is particularly important, because signal content across sensory modalities may combine or interact to influence perception, and ultimately mate-choice and reproductive success (Taylor et al. 2011; Taylor and Ryan 2013; Reichert and Hobel 2015; Ronald et al. 2017).

Sensory filtering is an energetically demanding process (Phelps 2007; Dangles et al. 2009); consequently, individuals may vary in their investment in sensory systems. This

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individual variation may result from differences in development or in current condition (reviewed in Ronald et al. 2012), and could lead to individual differences in how females filter male multimodal signals. These individual differences can subsequently lead to population-level patterns of sensory filtering. Imagine, for example, a female population that processes both male visual and acoustic courtship signals. We envision at least three population-level patterns for such a population. First, females may have high sensory filtering capacities in one sensory dimension but low in the other (hereafter, “sensory specialists”). Second, females may have high sensory filtering capacities in both dimensions (hereafter, “sensory generalists”). Third, female sensory filtering capacities across dimensions may not be related (e.g., independent sensory filtering across modalities). A first step towards testing these patterns of multimodal sensory filtering is to establish the degree of association (i.e., correlation) between sensory traits in different modalities across different receivers. Unfortunately, most of the evidence on associations between sensory traits is quite limited, and is primarily focused on pathology in human perception (Humes et al. 2009).

A population-level sensory specialist pattern can result when females resolve information better in one modality over the other; this pattern may arise from compensatory plasticity, whereby animals compensate for developmental deficits in one modality by redirecting energy to develop alternative sensory modalities (Rauschecker and Knierpert 1994; Lessard et al. 1998; Merabet and Pascual-Leone 2010). The outcome will be a trade-off between sensory traits in different sensory modalities (i.e., negative relationship). For example, human subjects born blind often have superior auditory abilities (Lessard et al. 1998; Collignon et al. 2009). Sensory specialists may also be the result of different selection pressures across modalities; for example, animals that live in visually complex environments may have evolved to place more emphasis on acoustic, rather than visual, signaling, and reception. As sensory systems are expensive to maintain (Dangles et al. 2009), this may result in greater filtering capacity in the acoustic modality and lesser filtering capacity in the visual modality, leading to sensory specialists.

A population-level sensory generalist pattern can result from individuals resolving information similarly across modalities, likely due to factors [e.g., body condition, age, hormone levels, etc (Eisner et al. 2004; Baur et al. 2009; Knott et al. 2010)] that simultaneously increase filtering capacities across modalities (i.e., a positive relationship). In adult human females, sensitivity to both acoustic (Al-mana et al. 2010) and visual stimuli (Eisner et al. 2004) is affected by hormonal changes throughout the menstrual cycle. Similarly, as humans age, they also experience a general reduction in sensory capacity across multiple modalities including

hearing (due to more noise exposure with age; Gates and Mills 2005) and vision (due to a gradual thickening of the lens; Glasser and Campbell 1998).

Finally, two scenarios may generate a non-significant population-level relationship in sensory filtering between modalities. First, there may be no individual variation in sensory filtering across modalities (e.g., signals are processed in the same way by all individuals). This is commonly assumed in the non-human literature (Ronald et al. 2012). Second, individuals may vary in their sensory filtering capacities, but this variation could be uncorrelated and thus leads to a lack of a specific population-level pattern.

We examined the relationship between visual and auditory sensory filtering capacity in female brown-headed cowbirds (*Molothrus ater*), an obligate brood-parasite, to test whether they are sensory specialists, generalists, or whether processing is uncorrelated across modalities. Male cowbirds court females with a fast, audiovisual display (less than 2 s) comprised of a song paired with a visual wingspread (West et al. 1981; O’Loughlen and Rothstein 2010). The visual display begins with body-feather puffing coupled with song, then transitions to the most visually intense portions (e.g., the wingspread) during the quieter portions of the song (Cooper and Goller 2004). The display ending is characterized by a high-frequency, temporally modulated note. Interestingly, the size of the two brain regions, the song control nuclei (i.e., area X) and the visual nuclei (i.e., nucleus rotundus), has been shown to be correlated with courtship skills in brown-headed cowbird males (Hamilton et al. 1998) which suggests a link between central processing and signal production. In this study, we are interested in sensory processing and signal reception of the sensory system.

