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1 **Sensory substitution reveals a manipulation bias**

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3

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10

11 **Abstract:**

12 Sensory substitution is a promising therapeutic approach for replacing a missing or diseased sensory
13 organ by translating inaccessible information into another sensory modality. What aspects of
14 substitution are important such that subjects accept an artificial sense and that it benefits their
15 voluntary action repertoire? To obtain an evolutionary perspective on affective valence implied in
16 sensory substitution, we introduce an animal model of deaf songbirds. As a substitute of auditory
17 feedback, we provide binary visual feedback. Deaf birds respond appetitively to song-contingent visual
18 stimuli, they skillfully adapt their songs to increase the rate of visual stimuli, showing that auditory
19 feedback is not required for making targeted changes to a vocal repertoire. We find that visually
20 instructed song learning is basal-ganglia dependent. Because hearing birds respond aversively to the
21 same visual stimuli, sensory substitution reveals a bias for actions that elicit feedback to meet animals'
22 manipulation drive, which has implications beyond rehabilitation.

23

24 **Main Text:**

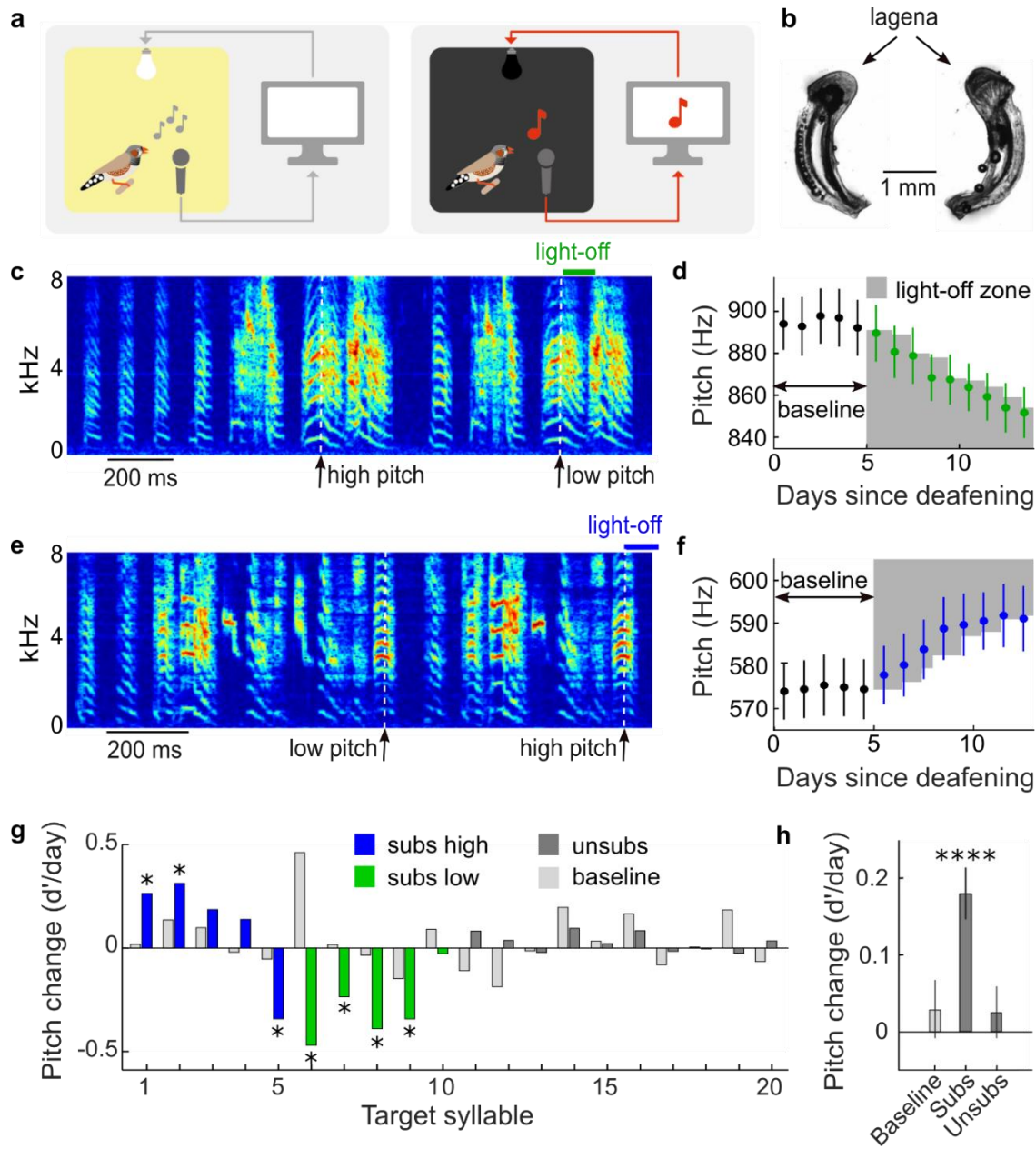
25 Sensory substitution is a transformation of stimuli from one sensory modality into another one¹. Such
26 transformation can be used as a therapeutic approach towards restoring perception from a defective
27 sensory modality². This approach has gained much interest in recent years thanks to both advances in
28 technology and the remarkable cross-modal flexibility of the central nervous system³⁻⁵. However, one of
29 the main obstacles hindering the wide adoption of substitution devices has been the amount of training
30 necessary to make use of the new sensory input; in fact, blind subjects often give up using a substitution
31 device before reaching a reasonable proficiency level because they feel overwhelmed and frustrated⁴.

32 How can this situation be remedied, and which are the general design principles that need to be
33 respected for sensory substitution to be willingly adopted? Currently, the motivational consequences
34 inherent in sensory substitution are poorly understood, partly because we are lacking a theory that
35 would predict how a subject will respond to substituting input. One key question is whether substitution
36 will increase or decrease the affective valence of a given motor action^{6,7}. Ideally, we would like to know
37 beforehand about actions that will suffer from a decrease in valence and therefore will be avoided by
38 subjects. Vice versa, if we could predict the actions that will experience a boost in valence from
39 substitution, we could provide better treatments to support skilled behaviors such as speech in the deaf.

40 This question concerns the motivational system that is best served by substitution. One idea is that
41 sensorially deprived subjects desire highly informative feedback about their actions. For example,
42 substituting input could help subjects to reduce uncertainties inherent in their motor output and allow
43 them to make better action choices. Accordingly, the artificial sensory input should perfectly
44 differentiate among distinct action outcomes. Formally, substitution may elicit the desire to explore⁸⁻¹⁰,
45 which is to seek knowledge about actions' effects. According to this knowledge seeking view, subjects
46 will preferentially choose actions with uncertain outcomes¹¹ or high predicted information gain¹²⁻¹⁴.

47 Another idea is that adaptive responses to substitution may focus on the intrinsic goal of manipulating
48 the environment¹⁵ rather than to obtain knowledge. For example, subjects may be drawn towards
49 actions for the sole reason that the latter trigger a significant sensory input. Substitution could thus
50 reveal a drive for impact¹⁶, which is to preferentially choose actions with noticeable effect.

