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Lombard effect onset times reveal the speed of vocal plasticity in a songbird

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1 Lombard effect onset times reveal the speed of vocal plasticity in a
2 songbird

3 Running title: Lombard effect onset times in a songbird

4
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21
22 Keywords: Lombard effect, bird song, amplitude, noise, bioacoustics, response time

23

24 **Summary statement:** We measured the speed at which canaries adjust the amplitude of their
25 songs to mitigate the effects of signal masking by noise and demonstrate rapid vocal plasticity
26 in this species.

27

28 Abstract

29 Animals that use acoustic signals to communicate often compensate for interference and
30 masking from background noise by raising the amplitude of their vocalisations. This response
31 has been termed the Lombard effect. However, despite more than a century of research little is
32 known how quickly animals can adjust the amplitude of their vocalisations after the onset of
33 noise. The ability to respond quickly to increases in noise levels would allow animals to avoid
34 signal masking and ensure their calls continue to be heard, even if they are interrupted by
35 sudden bursts of high amplitude noise. We tested how quickly singing male canaries (*Serinus*
36 *canaria*) exhibit the Lombard effect by exposing them to short playbacks of white noise and
37 measuring the speed of their responses. We show that canaries exhibit the Lombard effect
38 approximately 300 ms after the onset of noise and are also able to increase the amplitude of
39 their songs mid-song and mid-phrase without pausing. Our results demonstrate high vocal
40 plasticity in this species and suggest that birds are able to adjust the amplitude of their
41 vocalisations very rapidly to ensure they can still be heard even during sudden changes in
42 background noise levels.

43

44

45 Introduction

46 Acoustic communication is often constrained by the masking effects of background noise which
47 can prevent a signal from being heard by the targeted receiver. To overcome this problem
48 animals may adjust their acoustic signals in a variety of different ways including increasing the
49 duration of brief calls (Brumm et al. 2004), increasing the redundancy of their vocalisations by
50 giving longer and more repetitive call series (Brumm & Slater, 2006; Kaiser & Hammers, 2009),
51 shifting the timing of their vocalisations (Fuller et al. 2007; Vargas-Salinas & Amézquita, 2013),

52 or by increasing the pitch of their vocalisations (Slabbekoorn & Peet, 2003; Parks et al. 2007).
53 One of the most efficient and widespread methods by which animals reduce the impact of signal
54 masking is by raising the amplitude of their vocalisations (Brumm & Zollinger, 2011; Hotchkin
55 & Parks, 2013). This phenomenon has been termed the Lombard effect in honour of its
56 discoverer, the French otolaryngologist Etienne Lombard (Zollinger & Brumm 2011), and it has
57 been shown to be much more effective at increasing signal detectability in noise than either
58 increasing the duration or repetition of a vocalisation (Luo et al. 2015). Moreover, even increases
59 in the pitch of vocalisations in response to noise may in fact be a by-product of calling more
60 loudly, as higher pitched sounds can generally be produced at higher amplitudes (Nemeth et al.
61 2013).

62 The Lombard effect has now been shown across a diverse range of taxa including
63 mammals, such as humans, monkeys, cetaceans, and bats (Hotchkin & Parks, 2013) and
64 numerous species of paleognath and neognath birds (Brumm & Zollinger, 2011). The situation
65 in amphibians is still unresolved as one study recently found a noise-dependent regulation of
66 call amplitudes in a frog, (Halfwerk et al. 2015) whereas previous studies failed to find evidence
67 for the Lombard effect in other anuran species (Schwartz & Bee, 2013). Recently, the presence
68 of the Lombard effect was also reported in a fish (Holt & Johnston, 2014) but the data is difficult
69 to interpret because it is not clear whether and how the noise amplitudes were accounted for in
70 the signal measurements in this study.

71 The widespread taxonomic distribution of the Lombard effect suggests it is the basic
72 mechanism by which birds and mammals, and perhaps also other vertebrates, improve the
73 detectability of their vocalisations in noise. Furthermore, in birds the Lombard effect occurs
74 independently of whether vocalisations are learnt through vocal production learning (Cynx et
75 al. 1998; Brumm & Todt, 2002) or not (Potash, 1972; Leonard & Horn, 2005; Schuster et al. 2012).
76 In humans however, it has been shown that the strength of the Lombard effect can be affected

77 by the social context (Amazi & Garber, 1982; Lu & Cooke, 2008) or linguistic content of the
78 vocalisation (Patel & Schell, 2008), and may also be voluntarily controlled to some extent by
79 cognitive processes (Pick et al. 1989; Tonkinson, 1994).