Female cowbirds process male audiovisual signals during the breeding season when selecting a seasonal mating partner. Behavioral studies have shown that females prefer the multimodal display over the isolated song (O’Loughlen and Rothstein 2010) or the isolated visual signal (O’Loughlen and Rothstein 2012). In addition, the intensity of the visual signal (e.g., width of the wingspread and depth of the bow) and spectral/temporal components of the song can interact with one another to influence female preferences (see Ronald et al. 2017). This interaction suggests that the signal components provide different “messages” to the female about male quality (i.e., the multiple messages hypothesis of non-redundant signals) (Candolin 2003). The fast pairing of the auditory and visual components of the male signals, and the interaction of these signals, suggests that females may attend to these signals simultaneously. Furthermore, evidence suggests that females with greater neuronal numbers in IMAN, a song control center in the brain, show more choosiness in their mating decisions. This establishes a connection between processing (albeit central

processing) and eventual behavior decisions (Hamilton et al. 1997). Here, we examined whether there is a relationship between sensory filtering of visual and acoustic signals, because sensory filtering can also influence mating preferences (see Ronald et al. 2012).

Specifically, we characterized visual temporal resolution (i.e., ability to detect temporal changes in a visual signal) and auditory temporal resolution (i.e., ability to distinguish temporally modulated sounds). In cowbirds, visual temporal resolution can function to detect spatial movement in the wingspread, and auditory temporal resolution can function to detect song spectral changes. If the visual temporal resolution and auditory temporal resolution are positively correlated, it would indicate that the population-level sensory filtering pattern is a sensory generalist type and that some females may be better at discriminating between males based on the multimodal signal. If the visual temporal resolution and auditory temporal resolution are negatively correlated, it would indicate that the population-level sensory filtering pattern is a sensory specialist type and that some females may favor evaluating males using one signal modality in preference to another modality. If, however, sensory filtering is uncorrelated across modalities, then the capacity of females to process signals in one modality should, on average, not influence their capacity to process signal in the other modality.

Methods

Animal subjects

Twenty-four female cowbirds were wild-caught May 2013, in Sandusky, OH, and housed in individual enclosures. Birds were provided ad libitum access to seed and water. The lighting schedule followed the local conditions.

Subjects were first used in a mate-choice experiment described elsewhere (Ronald et al. 2017), which involved implanting them with estradiol (10 mm crystalline estrogen, Sigma Chemical Co., St. Louis, MO, into Silastic tubing, outer diameter 1.96 mm) after sedation with ketamine (40–60 mg/kg) and midazolam (6–8 mg/kg) via intramuscular injection. Females were randomly divided into seven experimental blocks with blocks of birds run sequentially. 29-day post-implantation a blood sample was taken for hormonal analysis (see electronic supplementary material). Females were then sedated as above and sensory traits were assessed via auditory and visual evoked potentials. Females recovered following auditory measurements for 2–7 days before visual measurements.

Auditory evoked potentials

Sensory filtering of temporal information is thought to be impacted by two aspects of the auditory system (Gall et al. 2012); the first is the width of the auditory filters on the cochlea, whose physical properties dictate a trade-off between temporal and frequency resolution (Moore 1993; Viemeister and Plack 1993). The second factor relates to the refractory nature of neurons. We used auditory evoked potentials (AEPs) (changes in electrical voltage when the brain-stem nuclei respond to sound) to evaluate both aspects in turn. Specifically, we measured auditory brain-stem responses (ABRs), which are responses to a sound onset (Hall 2007) to determine (1) auditory filter size (Gall and Lucas 2010; Gall et al. 2013) and (2) the slope of the recovery line from a double-pip protocol (Gall et al. 2012). Auditory filter size was measured at two frequencies (2–3 kHz) and then averaged to generate a single filter size. The double-pip-recovery experiment examined responses at 3 kHz. This small frequency range (2–3 kHz) was tested because this is the range where cowbirds are the most sensitive (Gall and Lucas 2010).