51 To test whether knowledge-seeking or impact-seeking better explains adaptive responses to sensory
52 substitution, in songbirds we partially replace auditory feedback from a complex vocal behavior by visual
53 feedback. We modified a widely applied operant conditioning paradigm involving the pitch of a song
54 syllable. Instead of using short white-noise bursts played through a loudspeaker^{17,18}, we substitute
55 auditory by visual feedback by briefly switching off the light in the sound-isolation chamber of the
56 singing bird whenever the pitch of a targeted syllable was below (or above) a threshold, Fig. 1. We set
57 the pitch threshold for light-off every morning to the median pitch value on the previous day. We
58 investigated whether adult male zebra finches deafened using bilateral cochlea removal would show any
59 kind of reaction in response to such pitch substitution by light-off (LO). We evaluated bird's responses to
60 substitution in terms of d' values, which are average daily pitch changes normalized by their standard
61 deviations (see Methods). From these values, we inferred the affective valence of substituted feedback:
62 whether it is neutral, aversive, or appetitive.



63

64 **Fig. 1: Light-off stimuli are positive reinforcers of vocal pitch in deaf songbirds.** *a*, Schematic of the
 65 experiment. A singing deaf bird inside a sound isolation chamber (left) experiences light off for a duration
 66 in the range of 100-500 ms (right) when the pitch of one of its song syllables (red note) exceeds a given
 67 threshold. *b*, Example picture of a pair of surgically removed cochleae. Complete deafness was confirmed
 68 by presence of the osseous spiral lamina and by verification of an intact loop including the lagena. *c, e*,
 69 Example song spectrograms in birds b2y2 (c) and b2p19 (e) with substituted feedback for low-pitched (c)

70 *and high-pitched (e) syllable renditions (the time points of pitch measurement are indicated by white*
71 *dashed lines). d, f, Daily mean pitches (dots) and their standard deviations during baseline (black) and*
72 *during substitution (green: low-pitch subs, d; blue: high-pitch subs, f). The light-off pitch zones are*
73 *indicated by gray shading. The birds adapted the pitch in the direction of increasing light-off rate. g,*
74 *Histograms of average daily pitch changes during substitution in birds with high-pitch substitution (subs*
75 *high, blue, n=5 birds, the first bar corresponds to b2p19 shown in e and f), low-pitch substitution (subs*
76 *low, green, n=5 birds, the 8th bar corresponds to b2y2 shown in c and d), and in control birds without*
77 *substitution (unsubs, dark grey, n=7 birds, target syllables 11 and 14 stemmed from the same bird and so*
78 *did syllables 13+18 and 15+19). The light grey bars to the left of the colored bars indicate the average*
79 *daily pitch change for each syllable during the last 5 baseline days. The asterisks indicate subs birds with*
80 *significant pitch changes compared to controls (two sample, two-sided t-test, $p < 0.05$). h, Shown are the*
81 *three fixed-effect terms of a mixed linear effect model and their standard errors (see main text for*
82 *details). The bars indicate the daily change in pitch (d'/day) during baseline (left, $p=0.44$), during*
83 *substitution in the direction of increasing light-off rate (subs, $p=2.0 \times 10^{-7}$), and in control birds (unsubs,*
84 *right, $p=0.46$).*

85

86 **Substituted feedback appetitively reinforces vocal pitch**

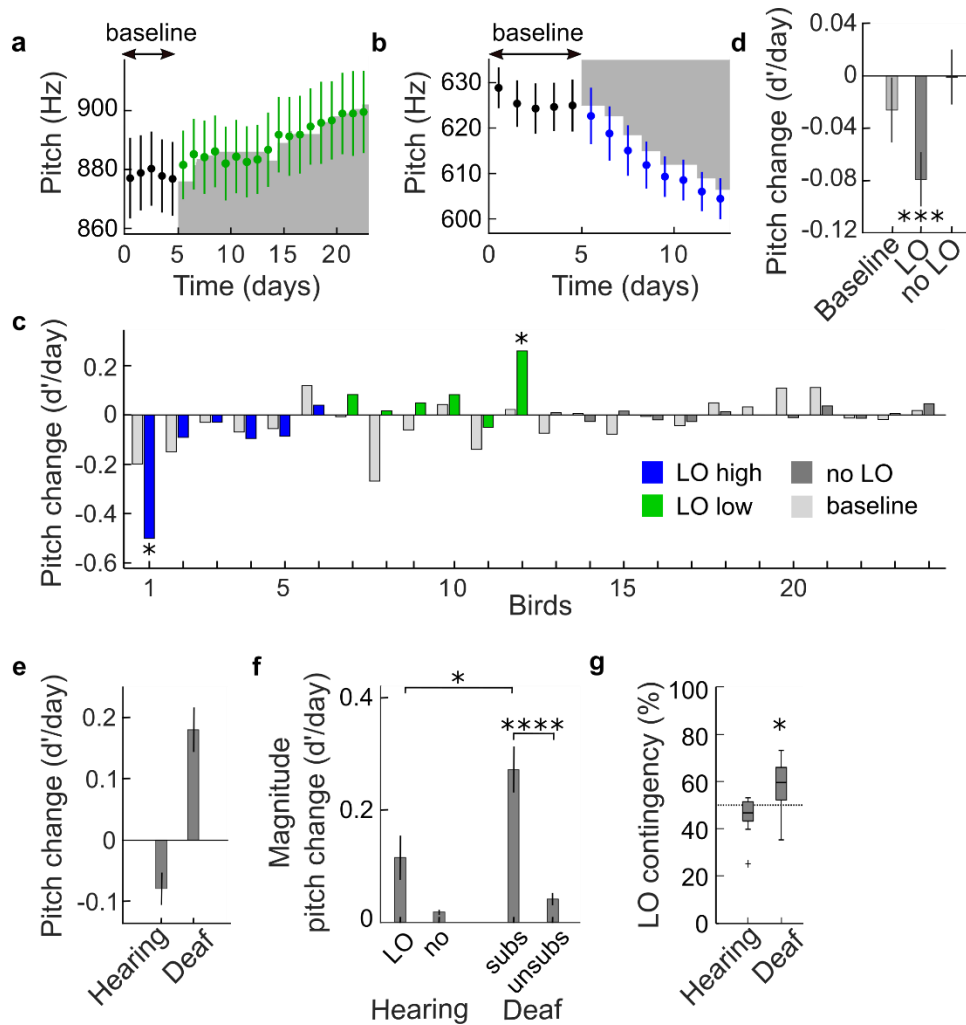
87 Because deafening by itself may induce a slow pitch drift with a nonzero bias^{19,20}, we evaluated pitch
88 responses in comparison to unsubstituted deaf control (unsubs) birds. Pitch changes in 7/10 subs birds
89 significantly deviated from the changes in control animals in matched time periods ($p < 0.05$ in 7 of 10
90 subs birds, two sample, two-tailed t-test of pitch change per day, see Methods, Fig. 1g).

91 Interestingly, subs birds tended to be attracted by light-off, because all birds except one changed their
92 pitch in the direction of increasing LO rate, Fig. 1g. If the direction of pitch drift were random in each

93 bird with probability $\frac{1}{2}$ in each direction (binomial model), then 9 of 10 birds would drift in the same
94 direction in less than 1% of cases, corresponding to a p-value smaller than 0.01, whence the attraction
95 was a non-random effect.