80 Although evidence for the Lombard effect in animals is extensive, it has so far only been
81 demonstrated in either wild animals living in continuously noisy environments, or in captive
82 animals exposed to long periods of synthetic noise (Tab. 1). Early studies of the Lombard effect
83 often used the term “Lombard reflex” (e.g. Egan, 1971; Junqua, 1996), possibly hinting that the
84 Lombard effect is typically exhibited very quickly in response to noise. This was shown in
85 humans by Bauer et al. (2006) who found an onset latency of 157 ms when the amplitude of the
86 auditory feedback of a speaker’s own voice was increased via headphones. Foery (2008) found a
87 similar onset latency of 127 ms in humans exposed to playbacks of noise.

88 However, despite this and more than a century of research on the subject, only one
89 study has yet directly tested how quickly the Lombard effect can be triggered in a non-human
90 animal. Hage et al. (2013) found that greater horseshoe bats (*Rhinolophus ferrumequinum*) with
91 their highly specialized auditory orientation system may adjust the amplitude of their
92 echolocation calls as fast as approximately 150 milliseconds, but data on other taxa, and
93 especially on vocalizations used for communication, are still lacking. This omission from the
94 literature is surprising given that many animals are often exposed to sudden changes in noise
95 levels. In undeveloped natural habitats, falling branches, gusts of wind or the calls of con- and
96 heterospecifics are potential sources of intermittent high amplitude noise bursts (Luther &
97 Gentry, 2013). In urban areas peaks in traffic during the morning and evening rush hours
98 contribute to a daily fluctuation in noise levels, while short bursts of often very loud noise from
99 sources such as car alarms, car horns, construction work or passing vehicles are common
100 throughout the day (Warren et al. 2006; Luther & Gentry, 2013).

101 The ability to rapidly increase the amplitude of their vocalisations would allow animals
102 to avoid signal masking and ensure their calls continue to be heard, even if their vocalisations
103 are interrupted by very sudden bursts of high amplitude noise. This is likely to be particularly
104 important for species whose vocalisations encode information as complex sequences of different
105 elements since masking of any part of these signals may prevent the correct messages from
106 reaching their targeted receivers. For species whose signals encode warnings about threats or
107 predators (e.g. Seyfarth et al. 1980; Templeton et al. 2005) it may be even more important to
108 ensure that they are successfully transmitted. As animal vocalisations are also often used for
109 territory defence and mate attraction (Seyfarth & Cheney, 2003), intermittent masking of these
110 vocalisations may lead to reduced breeding success in some species. The ability to avoid signal
111 masking during sudden bursts of noise is therefore likely to be strongly favoured by selection.

112 On a proximate level, the Lombard effect demonstrates that the auditory system
113 continuously monitors vocal output and uses this feedback to modulate the sound pressure level
114 of vocalisations according to the strength of the background noise (Eliades & Wang, 2012). The
115 speed at which the Lombard effect can act is therefore dependent on the neurons of the auditory
116 system, and the speed with which the muscles of the sound producing organ can respond to
117 neuronal stimulation (Suthers & Zollinger, 2008). In mammals the neurons which mediate the
118 Lombard effect are located in the brainstem (Nonaka et al. 1997; Hage et al. 2006) and in the
119 auditory cortex (Eliades & Wang, 2012). The ability of humans to voluntarily control the
120 Lombard effect to some degree also points towards some involvement of the motor cortex
121 (Brumm & Zollinger, 2011). These studies suggest that control of the Lombard effect is
122 sophisticated and likely requires well-developed auditory and motor control systems.

123 Understanding how quickly animals are able to exhibit the Lombard effect will provide
124 insight into how these systems function together and may also advance our understanding of
125 the flexibility and plasticity of vocal behaviours in animals.

126 We addressed this topic in a small passerine bird, the canary (*Serinus canaria*: Linnaeus).
127 Male canaries have diverse and well-studied vocal repertoires that are used in mate attraction
128 and stimulation (e.g. Leitner et al. 2001; Voigt & Leitner, 2008; Leboucher et al. 2012). The use
129 of minibreaths during rapid trills, which allows for uninterrupted songs of very long duration
130 and consisting of long repetitive phrases of the same element type, makes the canary an ideal
131 model to investigate mechanisms of rapid song modulation (Suthers et al. 2012). Furthermore,
132 different aspects of song production and vocal control mechanisms have been studied in this
133 species (e.g. Leitner & Catchpole, 2004; Bolhuis & Gahr, 2006; Suthers et al. 2012), which will
134 eventually allow placing new findings on the mechanisms of vocal plasticity into a broader
135 behavioural physiology context (Elemans et al. 2015). We examined changes in the sound
136 pressure level of the song of canaries during sudden short and sporadic bursts of broadband
137 white noise in order to discover how rapidly they exhibit the Lombard effect.