Stimulus presentation, ABR acquisition, and data storage were coordinated by a TDT system II modular rack-mount system. Acoustic stimuli were created in SigGen32 on a computer with an AP2 sound processing card. Stimuli were converted from digital to analogue signals with a TDT DA1, equalized across frequencies with a 31-band equalizer (Behringer Ultragraph model FBQ6200, Bothell, WA USA), and then amplified with a Crown D75 amplifier prior to being presented to the subject.

Following previous work, sedated birds were placed with their right ear facing upwards on a microwaveable heating pad in the center of an anechoic sound chamber (1.2 × 1.2 × 1.4 m) lined with 7.7 cm Sonex acoustic foam (Acoustic Solutions, Richmond, VA USA) (Gall and Lucas 2010; Gall et al. 2012, 2013). A temperature probe placed beside the bird allowed us to maintain the bird's external temperature between 39 ± 2 °C. Acoustic stimuli were presented from a magnetically shielded speaker (RCA Model 40–5000, RadioShack, Fort Worth, TX, USA; 140–20,000-Hz frequency response) 30 cm above the bird's head. We placed three needle electrodes just below the skin to record the ABR: a positive electrode was placed at the vertex of the skull, a negative electrode was placed in the mastoid just below the right ear, and a ground electrode was placed at the nape of the neck. These electrode leads were connected to a Tucker Davis Technologies (TDT; Alachua, FL, USA) headstage (HS4) and subsequently passed through a biological amplifier (TDT DB4). The neural responses were then bandpass filtered from 0.3 to 10 kHz, notch filtered at 60 Hz, and amplified (200,000×). The analogue signals were then digitized (TDT AD2) and connected to a Dell PC running

TDT BioSig32 in an adjacent room. We periodically played a broadband click (100 μs) to ensure that the amplitude and latency of the ABR response were not affected by changes in sedation level. Some individuals started to awaken before we could complete all experiments, so we detail the number of individuals that underwent each experimental protocol in each section below.

Auditory filter width

The auditory filter width serves as an estimation of an animal’s ability to resolve temporal information, because filter width mediates a trade-off between frequency and temporal resolution (Moore 1993; Viemeister and Plack 1993). Auditory filters function in signal integration over time; an animal with narrow filters can better discriminate between frequencies, because their filters integrate a signal over a longer time, but this comes at the cost of losing temporal resolution. In contrast, animals with wider filters tend to have better temporal resolution and poorer frequency resolution, because wider filters have shorter integration times (Moore 1993; Viemeister and Plack 1993). We used a notched-noise masking protocol (Patterson 1976; Patterson et al. 1982) to determine the width of the auditory filters ($N = 24$) following previous studies (Gall and Lucas 2010; Gall et al. 2013) (Fig. 1a). Stimuli for this protocol were 8-ms tone-bursts with 2-ms \cos^2 gating in alternating phases (90° and 270°) at 2–3 kHz. We varied the intensity of the stimulus from 16 to 72 dB in 8-dB steps for each frequency–notch width combination. Following previous protocols (Gall and Lucas 2010; Gall et al. 2013), we presented these tones in frequency–notched-white noise (spectrum level = 15.3 ± 2 dB re: $20 \mu\text{Pa}^2$ outside of the spectral notch) created by two waveform generators (TDT WG1) and

filters (TDT PF1, roll-off 156 dB/octave). Thresholds were estimated in duplicate and subsequently averaged at five normalized notch widths (half of the notch bandwidth divided by the center frequency) ranging from 0 to 0.4 at each center frequency (Gall and Lucas 2010).