96 To account for individual variability, we fitted mixed linear effect models to the pitch data. The models
97 contained three fixed terms: one term for the early time period before substitution and one term each
98 for the late time periods in subs and unsubs birds. In addition, there was one random term for each
99 syllable (n=17 birds, 20 target syllables, see Methods). We found that relative to baseline (early period),
100 subs birds exhibited pitch changes of 0.18 d'/day in the direction of increasing LO rate (nonzero fixed
101 effect, $p=2.0 \times 10^{-7}$, SE=0.03, tstat=5.33, DF=282, Fig. 1h), whereas unsubs birds did not change pitch
102 (0.02 d'/day, $p=0.46$, SE = 0.03, tstat=0.74, DF=282).

103 Syllables in deaf birds remained stable over the short period of the experiment; changes were specific to
104 pitch but did not affect other sound features ($p>0.05$, two-tailed t-test, duration, frequency modulation,
105 amplitude modulation, and entropy, see Methods), see Supplementary Fig. S1. In combination, these
106 results indicate that in deaf birds, substituted feedback is an appetitive reinforcer of song.



107
 108 **Fig. 2: In hearing birds, the valence of light-off reinforcers is negative.** **a, b,** Hearing birds change pitch
 109 in the direction of decreasing LO rate, here shown for a low-pitch light-off (LO low) bird (bird b2y2, **a**) and
 110 a LO high bird (bird p6s6, **b**). Legend as in Fig. 1d, f. **c,** Histograms of average daily pitch changes in LO
 111 high (blue, $n=6$), LO low (green, $n=6$), and in no LO birds (gray, $n=12$). **d,** The three mixed linear fixed
 112 effect terms and their standard errors. The bars indicate the daily change in pitch (d'/day) during
 113 baseline (left, $p=0.28$), during LO exposure in the direction of increasing LO rate (middle, $p=1.6 \cdot 10^{-4}$), and
 114 in control birds (no LO, right, $p=0.96$). **e,** Average directed pitch changes in LO (hearing) vs subs (deaf)
 115 birds. Hearing birds changed their pitch away from the LO zone (decreasing the number of renditions
 116 with LO) and deaf birds towards the LO zone (increasing the number of renditions with LO). The error

117 *bars indicate the standard errors of the mean. f, The magnitude of average pitch change is larger in subs*
118 *birds than in LO birds (* indicates $p < 0.05$ for average magnitude, two sample two-sided t-test), and*
119 *much larger than in unsubs birds (in time-matched periods, **** indicates $p < 0.001$). The error bars*
120 *indicate standard errors of the mean. g, Distribution of average daily LO contingency for hearing and*
121 *deaf birds. Deaf birds triggered light-off in more than 50% of cases (58%, $p = 0.04$, $t_{stat} = 2.45$, $SD = 0.11$*
122 *$DF = 9$, two-tailed t-test) whereas in hearing birds, the LO contingency did not significantly deviate from*
123 *50% (46%, $p = 0.08$, $t_{stat} = -1.91$, $SD = 0.08$, $DF = 11$, two-tailed t-test).*

124

125 **The same stimulus aversively reinforces vocal pitch in hearing birds**

126 We also evaluated adaptive pitch responses in hearing birds. A small number of hearing birds responded
127 to light-off: Pitch changes in two of 12 birds significantly exceeded the spontaneous pitch drift in hearing
128 controls (no LO, $p < 0.05$, two-tailed t-test on pitch changes per day, see Methods, Fig. 2c). A mixed linear
129 effect model revealed that hearing birds significantly changed pitch in the direction of decreasing LO
130 rate (-0.08 d'/day in the direction of subs, nonzero fixed effect of LO, $p = 1.6 \times 10^{-4}$, $DF = 385$, $SE = 0.02$,
131 $t_{stat} = -3.81$, $N = 24$ syllables from 24 birds including 12 controls), implying that overall, light-off was
132 aversive in hearing birds. In combination, our findings demonstrate that deafening causes an inversion
133 of affective valence of LO reinforcers.

134 Valence inversion was also signaled by the contrasting effects of light-off on singing rates. Subs birds
135 produced 280% or 1164 more song motifs on the last three days of substitution than their deaf controls
136 (non-zero fixed effect of light-off, $p = 5 \times 10^{-4}$, $DF = 58$, $SE = 318$, $t_{stat} = 3.66$, $N = 20$ syllables including 10
137 syllables from controls), suggesting that substitution increases the motivation of deaf birds to sing.
138 Hearing (LO) birds, by contrast, had a tendency to sing 10% or 201 fewer song motifs per day than their

139 hearing controls (fixed effect of light-off, $p=0.72$, $DF=70$, $SE=564$, $tstat=-0.36$, $N=24$ birds including 12
140 control birds).

141 Deaf and hearing birds exhibited different LO contingencies. While in hearing birds on average 46% of
142 syllable renditions triggered light-off ($p=0.08$, $tstat=-1.91$, $df=11$, two-tailed t-test of hypothesis that LO
143 rate is 50%), in deaf birds the average LO rate was 58% ($p=0.04$, $tstat=2.45$, $df=9$, two-tailed t-test of
144 hypothesis that LO rate is 50%, Fig. 2g). Thus, only deaf birds diverged from the 50% expectation set by
145 the previous day.

146 To analyze the sensitivity of birds' vocal response irrespective of whether they were attracted or
147 repelled by light-off, we quantified their magnitude pitch responses as the normalized pitch change per
148 day (d' value) aligned in the direction of global pitch change, implying that the average magnitude
149 change was always a positive number. The daily magnitude pitch change was larger by 135% in deaf
150 birds than in hearing birds (difference 0.16 d' /day, $p=0.01$, $tstat=2.73$, $df=20$, $n=12$ hearing and $n=10$
151 deaf birds, two-tailed t-test), Fig. 2f. Thus, visual feedback is much more salient when it substitutes
152 auditory feedback in deaf animals than as a supplemental feedback in hearing birds.

153 Nevertheless, deaf and hearing birds similarly changed their songs in response to substitution, their
154 pitch changes were confined to a temporal window within roughly 10 ms of the targeted time window
155 for LO delivery, Fig. S2 and S3.

156 **The inversion in valence does not reflect a preference for darkness in deaf birds**

157 A simple explanation of our findings could be that deafness induces an attraction to darkness for
158 whatever reason. This explanation was ruled out after we replaced light-off by light-on stimuli and found
159 strongly appetitive responses to such stimuli in deaf birds (0.71 ± 0.07 d' /day in the direction of
160 increasing light-on rate (0.61 and 0.77 d' /day), 2/2 birds significantly exceeded spontaneous pitch drift

161 in control (unsubs) birds, $p < 0.05$, two-tailed t-test on pitch changes per day, light-on contingency
162 $77\% \pm 8\%$ (75% and 79%), see Methods).

163 **A manipulation bonus seems to be required to explain valence reversal**

164 Our vocal-light substitution paradigm forms a simple but powerful touchstone for theories of intrinsic
165 motivation because 1) the vocal space of deaf birds is essentially binary (light on vs off), 2) the
166 environment has no intrinsic dynamics (light only depends on pitch), 3) there is no evolutionary
167 adaptation to LO stimuli, and 4) birds have no physiological need to sing a particular pitch (unlike their
168 need of food intake). Despite this simple framework, most models of behavioral learning cannot
169 accommodate valence inversion. In reinforcement learning (RL)²¹, stimuli have either appetitive or
170 aversive effects and standard RL models cannot accommodate valence inversion for example via
171 changes in baseline reward due to deafening^{22,23}.