Table one. Duration of noise exposure in studies of the Lombard effect in non-human animals.

Species	Context	Duration of noise exposure (sound pressure level re. 20 μ Pa unless stated otherwise)	Reference
Birds			
Japanese quail (<i>Coturnix coturnix japonica</i>)	Captive	Three hours prior to recordings (48 – 63 dB)	Potash (1972)
Zebra finch (<i>Taeniopygia guttata</i>)	Captive	Until a minimum of five vocalisations had been produced (60 – 90 dB in 5 dB increments)	Cynx et al. (1998)
Budgerigar (<i>Melopsittacus undulatus</i>)	Captive	Until the bird had produced 75 calls. During the first 25 calls noise was played at 55 dB followed by 70 dB for the second 25 calls and 55 dB again for the last 25 calls.	Manabe et al. (1998)
Common nightingale (<i>Luscinia megarhynchos</i>)	Captive	20 minutes or until the bird had sung 27 songs, repeated at 5 dB noise increments between 55 – 75 dB	Brumm & Todt (2002)
Bengalese finch (<i>Lonchura striata domestica</i>)	Captive	100 seconds per noise treatment played successively at 40 – 70 dB at 10 dB increments.	Kobayasi & Okanoya (2003)
Blue-throated hummingbird (<i>Lampornis clemenciae</i>)	Wild	Until the bird stopped producing chipping calls (35 and 40 dB)	Pytte et al. (2003)
Common nightingale (<i>Luscinia megarhynchos</i>)	Wild	Continuous urban noise (40 – 64 dB)	Brumm (2004)
Tree swallow (<i>Tachycineta bicolor</i>)	Captive and wild	Wild birds – continuous ambient noise (41 – 67 dB) Captive birds – At least one hour (55 and 65 dB)	Leonard & Horn (2005)
Domestic fowl (<i>Gallus gallus</i>)	Captive	Six minutes per treatment with four successive noise treatments (60, 67, 75 and 80 dB)	Brumm et al. (2009)
Budgerigar (<i>Melopsittacus undulatus</i>)	Captive	Until the bird had produced 60 vocalisations (40 – 90 dB)	Osmanski & Dooling (2009)
Noisy miner (<i>Manorina melanocephala</i>)	Wild	Continuous urban noise (50.83 – 65.80 dB)	Lowry et al. (2012)
Elegant crested tinamou (<i>Eudromia elegans</i>)	Captive	Until the bird had called 12 times (45 and 65 dB in 5 dB(a) increments)	Schuster et al. (2012)
Amphibians			
Cope's grey treefrog (<i>Hyla chrysoscelis</i>)	Captive	Six minutes (40, 50, 60, 70 dB), Lombard absent in this species	Love & Bee (2010)
Túngara frog (<i>Physalaemus pustulosus</i>)	Captive	One minute (54 – 94 dB)	Halfwerk et al. (2015)
Mammals			
Crab-eating macaque (<i>Macaca fascicularis</i>), and southern pig-tailed macaque (<i>Macaca nemestrina</i>)	Captive	Until 10 vocalisation had been produced at each of five playback levels in ascending and descending intensity (70, 80, 90, 80, 70 dB)	Sinnott et al. (1975)
Common marmoset (<i>Callithrix jacchus</i>)	Captive	30 minutes per noise treatment played successively in a random order at 40, 50, 60 and 65 dB.	Brumm et al. (2004)
Cotton-top tamarin (<i>Saguinus oedipus</i>)	Captive	Until 11 calls in both 50 and 70 dB noise had been produced	Egnor & Hauser (2006)
North Atlantic right whales (<i>Eubalaena glacialis</i>)	Wild	Continuous exposure to environmental noise (92 – 143 dB re: μ Pa)	Parks et al. (2011)
Mexican free-tailed bat (<i>Tadarida brasiliensis</i>)	Captive	A minimum of 100 echolocation pulses (55, 65, 75, 85 dB)	Tressler & Smotherman (2009)
Killer whale (<i>Orcinus orca</i>)	Wild	Continuous noise exposure from passing ships (approx- 96 – 118 dB re. μ Pa)	Holt et al. (2009)
Greater horseshoe bat (<i>Rhinolophus ferrumequinum</i>)	Captive	30 seconds (80, 90, 100 dB)	Hage et al. (2013)
Pale spear-nosed bat (<i>Phyllostomus discolor</i>)	Captive	28, 40, 52 dB (six minutes)	Luo et al. (2015)
Fish			
Blacktail shiner (<i>Cyprinella venusta</i>)	Captive	17 minutes to 2.5 hours. Playback noise equivalent to ambient noise levels in nesting sites and 10.2 dB louder than the quiet treatment (re. μ Pa)	Holt & Johnston (2014)