The notched-noise procedure determines filter width from the functions of threshold by notch width. In general, the threshold should decrease as notch width increases, because the signal-to-noise ratio in the filter increases. This masked threshold (P_s) for determining auditory filter shape can be expressed as

$$P_s = K \int_0^\infty N(f)W(f)df,$$

where K is the signal-to-noise ratio necessary to evoke a response, $N(f)$ is the average power spectrum of the noise measured from the stimulus, and $W(f)$ is a weighting function. We solved for $W(f)$ and K using an iterative Gauss–Newton polynomial fitting procedure in SAS (Proc NLIN; v. 9.3). $W(f)$ was modelled as a two parameter rounded exponential model [roex(p, r)] (Patterson et al. 1982), where p is the slope of the auditory filter near center frequency, and r modifies the filter’s dynamic range (Moore 1993). The weight of the filter thus becomes

$$W(g) = (1 - r)(1 + pg)e^{-pg} + r,$$

where g is the normalized width of the silent spectral notch in the masking noise. When we combine these two equations, the ABR masked threshold equation becomes

$$P_s(\text{nw})' = K' + 10 \times \log_{10} \sum_{i=1}^N \frac{\text{PSD}_{\text{nw}(i)} \times \int_i \text{roex}(p, r)}{4 \times 10^{-10}},$$

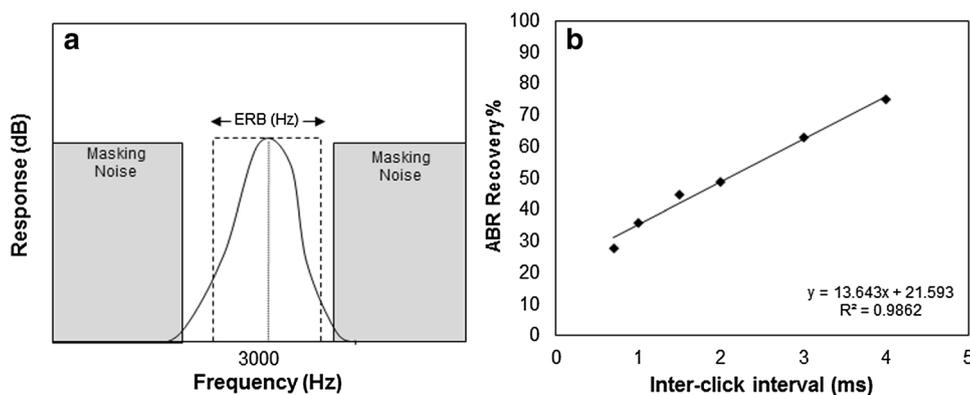


Fig. 1 **a** Method for determining auditory filter size using the notched-noise protocol. Here, we show a signal presented at 3000 Hz within notched-white noise. The filter size is determined using the equivalent rectangular bandwidth (ERB), where a rectangle the same size as the auditory filter is used to approximate the width of the filter in Hz. **b** Method for determining the auditory recovery function

slope. Percent recovery of the auditory brain-stem response (ABR) was found using ABR amplitude for the second of two tone pips as a function of the interval between pips. A higher slope reflects quicker system recovery after the first pip and, therefore, greater auditory temporal resolution

where nw is the width of the silent spectral notch and K' is the efficiency constant in decibels ($10 \times \log_{10} K$). N is the number of 25-Hz bins in the largest notch width, and $PSD_{nw(i)}$ is the power spectral density of the noise divided into each bin, each of which is multiplied by filter weight:

$$\int_i roex(p, r) = -(1 - r)p^{-1}(2 + pa)e^{-pa} + (1 - r)p^{-1}(2 + pb)e^{-pb} + r(a - b),$$

where a and b are the upper and lower frequency limits of each bin, respectively. We calculated the equivalent rectangular bandwidth (ERB), which describes a rectangle the same size and height as an auditory filter (Fig. 1a). We used the formula $ERB = 4/p \times \text{center frequency}$ to find the auditory filter size in Hz. We then averaged the filter size across the center frequencies we examined to obtain a single value of auditory filter size.