172 Our findings are also incongruent with computational models of directed exploration that involve an
173 exploration bonus for action policies that are either informative¹²⁻¹⁴, diverse^{8,9}, or simple²⁴, Table 1.
174 These theories have been designed to either improve the efficiency of reinforcement learning models or
175 to model human behavior within a restricted class of multi-armed bandit problems^{10,12,13}. In these
176 models, agents choose actions that maximize the information gained about the environment, which is
177 often modeled as an exploration bonus in proportion to the uncertainty of an action's value^{9,10}. Yet, in
178 binary (and pitch-symmetric) worlds, knowledge gain is maximal when agents uniformly sample from
179 their action repertoire, implying that such theories predict convergence of LO contingency to 50%^{12,13,25},
180 which contradicts the divergence we found in subs birds.

Reinforcement learning model characteristic	Additional info	Can it explain valence inversion?
Changes in baseline reward	Caused by deafening	No
Exploration bonus	For informative actions	No

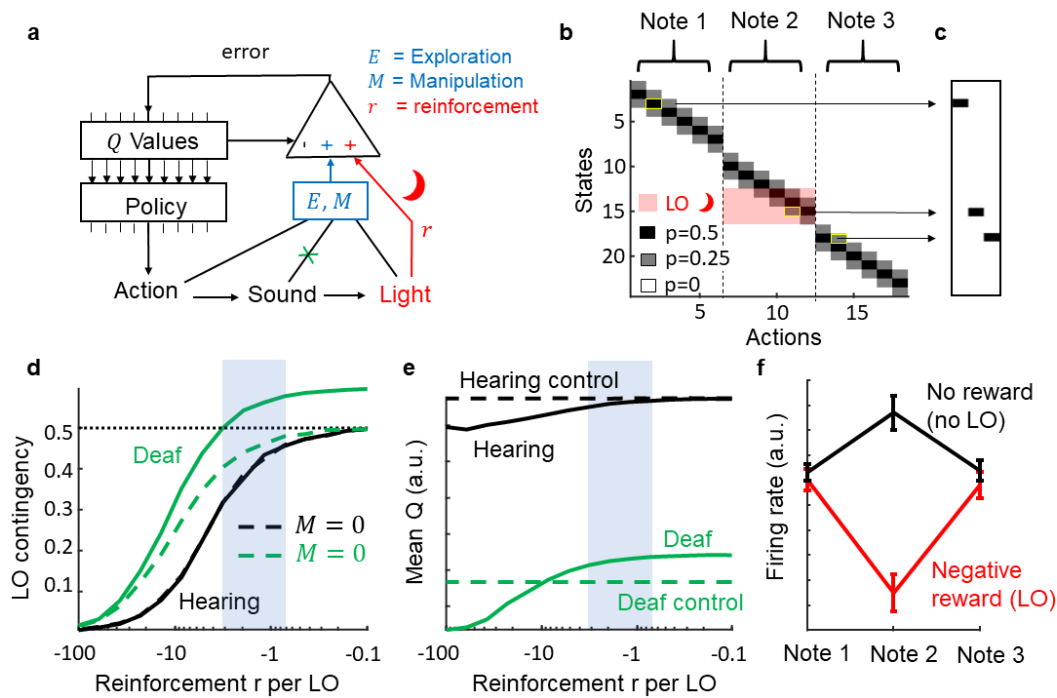
	For diverse actions	No
	For simple actions	No
Manipulation bonus	For impact	Yes

181 **Table. 1: Reinforcement learning characteristics and their compatibility with valence inversion.**

182 In essence, to step above a LO contingency of 50%, a manipulation bias is required towards actions that
 183 impact the environment (such as light off). We introduced such a bias by defining a manipulation bonus
 184 M_j associated with action j . This bonus $M_j = D_{KL}(\hat{\vartheta}_0 || \hat{\vartheta}_j)$ models the impact of action j in terms of the
 185 Kullback-Leibler divergence between the estimated sensory probability density $\hat{\vartheta}_j$ following action j and
 186 the same density $\hat{\vartheta}_0$ without any preceding action. Let us denote the LO probability following action j by
 187 $\hat{\vartheta}_j(off)$ and the LO probability without acting by $\hat{\vartheta}_0(off)$. Because $\hat{\vartheta}_0(off) = 0$, it follows that in deaf
 188 birds, the impact of action j is given by the Shannon surprise of light on: $M_j = -\log \hat{\vartheta}_j(on)$. The impact
 189 is the larger the more likely the action triggers LO (the smaller $\hat{\vartheta}_j(on)$). By experimental design, the
 190 impact is nonzero only for a small set of LO actions. An agent that maximizes impact will therefore
 191 exhibit a (manipulation) bias towards LO. In hearing birds, by contrast, the sensory environment includes
 192 vision and audition. Thanks to auditory feedback, all vocalizations in hearing birds elicit a nonzero
 193 impact. Thus, when hearing birds maximize impact, no particular action is singled out, which leads to
 194 absence of a manipulation bias towards light off.

195 In simulations, we modeled birds' intrinsic reward $R_j = E_j + M_j + r_j$ associated with action j as the sum
 196 of an exploration bonus E_j (given by information gain), a manipulation bonus M_j , and an extrinsic
 197 punishment $r_j \leq 0$ associated with light-off ($r_j < 0$ only in case of light off), Fig. 3a, b. We simulated a
 198 simple agent that maximizes R_j using SARSA^{26,27}, a standard RL framework. In simulations, we found that
 199 when the punishment term r_j per LO was such that deaf birds' LO contingency converged to values
 200 above and hearing birds' to values below 50%, Fig. 3d, the singing preference increased in deaf birds and
 201 it decreased in hearing birds, compared to their simulated controls, Fig. 3e, in excellent agreement with

202 data. A manipulation bonus was required to reproduce these findings, Fig. 3d. Thus, when a behavioral
 203 goal is to detect impact via sensory feedback, such intrinsic reward can account for valence inversion
 204 and for high salience of substituted feedback. Furthermore, by design²⁸, the model output in Fig. 3
 205 agreed with known firing behavior of dopaminergic neurons²⁹, which in hearing birds fire less than
 206 average on escape trials (no negative reinforcement) and more than average on hit trials (negative
 207 reinforcement), Fig. 3f.



208
 209 **Fig. 3: A manipulation bonus is compatible with valence inversion.** *a*, We modeled a simple agent that
 210 maximizes total reward formed by the sum of the extrinsic reinforcement r (red), an exploration bonus
 211 E , and a manipulation bonus M given by impact. The agent's greedy policy is to choose the action with
 212 maximal Q value (expected total reward). Deaf birds receive no auditory input (green cross). *b*, Markov
 213 model of an agent that generates one syllable composed of 3 consecutive notes, each associated with 6
 214 possible actions. An action triggers one of three possible sensory states with probabilities depicted with
 215 gray shading. States 13-16 trigger light-off (red). *c*, Example syllable generated by the model (the