139 Methods

140 Animals

141 Recordings were taken from seven adult male canaries (*Serinus canaria*: Linnaeus) kept under
142 license (license number: Az.: 311.5-5682.1/1-2014-021). One female canary was used to encourage
143 the males to sing. All birds were bred and raised in aviaries at the Max Planck Institute for
144 Ornithology (Seewiesen, Germany). Experiments were performed under a 14:10 light:dark cycle,
145 and constant access to *ad libitum* food and water supplemented with fresh vegetables,
146 cuttlebones and grit.

147 Apparatus

148 Prior to experiments, all male birds were kept together in an aviary (1.95 × 1.0 × 1.8 m). The
149 female was kept in a separate cage (120 × 80 × 60 cm). Recordings were made in a separate aviary
150 (1.95 × 1.0 × 1.8 m) lined with acoustic tiles which was visually and audibly separated from the
151 other birds. During recordings, individual males were placed inside the recording aviary inside
152 a wire cage (60 × 40 × 40 cm) within view of the female (in a separate cage 2 m away). An omni-
153 directional microphone (Sennheiser ME62) connected to a PC using an external soundcard
154 (Edirol UA-101) and the recording software Sound Analysis Pro (Tchernichovski et al. 2000;
155 version 1.085) were used for all audio recordings. Recordings were made with a sampling rate of
156 44.1 kHz and 16 bit accuracy. The microphone was placed 60 cm above the centre of the cage,
157 halfway between the two perches, to minimise variation in the recorded sound level caused by
158 lateral movements of the bird's body and head. Recordings were triggered automatically
159 whenever the bird sang using the trigger-record function in Sound Analysis Pro.

160 To induce the Lombard effect, white noise (0.1 – 16 kHz) was played towards the birds
161 during singing bouts. The noise was broadcast through a JBL Pro III loudspeaker placed 140 cm
162 away from the cage and connected to a Pioneer A109 stereo amplifier. The sound pressure level
163 of the noise was 75 dB (re. 20µPa) measured from inside the cage at the position of the perches.

164 A custom Matlab (version 7.5.0; Natick, USA; www.mathworks.com) routine was used to
165 automatically trigger noise playbacks whenever the sound pressure level and duration of a bird's
166 song crossed a pre-defined trigger threshold. The trigger function was controlled using a
167 microphone (Audio-Technica ATR3350) connected to an external soundcard (Edirol UA25) and
168 the Playrec toolkit for Matlab. Canary song is composed of a succession of phrases which are
169 each formed from long repeats of different song elements (Poulsen, 1959; Nottebohm &
170 Nottebohm, 1978). We set white noise playbacks to begin after a random delay of between 1 - 10
171 seconds after being triggered to ensure that the noise began during a different phrase and
172 element type in each recording. Playbacks of white noise were always exactly 20 seconds long.

173 Analysis

174 All acoustic analyses were carried out using the software Avisoft-SASLab Pro (version
175 5.2.09; Specht, 2002). First, different song element types were identified using spectrograms and
176 each song element type was given a number unique to the element type itself and to the bird it
177 came from. The sound pressure level for each element in both noise and quiet conditions was
178 measured with an averaging time of 10 ms.

179 The sound pressure level of the background noise was subtracted from these measurements
180 using the following logarithmic computation procedure given by Brumm & Zollinger (2011) in
181 order to calculate the sound pressure level of the song elements alone (L_{signal}):

$$182 \quad \text{Eqn 1. } L_{\text{signal}} = 10 \log(10(L_{\text{signal} + \text{noise}}/10) - 10(L_{\text{noise}}/10))$$

183 Where $L_{\text{signal} + \text{noise}}$ is the sound pressure level of the song element and the background noise
184 and L_{noise} is the sound pressure level of the background noise alone.

185 The software was calibrated by recording a sine tone of constant amplitude using the
186 same microphone and software settings as used for the recordings of birdsong. The sound

187 pressure level of this tone (68 dB, 1000 Hz) was directly measured using a sound pressure level
188 meter (Voltcraft SL-400) at the position of the microphone.