Auditory recovery function slope

Double-pip auditory recovery function slope gives an indication of the second aspect limiting temporal resolution in the auditory system: the neural refractory period. Here, AEPs were recorded in response to two tone pips separated by a time interval (Henry et al. 2011; Gall et al. 2012); with large time intervals, the amplitude of the ABRs generated by the tone pips is expected to be generally the same. However, as the interval between the two stimuli is reduced, the auditory system fails to recover quickly enough after the first pip to generate a normal ABR for the second pip. Thus, most studies investigate the amplitude of the ABR generated by the second pip as a function of inter-click interval (Henry et al. 2011; Gall et al. 2012). We examined the slope of the relationship between ABR amplitude for the second of two tone pips as a function of the interval between pips (Fig. 1b, $N = 16$). The function slope reflects the auditory system's ability to recover and detect sounds separated by a silent interval (Gall et al. 2012). A higher slope reflects quicker system recovery after the first pip and, therefore, greater auditory temporal resolution.

We followed a previously established procedure for measuring ABR recovery to paired-pips (Henry et al. 2011) which has been used to assess temporal resolution in cowbirds (Gall et al. 2012). Briefly, the stimuli included both paired clicks and single clicks. These clicks were generated by applying a 0.25 ms Blackman onset and offset ramps to a 0.67 ms, 3 kHz sinusoid with an amplitude of 60 dB (Henry et al. 2011). Paired click stimuli included two clicks, with the second click occurring after an inter-click interval of 4, 3, 2, 1.5, 1.0, or 0.7 ms (tested in decreasing order). At short inter-click intervals (<3 ms), the ABRs to both clicks

overlapped one another. We used point-to-point subtraction to isolate the ABR of the second click by subtracting the response to the single click from the average response to the double click. We then found the slope of the function between inter-click interval and ABR recovery (i.e., amplitude of the response to the second click divided by the amplitude of the response to the single click times 100) (Fig. 1b). Here, steeper (i.e., higher) slopes indicate faster ABR recovery and greater temporal resolution.

Visual evoked potentials

We measured temporal visual resolution with visual evoked potentials (i.e., changes in voltage in the retina and optic nerve to pulsing light, $N = 24$). The flicker fusion frequency (FFF) is the threshold frequency at which a pulsing light is perceived as a continuous, steady beam (Lisney et al. 2012). Higher FFF values indicate higher visual temporal resolution.

Birds were sedated as above and then positioned in a custom foam cradle on top of a microwaveable heating pad so that the head and beak were stabilized and body temperature could be maintained at 39 ± 2 °C. We measured responses from the left eye of each individual to be consistent between individuals and control for any laterality; this eye was held open with a Barraquer eye speculum (Arivet Inc, Utah, USA). Throughout the experiment, we applied a 1% carboxymethylcellulose solution (refresh tears lubricant eye drops) to the left eye to keep the eye moist and aid in electrical conductivity.

We used a custom-built stroboscope (Dr. Ellis Loew, Cornell University, Ithaca, NY, USA) to record our visual evoked potentials. White light stimuli were generated with a high-power xenon light (Monarch instruments 6206-010) fitted with a trigger and dial which allowed us to change the light pulse frequency (i.e., the length of time between pulses). We tested five different frequencies per bird from 80 to 100 Hz in 5-Hz increments. Stroboscopes have been previously used to record visual evoked potentials (Biel et al. 1999; Tanimoto et al. 2014). Birds were positioned within 12 cm of the light source, and the left eye was fully illuminated by the stroboscope. We maintained our stimulus light intensity at 455,014 cd/m². We used a background light (82,166 cd/m², Ludl Electronic Products, serial #41544, Hawthorne NY, USA) to measure the FFF under photopic conditions as cowbirds are diurnal birds. Stimulus light intensity measurements were done with a spectrometer (Jaz Spectrometer, Jaz-A-IRRAD application, Ocean Optics, Inc., Dunedin, Florida USA). Background light intensity measurements were collected via a LX1330B Digital Illuminance meter.