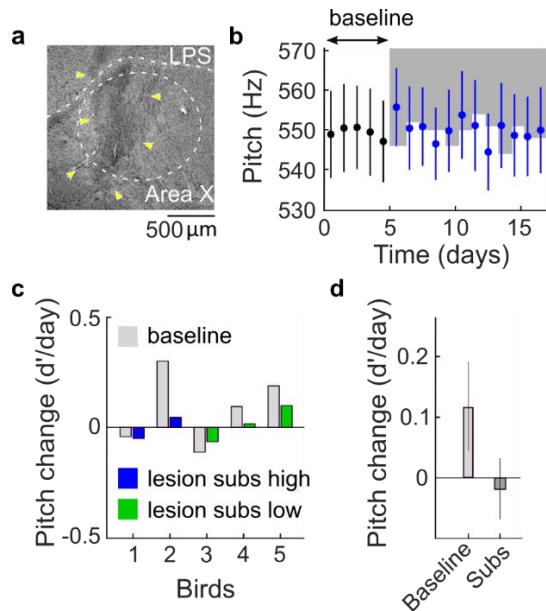
216 *underlying action-state pairs are delimited in yellow in b). d, Hearing birds trigger light-off on less than*
217 *50% of syllables for all choices of negative reinforcement r per LO. Deaf birds go above the 50% LO*
218 *contingency (green). Without manipulation bonus ($M = 0$, dashed line) this is not the case ($\beta = 0$). e,*
219 *Simulated subs birds are more motivated to sing than their controls (unsubs), the mean Q value (green,*
220 *arbitrary units) for subs is above that of unsubs (dashed green). In hearing birds, the situation is*
221 *reversed, they are less motivated than their controls. The blue dashed area indicates the plausible*
222 *reinforcement-per-LO region that qualitatively matches our results. f, simulated firing rate of Area-X*
223 *projecting dopaminergic neurons in hearing birds, modeled as reward prediction errors of a simple Q*
224 *learning rule²⁶. On aversively reinforced trials during Note 2 (modeling a brief LO or an acoustic white*
225 *noise stimulus), the firing rate decreases (red), whereas on escape trials (no reinforcer, no LO), the firing*
226 *rate increases (black). Error bars depict standard deviations (across simulated model birds).*

227

228 **Basal ganglia lesions prevent visual reinforcement of pitch**

229 Our reinforcement learning model suggests an involvement of the basal ganglia in mediating a
230 manipulation bias. Dopaminergic neurons can drive selective pitch changes via their action in Area X³⁰⁻³²,
231 a region homologous to the mammalian basal ganglia^{18,33}. To probe for a manipulation bias in Area X, we
232 made irreversible bilateral lesions in Area X of deaf birds. When these birds were subjected to
233 substituted LO feedback, none of them (N=5) changed pitch in excess to deaf controls ($p > 0.05$ for all
234 birds, two-sampled t-test), Fig. 4a-c. One bird in which the lesion did not overlap with either Area X or
235 LMAN in both hemispheres changed pitch significantly compared to deaf controls ($p = 0.01$, two-sampled
236 t-test). In lesioned subs birds, the magnitude of average pitch change per day was smaller than in
237 unlesioned subs birds (difference -0.22 d'/day, $p = 0.003$, $t_{stat} = -3.62$, $df = 12$, two-tailed two-sample t-
238 test), and the daily pitch change in lesioned subs birds was not significantly different from zero (-0.02

239 d'/day , $p=0.70$, $SE=0.05$, $t_{\text{stat}}=-0.39$, $df=97$, $n=5$ birds, fixed effect), Fig. 4d. In combination, these
240 findings show that Area X is necessary for expressing adaptive pitch responses to substituted feedback.



241
242 **Fig. 4: A basal ganglia pathway is necessary for adaptive responses to substituted feedback. a,**
243 *Example sagittal brain section of a bird with lesion (yellow arrows) in Area X (dashed white ellipse). The*
244 *lamina pallio-subpallialis (LPS) is indicated by the white dashed line. Anterior is towards the left,*
245 *posterior to the right. b, Means (dots) and standard deviations (whiskers) of daily pitch distributions of*
246 *an example deaf bird with bilateral lesions in Area X. There is no clear adaptive response to substitution.*
247 *c, The average pitch changes (d'/day) in deaf birds with Area X lesions during baseline (light grey), during*
248 *high-pitch substitution (blue), and during low-pitch substitution (green). d, The two fixed-effect terms of*
249 *a mixed linear effect model and their standard errors: the daily pitch changes 1) during baseline (left bar,*
250 *$p=0.10$), and 2) during substitution in the direction of increasing LO rate (right bar, $p=0.70$).*

251

252 **Discussion**

253 We found that elimination of auditory feedback induces appetitiveness of an otherwise aversive visual
254 reinforcer of song. This finding helps to refine our understanding of the neural basis of vocal learning.
255 Namely, because targeted changes of vocal skills can occur without hearing, it follows that evaluation of
256 auditory performance is not a prerequisite for vocal plasticity in adulthood, unlike commonly
257 assumed^{29,33}. Our findings do not rule out the use of vocal performance for template-based song
258 learning³⁴, but they showcase that some forms of vocal learning do not rely on auditory representations
259 of song, but rather on motor representations.

260 This means that the song system is able to assign a cross-modal signal such as light the role of an
261 instructive signal that can selectively bias motor variability. To enable flexible assignment of visual
262 signals (light brightness) to specific motor features (pitch), the visual system must feed into the song
263 system in a computationally powerful way. We find that this cross-modal circuit involves the basal
264 ganglia, which provides some clues as to the underlying neural mechanisms. For one, given that cerebral
265 neurons efferent to the basal ganglia do not even respond to auditory feedback during singing³⁵⁻³⁷, it is
266 unlikely that multimodal visual-vocal neurons are involved in this cross-modal learning flexibility. Rather,
267 a large body of work on the basal ganglia suggests existence of an error-like signal that reinforces time-
268 resolved motor representations of song^{29,31,38}. Our work therefore suggests that the avian basal-ganglia
269 part of the song system has evolved to support multimodal learning independent of the sensory
270 modality of reinforcement.

271 We found that substitution uncovers a strong drive to manipulate. This drive better explains our
272 observations than intrinsic motivations such as activity and exploration¹⁵. Normally, in healthy
273 vocalizers, the need to manipulate is satisfied and does not constrain the brain's valence system.
274 However, when sensory feedback is lacking, this need becomes overwhelming to the point that it can
275 override the valence even of aversive stimuli. This remarkable dictatorship of the manipulation drive

276 emphasizes one of the most basic needs associated with motor actions, which is to perceive sensory
277 feedback.

278 By design, the slightly aversive LO events are the only feedback that deaf birds experience, which is why
279 to satisfy their manipulation drive, they prefer it over no response at all ('something' is preferable for a
280 curious agent over 'nothing'). One function of song in birds may thus be to exert an influence on the
281 environment to signal the singer's presence, even if confirmed only by visual feedback as in our
282 experiment. Birds' tendency to avoid overlap in their vocalizations⁴⁰ is evidence for such a need of
283 undisturbed signaling.

284 In humans, there exists a compelling analogy of the remarkable transformation of affective stimulus
285 valence we observed. Namely, a manipulation drive shows up during boredom, which can prompt
286 subjects to display behaviors that evidence paradoxical preference of otherwise aversive stimuli^{41,42}.
287 Lacking an alternative, subjects prefer an unpleasant experience rather than none at all.

288 Regarding substitution as a therapy, perhaps the frustration experienced by users of substitution devices
289 is linked with the level of uncontrollability of the substituting input. Our findings suggest that users of
290 substitution devices might avoid motor actions unless these elicit some form of substituting sensory
291 feedback. Although the intention behind a substitution system usually is to maximize the conveyed
292 information, to merely maximize information can conflict with a manipulation bias that may draw the
293 use of a device away from its intended purpose.