189 The proportional increase in the sound pressure level (SPL) of song elements in noise
190 was calculated using the equation:

191
$$\text{Eqn 2. SPL increase} = \sqrt{2}^{(\text{dB increase}/6 \times 2)}$$

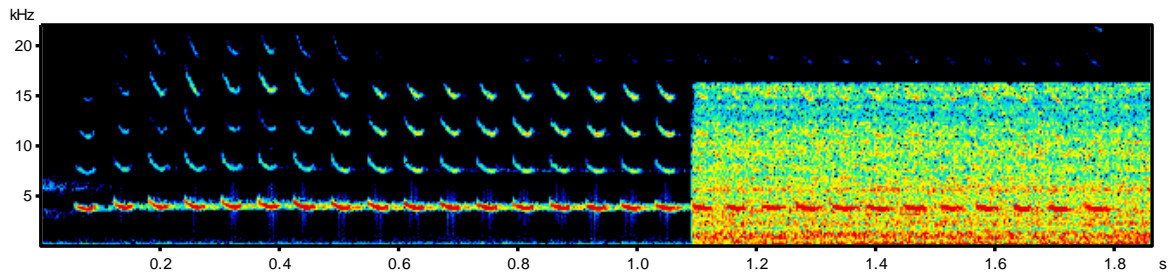
192 Where *SPL increase* is the proportional increase in the sound pressure level and *dB increase* is
193 the measured increase in dB of a song element.

194 For every song element sung during noise playbacks we also recorded how many seconds
195 of the noise playback the bird had been exposed to before the element was sung (maximum 20
196 seconds). With this information we created a subset from our full dataset for song elements
197 sung during the first one second after the onset of noise exposure. These data were used to
198 determine if canaries exhibit the Lombard effect within one second of exposure to noise.

199 In most of our recordings canaries stopped singing immediately after the noise playback
200 began, before quickly resuming song again in the noise. However, in some cases the canaries
201 continued to sing the same phrase uninterrupted during the quiet period and into the noise
202 (Fig. 1). From these recordings we created a separate dataset of sound pressure level
203 measurements to test if canaries can adjust the sound pressure level of their songs mid-song
204 and mid-phrase without pausing.

205

206



207

208 **Figure 1. Spectrogram showing canary song which began during quiet conditions and**
 209 **continued after noise began.**

210

211 Statistical analyses

212 To determine if the Lombard effect occurred within 20 seconds and within one second of the
 213 onset of noise, and to determine whether canaries are able to exhibit the Lombard effect mid-
 214 phrase without first interrupting their song, we analysed our data using generalised linear mixed
 215 models (GLMMs) in R (version 3.0.2; R core team, 2013) using the package lme4. We modelled
 216 the influence of noise exposure (binary fixed factor: present or absent) on the sound pressure
 217 level of the song elements (dependent variable) with normally distributed errors and an identity
 218 link function. The ID of the birds, the song element code and the recording (the audio file the
 219 data were taken from) were all included as random factors. We also included noise as a nested
 220 random factor within recordings to account for audio files containing song elements recorded
 221 both during quiet and during noise exposure. We assessed the effect of noise exposure on the
 222 sound pressure level of canary song by comparing models including noise exposure to null
 223 models using likelihood ratio tests with one degree of freedom. Where multiple analyses were
 224 carried out on the same dataset Bonferroni corrections were used to account for multiple
 225 comparisons.

226 To more precisely determine the speed of the onset of the Lombard effect we further
 227 analysed one exemplary element type from one individual (for which the most data were

228 available) using a broken-line regression model fitted using the segmented package in R
229 (Muggeo, 2008; Muggeo & Adelfio 2010). This allowed us to precisely identify at what time after
230 the onset of noise this element type was sung at a significantly higher sound pressure level than
231 before the noise began.