Visual evoked potentials were recorded from the bird with three electrodes: (1) a subdermal, positive electrode

was placed at the vertex of the skull; (2) a gold wire, negative electrode was placed gently resting on the cornea; and (3) a subdermal, ground electrode was placed at the nape of the neck. The electrode leads were connected to a biological amplifier (Grass EEG Amplifier, Natus Medical Incorporated, CA, USA). The neural responses were band-pass filtered from 3 to 1000 Hz, notch filtered at 60 Hz, and amplified 100×. The analogue signals were then digitized at a sampling rate of 48,000 Hz using a data acquisition program (Daqarta; Data Acquisition And Real-Time Analysis; www.daqarta.com) running on a Dell Latitude D610 laptop computer. We collected data over 40 ms and averaged the responses over 300 data collections. A response from each frequency (i.e., 80, 85, 90, 95, and 100 Hz) was collected in duplicate. Following a previous study (Lisney et al. 2012), we also recorded the background noise amplitude to analyze the response amplitude over the noise floor (i.e., responses, where no light was presented to the individual) at each frequency tested.

Visual evoked potentials are characterized by a trough (i.e., the a-wave), followed by a peak (i.e., the b-wave). We examined the amplitude of the b-wave as an indication of neuronal response from the retina by measuring the trough of the first a-wave to the peak of the first b-wave (as in ‘Method 2’ from Rubin and Kraft 2007; Lisney et al. 2012). Data files were first run through a custom Matlab code which smoothed the average curve and allowed the user to define the peak and trough of the evoked potential. We then examined the function of b-wave amplitude and stimulus frequency, and found that although the relationship was generally linear (Fig. 2), occasionally, the data were too variable to generate a robust estimate of FFF. Therefore, we used the regression with the highest R^2 value for each FFF treatment (R^2 range 0.78–0.98).

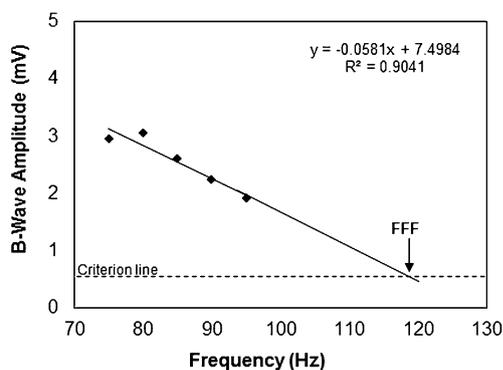


Fig. 2 Method for determining the flicker fusion frequency (FFF). Visual evoked potentials were recorded at different stimulus flashing frequencies and a linear regression was fit through B-wave amplitude as a function of flicker frequency. The FFF was determined as the intersection of this regression line and the criterion level of the noise, plus 1

We determined the average background amplitude for each individual and used this value as a threshold (criterion average noise amplitude plus one standard deviation, Lisney et al. 2012), below which the individual responses could not be differentiated from the noise floor. The intersection between the linear regression line and the criterion indicates the point at which the individual transitions from seeing a pulsing light to a steady beam of light (Fig. 2). Therefore, this value plus one is defined as the FFF and is the frequency at which the individual no longer perceives the pulsing light as flashing (Lisney et al. 2012).