294 We suspect that substitution devices are preferred when they provide feedback about motor actions,
295 making subjects feel empowered through the new sense. By designing substitution systems as part of
296 closed sensorimotor loops⁴, the systems may stimulate motor learning, which can be fun as in tennis
297 practice or piano playing rather than strenuous as in learning a foreign language (analogies between
298 learning to make use of substituted input and reading have been drawn¹). Perhaps, acceptance of

299 substitution devices would also increase when training setups are designed to let subjects predictably
300 manipulate the substituting sensory input, in line with insights from interviews conducted with users of
301 substitution devices⁴³.

302 To focus on manipulation biases in substitution therapies must not necessarily interfere with
303 information gain; rather, such biases may be exploitable on their own when they point towards
304 desirable actions. Binary feedback signals are known to promote robust motor learning⁴⁴. For example,
305 the blind might benefit from a signal that reports the inverse distance of a hand to an object of choice.
306 Or, in the context of speech rehabilitation, the hearing impaired may benefit from short-latency
307 feedback when their variable speech agrees with signals of high comprehensibility; such feedback could
308 be provided as visual signal (e.g. displayed in augmented reality devices) or as vibro-tactile signal⁴⁵.

309 Manipulation biases might also be relevant in neuroprosthetic systems that aim to increase the
310 perceptual space of subjects. In sensory neuroprosthetics, the sensor is not substituted but bypassed by
311 electrical stimulation of downstream neurons. While neuroprosthetic closed-loop systems have only
312 recently started to be explored in the sensory domain⁴⁶, closed-loop systems are very common in the
313 motor domain⁴⁷, where animal models have played a crucial role in the development of a wide range of
314 those systems^{47,48}. Closed-loop motor systems achieve better performance than open-loop systems^{47,48}
315 and there is a distinct performance benefit of high feedback rates⁴⁹. These facts lend support to the idea
316 that sensory neuroprosthetic systems will also benefit from closed-loop design. The zebra finch as an
317 animal model may lend itself to exploring the closed-loop benefits of sensory neuroprosthetics.

318 Key to our findings is that songbirds have a strong manipulation drive. Abstracted as a principle of
319 software agents, such a drive can serve some computational functions. Conceptually, manipulation
320 seeking can be preferable to knowledge seeking because the latter is uninformative about relevance.
321 For example, a manipulation drive can prevent an agent from getting stuck in front of a computer screen

322 displaying random stimuli, which would otherwise be the most absorbing stimulus for a purely
323 knowledge-driven agent that does not distinguish between self-generated and external stimuli. It is
324 therefore not surprising that concepts such as manipulation and impact are gaining in importance in
325 machine learning. In a recent curiosity-driven RL approach, it was found that a focus of actions on self-
326 generated sensory feedback can dramatically expedite learning progress⁵⁰.

327 Further impulses for understanding the motivational drives of spontaneous behaviors are highly needed.
328 We propose that sensory substitution is a promising paradigm not just to experimentally characterize
329 the motivation to manipulate, but also to dissect the neural representations of affective valence⁵¹ and to
330 probe how substituting input is integrated into an existing circuit on the level of single cells, which so far
331 is only understood on the level of brain areas^{1,39}. Because the manipulation drive seems to have access
332 to cross-modal learning mechanisms that are as fast and efficient as those of normal motor learning,
333 sensory substitution and the manipulation drive it reveals may provide a glimpse on some of the
334 enabling factors of evolutionary adaptations.

335

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341 Data and scripts can be accessed at the ETH Research Collection.

342 **Author Contributions**

343 Conceptualization, A.T.Z. and R.H.R.H.; Formal Analysis, A.T.Z. and R.H.R.H.; Investigation, A.T.Z. and
344 S.C.L., Data Curation, A.T.Z. and M.R.; Writing – Original Draft, A.T.Z. and R.H.R.H.; Writing – Review
345 & Editing, A.T.Z., N.G. and R.H.R.H.; Supervision, N.G. and R.H.R.H.

346 **Declaration of Interests**

347 The authors declare no competing interests.

348

349 **Materials and Methods**

350 **Subjects and song recordings:** We used 50 adult male zebra finches (*Taeniopygia guttata*) raised in our
351 breeding facilities in Zürich (Switzerland) and Orsay (France). At the beginning of the experiment, birds
352 were between 90 and 200 days old. During the experiment, birds were housed individually in sound-
353 attenuating recording chambers on a 14/10 h day/night cycle. Access to food and water was provided *ad*
354 *libitum*. After 2-5 days of familiarization in the experimental environment, birds resumed singing at a
355 normal rate. Songs were recorded with a wall-attached microphone, band-pass filtered, and digitized at
356 a sampling rate of 32 kHz. All experimental procedures were approved by the Veterinary Office of the
357 Canton of Zurich and by the French Ministry of Research and the ethical committee Paris-Sud and Centre
358 (CEEA N°59, project 2017-12).

359 **Visual substitution of pitch:** To provide pitch substitution, we ran a custom LabVIEW (National
360 Instruments, Inc.) program. We targeted a harmonic syllable using a two-layer neural network trained
361 on a subset of manually clustered vocalizations. We evaluated pitch (fundamental frequency) in a 16-ms
362 window at a fixed delay after the syllable detection point (which occurred at a roughly constant time lag
363 after syllable onset). We estimated pitch using the Harmonic Product Spectrum algorithm⁵², our code is
364 published at the ETH Research Collection, also in the Matlab (Mathworks Inc.) language.

365 We provided pitch substitution by switching off the light (using a relay) in the sound recording chamber
366 after a delay of 12 ms and for a duration in the range of 100 to 500 ms. Two birds were put in dim light
367 and substitution was provided turning on an additional light instead of switching off the light. We
368 substituted either high or low pitch, depending on a manually set threshold.

369 To cumulatively drive pitch of the targeted syllable away from baseline, every morning, we adjusted the
370 pitch threshold to the median pitch value from the previous day based on all noncurated neural network
371 detections (in 24/328 days from 15/29 birds, we did not set the threshold to the median value because
372 of a software crash on the previous day). In 15 birds (6 hearing and 9 deaf, among which 2 were Area X
373 lesioned birds and 1 missed lesion) we delivered substitution on high-pitched syllable renditions, and in
374 15 birds (6 hearing and 9 deaf, among which 3 were Area-X lesioned birds) on low-pitched syllable
375 renditions. **Subs birds** were deaf birds with LO substitution, **unsubs birds** were deaf and unsubstituted
376 birds; **LO birds** were hearing and subjected to LO, and **no LO birds** were hearing and not subjected to
377 LO.

378 **Surgeries:** Before the onset of surgery, we provided analgesia with the nonsteroidal anti-inflammatory
379 drug carprofen (2-4 mg/kg, Norocarp, unfamed AG, Sursee, Switzerland) given intra muscularly (IM). Birds
380 were deeply anesthetized using isoflurane (1.5-3 %) and placed in a stereotaxic apparatus. We applied
381 the antiseptic povidone-iodine (Betadine, Mundipharma Medical Company, Basel, Switzerland) to the
382 skin at the incision site, followed by the local anaesthetic lidocaine in gel form (5 %, EMLA, AstraZeneca
383 AG, Zug, Switzerland).