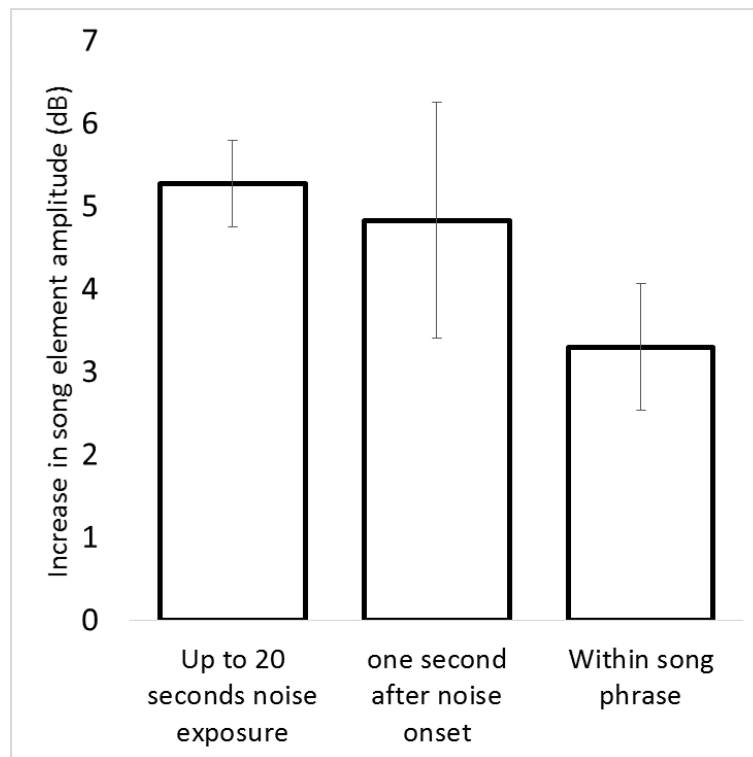
232 Results

233 In total we measured 4140 song elements from seven birds ($n = 1750$ before the onset of noise,
234 2390 during white noise exposure, song element types $n = 31$). The sound pressure level of song
235 elements sung during the full 20 seconds of exposure to white noise was on average 5.27 dB (\pm
236 0.52 s.e.m.) higher than song elements sung before the onset of noise ($\chi^2 = 60.166$, d.f. =
237 1, Bonferroni corrected $P < 0.0001$), while the sound pressure level of song elements sung during
238 the first one second of noise exposure ($n = 636$ before the onset of noise, 38 during white noise
239 exposure, birds $n = 3$, song element types $n = 5$) was on average 4.83 dB (± 1.42 s.e.m.) higher
240 than song elements sung before the onset of noise ($\chi^2 = 9.430$, d.f. = 1, Bonferroni corrected $P =$
241 0.004). These results represent increases in sound pressure level of 84 % and 75 % respectively
242 (Fig. 2).

243 In many of our recordings we found that canaries often briefly stopped singing
244 immediately after the noise playback began. However, in some of our recordings the birds began
245 to sing a song phrase during quiet conditions and continued to sing the same phrase
246 uninterrupted as a noise playback began (Fig. 1; $n = 159$ elements sung before the onset of noise,
247 80 during white noise exposure, birds $n = 4$, mean phrase length 1.5 s). These recordings allowed
248 us to test if canaries are able to exhibit the Lombard effect mid-song and mid-phrase without
249 pausing. In these recordings, the sound pressure level of song elements sung during noise
250 exposure was on average 3.3 dB (± 0.76 s.e.m.) higher than song elements sung before the onset
251 of noise ($\chi^2 = 8,940$, d.f. = 1, $P = 0.002$) representing a 46 % increase in the sound pressure level
252 (Fig. 2).

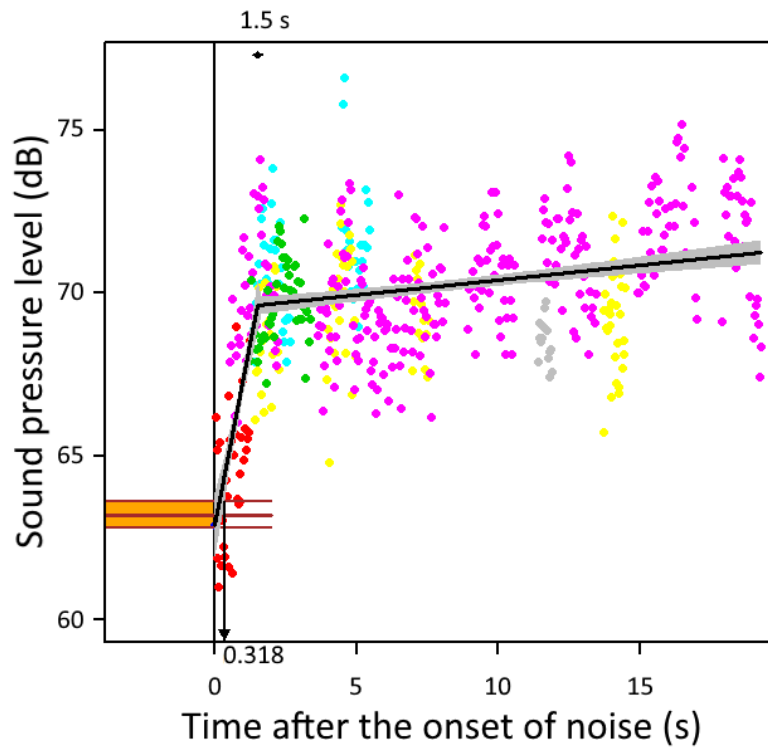
253 For the element type analysed using the broken-line regression model we found that the
254 sound pressure level of song elements sung more than 0.318 seconds after the onset of noise was
255 significantly higher ($P = <0.05$) than song elements sung before the onset of noise (Fig. 3).