Statistical analyses

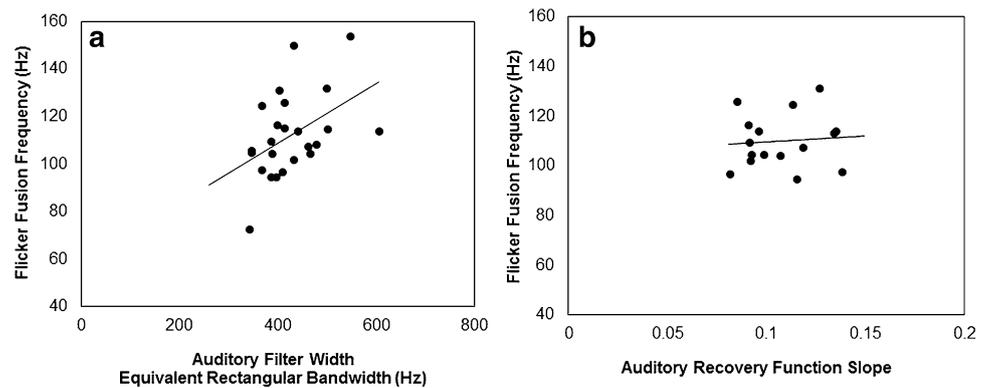
We used general linear models (Proc GLM in SAS 9.3) to investigate visual temporal resolution (FFF) as a function of auditory temporal resolution (recovery function slope or auditory filter width). Independent factors included the auditory temporal resolution and body mass, as body size has previously been positively correlated with visual temporal resolution (Healy et al. 2013).

Results

Temporal visual resolution (FFF) and temporal auditory resolution (auditory filter width) were positively associated ($F_{1,21} = 4.83$, $P = 0.04$), with an R^2 value of 0.21. Females with higher visual temporal resolution also had higher auditory temporal resolution (Fig. 3a). This finding suggests that females vary in their sensory processing across modalities. The association between FFF and recovery function slope was not significant ($F_{1,14} = 0.04$, $P = 0.85$; Fig. 3b), but variation between females was still evident. Body mass did not significantly affect the relationship between FFF and auditory filter width ($F_{1,21} = 0.64$, $P = 0.43$) or FFF and recovery function slope ($F_{1,14} = 0.17$, $P = 0.69$). When we removed body mass from the analyses, the relationship between FFF and filter width becomes more statistically significant ($F_{1,22} = 5.80$, $P = 0.02$), but the model has a lower fit (i.e., a higher AIC value without body mass, 201.7, than with body mass, 190.0); therefore, to be conservative, we kept body mass in the model.

We then explored the possibility for potential outliers in our data set. We found that the studentized residuals were well within the threshold for acceptance (i.e., 3; Yan and Su 2009); thus, we had no evidence of statistical outliers in our data set. Nevertheless, because of our relatively small sample size ($N = 24$), we decided to investigate the effect of removing a single data point at a time (with replacement) on both the R^2 and P values (see electronic supplementary material). Overall, regardless of any point we removed the positive relationship between auditory filter width and FFF

Fig. 3 **a** Positive linear relationship between auditory temporal resolution (i.e., auditory filter width) and visual temporal resolution (i.e., FFF). **b** No significant relationship between auditory temporal resolution (i.e., auditory recovery function slope) and FFF



stayed the same, with an R^2 range of 0.11–0.32 and the relationship was significant in 19 of the 24 models we ran (see electronic supplementary material).

Discussion

Our findings provide the first non-human evidence, to our knowledge, of an association between visual and auditory temporal resolution that may influence how females process the temporal components of male multimodal signals. This association suggests that females vary from one another in their sensory filtering of multimodal stimuli. We found support for females being sensory generalists for the sensory traits tested.