384 **Deafening procedure:** In the stereotax, the head angle formed by the flat part of the skull above the
385 beak and the table was set at 90°. The skin was opened above the hyoid bone and the neck muscles
386 were gently pushed back to expose the semi-circular canals. A hole was made in the skull to access the
387 inner ear below the semi-circular canals. The cochlea was visually identified based on the surrounding

388 bone structure and a small hole was made with forceps into the cochlear base. We removed the cochlea
389 from the cavity with a custom-made tungsten hook and took a picture of both intact cochleae including
390 the lagenas to document the success of the procedure, Fig. 1b.

391 **Area X lesions:** We set the head angle formed by the flat part of the skull above the beak and the table
392 to 35° and drilled a window into the skull above Area X. Area X was localized based on stereotaxic
393 coordinates and identified through presence of tonically firing neurons, recorded with a 0.6-1.7 MΩ
394 tungsten electrode attached to a vertical manipulator. We injected in each hemisphere 1 μl of ibotenic
395 acid (Tocris) near the center of Area X. Injection sites were located on average 1.5-1.9 mm medial-lateral
396 (ML), 5.5-6.0 mm anterior-posterior (AP), and 2.8-3.5 mm dorsal-ventral (DV) from the bifurcation of the
397 midsagittal sinus (lambda). Injections were performed using a borosilicate glass pipette (BF-120-69-10,
398 Sutter instrument) pulled with a Picospritzer (Parker Inc.) and broken with forceps to a tip diameter of
399 about 10 μm.

400 **Histology:** At the end of the experiment, birds were euthanized with an overdose of intraperitoneal
401 injection of sodium pentobarbital (200 mg/kg, Esconarkon, Streuli Pharma AG, Uznach, Switzerland) and
402 intracardially perfused with 4% paraformaldehyde (PFA) before brains were removed for histological
403 examination. Brains were rinsed in a 0.01 M phosphate buffer solution. The hemispheres were
404 separated from each other, glued on a metal plate, and embedded in 3% agar. Sagittal slices of 80 μm
405 thickness were cut with a Thermo Microm HM650V microtome and mounted on slides for Nissl staining.

406 **Statistical pitch analysis:** We curated the neural network detections manually by visually removing
407 misdetections (detection of noises or timepoints in the song that did not correspond to the selected
408 target syllable). We quantified the effects of light-off (LO) on pitch using **d-prime values** $d'_{i,j}$:

409
$$d'_{i,j} = \frac{\bar{p}_j - \bar{p}_i}{\sqrt{\frac{1}{2}(\sigma_i^2 + \sigma_j^2)}}$$

410 where \bar{p}_i and \bar{p}_j are the mean pitches on days i and j , and σ_i^2 and σ_j^2 are the variances, respectively.

411 **LO start criterion:** LO started after at least 5 days of stable singing ($|d'_{i-4,i}| < 0.5$ with i being the last
412 day of baseline); in two birds, LO started earlier and in one bird, LO started later because of technical
413 issues and unforeseen scheduling constraints. In deaf (subs) birds, LO started on average 15 days after
414 deafening (range 7 to 33 days) and in hearing (LO) birds it started after at least 7 days in isolation.

415 **LO end criterion:** We ended the LO paradigm when the absolute mean pitch change (relative to
416 baseline) either exceeded at least $2.5d'$ or when it stabilized near zero, which was defined as $|d'_{i-4,i}| <$
417 0.5 with the index i referring to the last day of light off (in one bird, we ended substitution before this
418 criterion was reached because the song degraded too much for reliable syllable detection). The duration
419 of the substitution paradigm did not differ significantly between birds in the hearing and deaf groups (p
420 = 0.39, two-tailed two-sample t-test, mean hearing = 13 days, mean deaf = 11 days). Thus, the observed
421 differences between hearing and deaf birds in Fig. 2e, f were not due to differences in time spent in the
422 experimental chamber.

423 The **average daily pitch change** $\overline{d'_{LO}}$ **during substitution** in each animal (Figs. 1g and 2c) we quantified
424 as $\overline{d'_{LO}} = \langle d'_{i-1,i} \rangle_i$, where the angle brackets denote averaging across all days i with LO (starting from
425 the second day).

426 Similarly, the **average daily pitch change** $\overline{d'_B}$ **during the baseline period** in each animal (light grey bars
427 in Figs. 1g and 2c) we quantified as $\overline{d'_B} = \langle d'_{i-1,i} \rangle_i$, where the average runs across the last 4 days i
428 before LO.

429 **Magnitude pitch change:** We assessed the magnitude pitch change in each bird irrespective of its
430 preference (attraction or repulsion by LO). To discount for preference, we first defined the **global**
431 **direction δ of pitch change** during substitution as $\delta = \text{sign}(d'_{b,i})$, where b is the last day of baseline and

432 l is the last day of LO exposure (δ corresponds to the direction of the colored bars in Figs. 1g and 2c).
433 Thus, if birds shifted pitch upward towards higher values, $\delta = 1$, and if birds shifted pitch down, $\delta =$
434 -1 . In each animal, we computed the **mean aligned pitch change** \bar{a}' during substitution as the average
435 daily change $d'_{i-1,i}$ multiplied with δ : $\bar{a}' = \langle \delta \cdot d'_{i-1,i} \rangle_i$, ($i=6, \dots, \text{end}$). Fig. 2f shows \bar{a}' averaged over all
436 birds. For control birds (unsubs, no LO), the direction of change δ was calculated analogously.

437 **Sound features other than pitch:** To test whether substitution-induced sound feature changes of the
438 target syllable were specific to pitch, we inspected sound features including syllable duration, amplitude
439 modulation (AM), frequency modulation (FM), and entropy. Syllable duration was defined by the
440 interval between consecutive threshold crossings of RMS sound waveform, the threshold for each
441 animal was kept constant for all days analyzed. AM, FM, and entropy were computed as means over the
442 entire syllable. For the analysis, we combined low-pitch and high-pitch substituted birds, all feature
443 values in low-pitch birds were first multiplied by -1 to account for the anti-symmetry between their
444 treatments. As a group, we compared the feature d' values between the last LO day and the last day of
445 baseline (paired two-tailed t test), Supplementary Fig. S1a.

446 **Control birds:** To evaluate whether an individual bird responded to substitution, we compared the daily
447 pitch changes $\{d'_{i-1,i}\}_{i \in LO}$ of its targeted syllable to daily pitch changes of harmonic syllables (containing
448 a harmonic part longer than 100 ms) in many control birds (not exposed to LO). In subs birds, the control
449 group was formed by 12 harmonic syllables in 9 deaf animals, and in LO birds, the control group was
450 formed by 12 harmonic syllables in 12 hearing birds. To account for possible pitch drifts caused by
451 deafening or by time spent in the experimental chamber, the time window for pitch analysis in unsubs
452 birds was matched to the substitution period in the subs bird, i.e., the first day analyzed in control birds
453 occurred at the same time lag after deafening as the first LO day. Also, the number of days analyzed was
454 identical in the subs bird and in control birds (same for LO and no-LO birds). We paired a subs bird only

455 to controls that produced more than 100 song motifs on each day during the matched time periods. Two
456 unsubs birds had to be excluded because they produced fewer than 100 renditions on days 11 and 12
457 after deafening (these birds could not be time-matched to any subs bird, resulting in 10 harmonic
458 syllables from 7 control birds).