256



257

258 **Figure 2. Mean (\pm s.e.m.) increases in the sound pressure level of song elements sung**
259 **during noise compared to the period before the onset of noise.** Graph shows the increase
260 in the sound pressure level of song elements sung up to 20 seconds after the onset of noise
261 exposure ($n = 1750$ before the onset of noise, 2390 during white noise exposure, song element
262 types $n = 31$), during the first one second of noise exposure ($n = 636$ before the onset of noise, 38
263 during white noise exposure, birds $n = 3$, song element types $n = 5$) and within song phrases
264 which began during the quiet period and continued uninterrupted into the noise ($n = 159$
265 elements sung before the onset of noise, 80 during white noise exposure, birds $n = 4$). All bars
266 show a significant increase in the sound pressure level of elements sung after the onset of noise
267 when ($P = <0.05$).



268

269 **Figure 3. Scatterplot showing the sound pressure level of individual song elements**
 270 **before and after the onset of noise.** Shown is one element type taken from a single bird for
 271 which the most data were available ($n = 46$ elements measured before the onset of noise; 207
 272 during white noise). Each point depicts a single vocalisation and different colours show
 273 measurements taken from different recordings. The mean sound pressure level of song elements
 274 sung in the five seconds before the onset of noise is depicted by the brown line with orange
 275 bands showing the 95 % confidence intervals. The black line was fitted using a broken-line
 276 regression model with grey bands showing the 95 % confidence intervals. The onset of the
 277 Lombard effect is defined as the point at which the 95 % confidence intervals for elements sung
 278 before and after noise no longer overlap and occurred here at 0.318 seconds after the onset of
 279 noise. Elements sung after this time point were significantly louder ($P = <0.05$) than elements
 280 sung before the noise began. The initial rapid increase in the sound pressure level of song
 281 elements stopped at 1.5 seconds as shown at the top of the panel. After this point the increase
 282 in the sound pressure level slowed markedly.

283 Discussion

284 This is the first study, to our knowledge, to directly test the onset latency of the Lombard effect
285 in a bird and the first to show that the Lombard effect is exhibited by canaries. Our results show
286 that male canaries exhibit the Lombard approximately 300 ms after the onset of noise, and are
287 able to do this mid-song and mid-phrase without pausing. Thus, we show that canaries possess
288 a remarkably fast vocal plasticity which allows them to adjust their vocalisations in real time to
289 mitigate the masking effects of sudden bursts of noise. Given that the Lombard effect is an
290 ancient trait which is likely shared by all extant bird species (Brumm & Zollinger, 2011) it is
291 probable that all vocalising species exhibit similarly rapid response times. Moreover, while
292 humans exhibit the Lombard effect within 150 ms (Bauer et al. 2006; Kristen R. A. Foery,
293 Triggering the Lombard Effect: Examining Automatic Thresholds, master's thesis, University of
294 Colorado at Boulder, 2008), greater horseshoe bats (*Rhinolophus ferrumequinum*) have been
295 shown to increase the sound pressure level of their echolocation calls almost instantaneously
296 when exposed to noise (Hage et al. 2013), These studies suggest that similarly rapid Lombard
297 responses may be present in taxa other than birds.

298 In recent years numerous studies have identified adjustments to the vocalisations of
299 animals living in noisy environments which help them to mitigate the problem of signal
300 masking (Brumm, 2013). Most of these studies contrast the vocalisations of populations living
301 in noisy and quiet environments and identify differences which may be adaptive. However, it is
302 still not fully understood exactly how these differences arise. Several hypotheses have been
303 proposed, including short term vocal plasticity, long-term ontogenetic vocal adjustments,
304 selective attrition of vocalisations which transmit poorly in noise, passive acquisition of
305 vocalisations which transmit well in noise, and microevolutionary change (Patricelli & Blickley,
306 2006). The Lombard effect is a clear example of short-term vocal plasticity. The very fast
307 reaction times demonstrated in our study suggests, in combination with the evidence for the

308 perceptual efficiency of the Lombard effect for signal detection in noise (Nemeth & Brumm 2010,
309 Luo et al. 2015), that vocal plasticity is the key factor allowing animals to cope with the problem
310 of signal masking in environments with unpredictable and fluctuating noise levels.