Female cowbirds are sensory generalists

Females with better temporal resolution of a visual signal, such as moving wings during the wingspread, also had wide auditory filters, which may allow for better capacity to filter temporally modulated auditory stimuli, such as complex trills. In the cowbird specifically, the timing of the wingspread and song is mechanically linked and these two signaling components are thought to have evolved together (Cooper and Goller 2004). This may help explain the association that we found in two sensory modalities of females. Female cowbirds may benefit, for instance, by quickly being able to discriminate between multiple singing males based on the performance of the visual display. This could be particularly useful as cowbirds flock together and females are often being courted simultaneously by more than one male (Rothstein et al. 1988). Interestingly, although the majority of data in humans suggests a general lack of relationship between modalities, a fairly recent study found that the ability to resolve temporal stimuli across modalities was positively correlated. Indeed, participants who were relatively better at detecting temporal gaps in auditory stimuli were

also more likely to detect temporal gaps in visual and tactile stimuli (i.e., absence of visual or tactile stimuli) (Humes et al. 2009).

Independent variation across sensory modalities

We did not find a relationship between auditory recovery slope and FFF (i.e., no relationship between auditory and visual temporal resolution). This may not be surprising, however, as other studies have found mixed support for a relationship between auditory filter width and recovery function slope in cowbirds (Gall et al. 2012) and other avian species including Carolina chickadees (*Poecile carolinensis*) (Henry et al. 2011), zebra finches (*Taeniopygia guttata*), and budgerigars (*Melopsittacus undulatus*) (Okanoya and Dooling 1990). The two scenarios that may generate this null-relationship (i.e., no individual variation in sensory filtering capacity or random individual variation in sensory capacity) should also result in different selective pressures on male signals. Under the first scenario, males may adopt a single signaling strategy as all females are essentially the same; under the second scenario, males may vary in their signaling strategies in a random manner. Independent variation across sensory capacities may result in weak selection on multimodal signals, or if signaling is costly, selection on males to emphasize components processed in a single modality.

We may expect to see independent variation across receiver sensory filtering especially in systems where one signaling component is dominant to another (Partan and Marler 2005). This occurs when one multimodal signaling component is both necessary and sufficient to eliciting a receiver response, while a secondary component does not influence receiver response during the multimodal playback (Partan and Marler 2005). Such is the case in wolf spiders (*Schizocosa stridulans*), where males court females with a combination of seismic and visual signals (Hebets 2008). Female spider receptivity, in turn, was found to be influenced only by male seismic signals (Hebets 2008). In this

scenario, there may be limited selection on both the male visual signal and female visual sensory filtering, resulting in a limited association between visual and seismic multimodal sensory filtering. Nevertheless, a recent review (Ronald et al. 2012) highlights that individual variation in sensory biology may be more common than expected, even if there is no correlation between sensory filtering capacities across multiple modalities.

Female sensory filtering can influence the selection on male signals

More generally, variation in female filtering capacity may alter the perception and, consequently, the evolution of male multimodal signals (Ronald et al. 2012). This may especially be the case where the information from different modalities eventually interacts to influence preference, like in brown-headed cowbirds (Ronald et al. 2017). For example, if females are sensory generalists, we may expect females to prefer males that can signal their quality equally across modalities. If current condition is reflected in the production of honest signals and receiver multimodal sensory filtering capacity, this could lead to a form of assortative mating, where females can resolve certain signals preferentially mate with males that can produce those signals, whereas females that do not have these sensory capabilities may be less selective (Hamilton et al. 1997; Maguire et al. 2013). Therefore, the strength of directional selection will vary with the distribution of sensory capabilities in the female population (Ronald et al. 2012). These predictions differ from those in the classical model of assortative mating. In the classical model of assortative mating, for instance, females are assumed to be accurate at determining their own rank and the prospective mate's ranking in one modality (e.g., modality A); this consequently leads to the appropriate mate choice, in an assortative pattern. If, however, there is variation between females in their sensory filtering capacity, this may result in some females unable to discriminate between males either to choose randomly between males based on modality A, or to rank males based on a different signaling modalities (e.g., modality B). Thus, in our model of assortative mating, variance in the ability of females to discriminate among the male signals will determine if males are selected.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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