459 **Pitch response testing:** To test whether an individual bird significantly changed its pitch in response to
460 LO, we compared all its daily pitch changes during LO to all daily pitch changes in control birds in
461 matched time windows (at significance level $p=0.05$, two-tailed two sample t-test, indicated by asterisks
462 in Figs. 1g, 2c).

463 For the population analysis, we compared daily pitch changes in all subs/LO birds against all unsubs/no-
464 LO controls. We randomly paired 10 syllables in control birds (dark grey bars in Fig. 1g) with the 10
465 syllables in subs birds (under the constraint that analysis days could be temporally matched). The pairing
466 is depicted in Fig. 1g such that target syllable 11 was paired with subs bird 1, target syllable 12 with subs
467 bird 2, etc. We did the same for the 12 syllables in LO birds in Fig. 2c, i.e., target syllable 13 was paired
468 with LO bird 1, target syllable 14 was paired with LO bird 2, etc. All pairings were time-matched, i.e., the
469 early (baseline, light gray bars in Fig. 1g) and late time periods in controls were defined according to the
470 baseline and LO periods in the treated bird.

471

472 **Linear mixed effect model:** To test whether subs/LO birds exhibited a common direction of pitch change
473 (either towards LO or away from it), we modeled daily pitch changes $d'_{i-1,i}^j$ in bird j in response to LO
474 with a linear mixed effect model:

$$475 \quad d'_{i-1,i}^j = b\vartheta_i + a\theta_i + d\varphi_i + r_j,$$

476 where the three fixed effect terms b , a , and d common to all birds were: the daily pitch change b during
477 baseline ($\vartheta_i = 1$ if day i is during baseline and $\vartheta_i = 0$ otherwise), the pitch drift a without LO ($\theta_i = 1$ in

478 control birds if days i and $i - 1$ occurred after baseline and $\theta_i = 0$ otherwise), and the daily pitch
479 change d caused by LO ($\varphi_i = 1$ for LO high and $\varphi_i = -1$ for LO low birds, provided both days $i - 1$ and
480 i were LO days). The r_j are zero-mean Gaussian noise terms that account for variability among birds. We
481 separately fitted linear mixed effect models to deaf and to hearing birds.

482

483 When we reduced the model to two fixed effects (combining the terms b and a into a single term
484 describing spontaneous pitch drift during both baseline in LO-treated birds and all days in control
485 animals) we found the results displayed in Fig. 1h and Fig. 2d to be qualitatively unchanged.

486 **Song degradation:** To assess song degradation caused by deafening (Supplementary figure S1b-e), we
487 inspected non-targeted syllables, comparing renditions at the beginning and the end of the experiment.
488 Tschida and Mooney showed that both entropy and entropy variance significantly change after
489 deafening²⁰. Mean entropy is a measure of syllable noisiness and variance entropy of syllable
490 complexity. To follow suit and inspect mean and variance entropy, we first semi-automatically clustered
491 all (non-targeted) syllables using a nearest neighbor approach in the spectrogram domain. We only
492 considered syllables that were sung more than 100 times on each day (21 syllables in hearing birds and
493 18 syllables in deaf birds). We calculated for each syllable type the magnitude mean-entropy change as
494 the absolute difference in mean entropy between the last day before deafening and the first day after
495 LO ended. For hearing birds, we chose the first day analyzed such that the duration of the analysis
496 window matched the window in deaf birds. As a result, the intervals between the first and last day of
497 the experiment did not significantly differ between birds in the hearing and deaf groups ($p = 0.86$, two-
498 tailed two-sample t-test, mean hearing = 32 days, mean deaf = 31 days). Thus, differences between
499 hearing and deaf birds in Supplementary Fig. S1b-e were not due to differences in time spent in the
500 recording chamber.

501 In agreement with Tschida and Mooney, we found that deaf birds have a larger magnitude variance-
502 entropy change than hearing birds (difference 0.32, $p = 9.3 \times 10^{-4}$, $t_{\text{stat}} = 3.60$, $df = 37$, two-tailed two-
503 sample t-test, Suppl Fig. S1c). However, we found no difference in magnitude mean-entropy change
504 ($p=0.61$, Suppl Fig. S1b). Note that Tschida and Mooney did not perform time-matched comparisons
505 against a group of hearing birds as we did, but they compared entropy to baseline measurements taken
506 before deafening, implying that mean entropy changes in their study could have been caused by birds'
507 gradual adaptation to the recording chamber, irrespective of the deafening procedure.

508 For non-targeted syllables, we calculated the pitch coefficient of variation CV_i on day i as $CV_i = 100 \frac{\sigma_i}{\bar{p}_i}$.
509 As we had done for targeted syllables, we calculated the pitch within a fixed 16 ms window during a
510 harmonic part of the syllable (provided the latter existed, i.e., a harmonic part was found in 9/18
511 syllables in deaf animals and in 9/21 syllables in hearing animals). The difference between the
512 coefficients of variation on the last day of deafening and on the first day after LO is shown in Suppl Fig.
513 S1d. In deaf birds, this difference was larger than in hearing birds.

514 To compute spectral changes due to deafening we performed a bias-variance decomposition. To
515 calculate spectrograms, we first tapered the sound waveform using a Hamming window of 512 samples.
516 The windowed signal was transformed into a linear-power sound spectrogram using the discrete fast
517 Fourier transform computed over segments of 512 samples and nonoverlaps of 128 samples
518 (corresponding to 4 ms). The log-power sound spectrogram was then obtained by taking the natural
519 logarithm of the linear-power sound spectrogram after adding an offset of 0.1 (corresponding roughly to
520 the 75th percentile). We computed the spectrograms of non-targeted syllables within a time window
521 defined by the duration of the shortest syllable rendition. To achieve robustness to low-frequency noise
522 present in the recordings, we ignored the lowest 10 frequency bins corresponding to a frequency cutoff
523 at 625 Hz. The spectrogram bias of a particular syllable was defined as the Euclidean distance between

524 the average spectrograms on two separate days: on the last day before deafening and the first day after
525 the end of the LO period. The spectrogram variance was defined as the average pixel-wise variance on a
526 given day. There was no significant difference between hearing and deaf birds in terms of either
527 spectrogram bias or variance (bias: $p=0.45$, $t_{stat}=0.77$, $df=39$, variance: $p=0.32$, $t_{stat}=-1.01$, $df=39$, two-
528 tailed two-sample t-test, Suppl Fig. S1e and f). Thus, the substitution period was too short to lead to a
529 major spectral song degradation.

530

531 **Localization of pitch changes:** Next we assessed the temporal dynamics of pitch changes in response to
532 light off. We computed pitch traces over the entire syllable in a sliding window of 16 ms and plotted
533 their temporal statistics at a time resolution of 1 ms, supplementary Fig. S2. In each bird, to compare
534 pitch traces from the last day of light off with traces from the last day before light off, we computed d'
535 values between the two distributions at 1-ms time scale relative to the window of LO delivery,
536 Supplementary Fig. S3. For bird 1, the syllable detection point was not stable and over the experiment
537 the pitch window slightly shifted relative to syllable onset (see Supplementary Fig S2a, bird 1). To avoid
538 the visualization of spurious pitch changes due to syllable detection jitter, we corrected for this temporal
539 jitter before plotting pitch difference traces across the LO period in individual birds and their averages,
540 Supplementary Fig. S3 (we aligned all syllables to their onsets and defined the pitch window at the mean
541 time lag of all windows on the day before light off).

542

543

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