311 Studies on the speed of behavioural song plasticity in birds are rare but the available
312 evidence suggest that other song parameters can be modified in response to changes in the
313 environment on different or similar time scales as the one we found for the Lombard effect.
314 House finches (*Carpodacus mexicanus*) have been shown to shift the frequency of their song
315 notes within the time it takes them to sing three songs to avoid masking by high-amplitude
316 noise playbacks (Bermúdez-Cuamatzin et al. 2010), while black-capped chickadees (*Poecile*
317 *atricapillus*) increase the frequency of their song notes on average after more than one minute
318 to avoid spectral overlap with lower frequency masking tones played back to them (Goodwin &
319 Podos, 2013). In contrast, the onset of singing activity in nightingales (*Luscinia megarhynchos*)
320 can be triggered on average within 0.9 seconds to reduce temporal overlap by heterospecific
321 songs (Brumm, 2006). In duetting bird species, the two partners of a pair may react even faster
322 to integrate their duet parts into one coherent song (Hall, 2009; Tempelton et al. 2013). Thus,
323 the regulation of vocal onset in birds operates on a similar time scale as the Lombard effect,
324 suggesting a similar role for the fast adjustment of signalling in fluctuating environments.

325 The rapid onset of the Lombard effect also indicates how quickly the auditory system
326 can be integrated with the different motor systems to enable fast vocal plasticity (Bauer et al.
327 2006). For the Lombard effect to occur, a singing bird first needs to detect an increase in noise
328 and in a second step increase the contraction of abdominal and intercostal muscles to increase
329 bronchial pressure, which eventually leads to an increase in song amplitude (Plummer & Goller,
330 2008). To stay on pitch during Lombard song, birds need to decouple amplitude from frequency
331 during vocal production, which could be achieved by a reduction of labial tension via the

332 syringeal muscles or a reduction of air pressure in the interclavicular air sac via the respiratory
333 muscles (Elemans et al. 2015).

334 Our study also sheds light on the question of what the smallest unit of vocal production
335 in birds is. Cynx (1990) approached this question by interrupting the song of zebra finches
336 (*Taeniopygia guttata*) and observing at what point in their songs the birds stopped singing. He
337 found that zebra finches always stopped singing at discrete locations between song elements
338 and never stopped halfway through a song element. That song elements in zebra finches may
339 represent the smallest motor unit of song production was further supported by the discovery of
340 Yu & Margoliash (1996) of precisely timed temporal correlations between discharge patterns in
341 the vocal motor nucleus RA (Robust nucleus of the archopallium) and individual song elements
342 in singing birds. Franz & Goller (2002) later confirmed this result in the peripheral vocal
343 production system, by showing that each song element sung by zebra finches corresponds to a
344 single expiratory pressure pulse from the lungs. Evidence from measurements of peripheral
345 vocal motor patterns in canaries also support the hypothesis that individual elements represent
346 the smallest units of song production in this species. Even in trills with a repetition rate of up
347 to 30 elements per second, canaries take a rapid minibreath between each element,
348 demonstrating that each element in these trills represents a discrete production unit (Suthers
349 & Zollinger, 2008). However, unlike in zebra finches (Yu and Margoliash, 1996), almost nothing
350 is known about the smallest motor units of song production in the canary brain. In our study
351 canaries often interrupted their song almost immediately in response to the sudden onset of
352 noise. As in zebra finches, we observed that canaries always stopped singing at discrete intervals
353 between elements. Our recordings therefore suggest that song elements are also the smallest
354 units of sound production in this species. Furthermore, as repeats of individual syllables in
355 canary song are controlled by the HVC and the song pattern by the RA (Halle et al. 2003), the
356 ability to stop singing so quickly after the onset of noise suggests extremely rapid modulation
357 of this pathway.

358 In conclusion, our study adds to the growing number of studies which show that animals
359 use the Lombard effect to communicate in to noise. Furthermore, we show for the first time
360 that the Lombard effect can be exhibited extremely rapidly in response to sudden bursts of
361 noise. For animals that live in environments with highly variable and unpredictable background
362 noise this ability is likely to be of particular importance as it would allow them to maintain
363 signal transmission despite sudden changes in noise levels.

364

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377 analysis of sound recordings and to the manuscript; K. K. assisted with statistical analyses and
378 contributed to the design of the experiment and to the manuscript; S. L. Provided experimental
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