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**Learning strategies and the social brain: Missing elements  
in the link between developmental stress, song, and  
cognition?**

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## 1 **Abstract**

2 Bird songs may advertise aspects of cognition because song learning and learning  
3 speed in cognitive tasks are both affected by early-life environments. However, such  
4 relationships remain ambiguous in the literature. Here, I discuss two lines of research  
5 that may help to demystify links between song learning and cognition. First, learning  
6 strategies should be considered when assessing performance to ensure that individual  
7 differences in learning ability are not masked by individual differences in learning  
8 strategies. Second, song characteristics should be associated with social behaviour  
9 because songs have a social purpose and consequently should be strongly related at  
10 functional and neural levels. Finally, if song learning and cognitive abilities are  
11 correlated because they develop concurrently and/or share or compete for the same  
12 resources, I discuss ways glucocorticoids may link early-life stress, song learning and  
13 cognitive ability, focusing particularly on oxidative stress as a potential mechanism.

## 14 **Keywords**

15 Early-life stress; song learning; spatial memory; learning strategies; social behaviour;  
16 cognition

## 17 **Main text**

18  
19 Birdsong is a condition-dependent signal that potentially provides receivers with  
20 different types of information about the singer (Gill & Gahr 2000; Buchanan et al.  
21 2013). For instance, song characteristics such as song complexity and performance  
22 consistency are influenced by physiological factors (e.g. endocrine and immune system  
23 activity; Pfaff et al. 2007; Schmidt et al. 2012), age (Forstmeier & Hasselquist 2005;  
24 Ballentine 2009), social factors (natal region, audience type; Marler & Tamura 1962;  
25 Vignal et al. 2004), and environmental factors (season, temperature; Verhencamp et al.  
26 2013).

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29 Over the past 20 years, there has been a proliferation of research on how adverse  
30 conditions during development influence individual differences in song learning,  
31 production, and perception. This body of work has been greatly motivated by the  
32 conception of the developmental stress hypothesis (formerly called the “nutritional  
33 stress hypothesis” and hereafter referred to as DSH; Buchanan et al. 2003), which  
34 proposes that some songs are more attractive to females because they are more costly  
35 to develop, and the costs of developing these attractive songs are what maintains the  
36 honesty of songs as reliable indicators of singer quality (Nowicki et al. 1998, 2002).  
37 Song learning is costly in the sense that individuals must invest resources into growing  
38 specific song-related brain regions to support memorization of tutor songs, as well as  
39 practice matching their vocal output to memorized tutor songs (Bolhuis & Gahr 2006).  
40 According to the DSH, conditions that impede growth such as poor nutrition and  
41 disease negatively affect songs because i) activation of the stress response causes  
42 resources to be diverted away from song learning and towards processes necessary  
43 for immediate survival (differential allocation), or ii) chronic activation of the stress  
44 response leads to prolonged elevation of glucocorticoid hormones, which produces  
45 adverse effects on growth and maintenance of neural and somatic tissue (harmful  
46 corollary of stress response; MacDougall-Shackleton & Spencer 2012). Song quality is  
47 therefore an advertisement of phenotypic quality – specifically, the degree to which an  
48 individual can cope with early-life adversity. In support of the DSH, juvenile songbirds  
49 raised in unfavourable conditions show reduced song quality (e.g. song repertoire size,  
50 which is the number of song types, and song complexity, which is the number syllables  
51 in a song) and song perception (e.g. song preference) in adulthood (Spencer et al.  
52 2003, 2005; Holveck et al. 2008; Holveck & Riebel 2010; Farrell et al. 2011; Schmidt et  
53 al. 2013a, 2013b; Nowicki et al. 2002). Likewise, the volumes of brain regions  
54 responsible for song learning and production are reduced in adult birds exposed to

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4 55 developmental stress (e.g. Buchanan et al. 2003, 2004; Schmidt et al. 2013a; Nowicki  
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6 56 et al. 2002; but see Gil et al. 2006; Kriengwatana et al. 2014).

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10 58 Song learning is not the only cognitive trait affected by poor developmental conditions.  
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12 59 Spatial memory and associative learning are also affected by developmental stress  
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14 60 (Pravosudov et al. 2005; Fisher et al. 2009; Farrell et al. 2011, 2015; Brust et al. 2014;  
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16 61 Kriengwatana et al. 2015), and song complexity is associated with better performance  
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18 62 (Farrell et al. 2011; Boogert et al. 2008; Anderson et al. 2017). Spencer and  
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20 63 MacDougall-Shackleton (2011) have suggested that song learning may be correlated  
21  
22 64 with other cognitive abilities if they develop at the same time, compete for or share the  
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24 65 same resources, and are sensitive to developmental environments (i.e. not highly  
25  
26 66 canalized). Since song learning occurs over a protracted period of time – starting early  
27  
28 67 in development and continuing throughout adolescence for many songbird species (i.e.  
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30 68 close-ended learners; Nowicki et al. 1998; Nowicki & Searcy 2011) – it likely coincides  
31  
32 69 with the development of other cognitive abilities, which could lead them to appear  
33  
34 70 correlated in adulthood, even if there is no functional relationship (e.g. song learning  
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36 71 and spatial memory; Sherry & Schacter 1987; Spencer & MacDougall-Shackleton  
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38 72 2011). For songbirds that can modify their songs or learn new songs as adults (i.e.  
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40 73 open-ended learners), the correlation between song learning and cognitive ability could  
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42 74 be weaker, but stressful developmental conditions are still expected to have long-  
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44 75 lasting organizational effects in the brain that cannot fully be compensated for later in  
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46 76 life.

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52 78 However, the relationship between song learning and cognitive ability is far from clear.  
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54 79 In this paper, cognitive ability is defined as learning ability (i.e. learning speed or  
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56 80 accuracy), as it is the measure used by the majority of studies on the topic. Song  
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58 81 sparrows (*Melospiza melodia*) with a larger song repertoire size were faster to inhibit  
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4 82 inappropriate responses and find a more useful one (an ability important for problem-  
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6 83 solving) but there was no strong evidence to suggest that song repertoire size was  
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8 84 associated with faster motor learning, colour associative learning, or reversal learning  
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10 85 (Boogert et al. 2011). Other researchers failed to find convincing evidence that song  
11  
12 86 repertoire size of song sparrows was related to any of the measures of cognitive  
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14 87 abilities used in Boogert et al. (2011) or to spatial memory (Anderson et al. 2017). In an  
15  
16 88 earlier study, the rate of motor learning increased as song complexity increased in  
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18 89 zebra finches (*Taeniopygia guttata*) tested on the same motor learning task used by  
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20 90 Boogert et al. (2011) (Boogert et al. 2008), although this result was not replicated when  
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22 91 zebra finches were tested in groups (which is a more naturalistic situation for the  
23  
24 92 socially gregarious zebra finch; Templeton et al. 2014). In swamp sparrows, cognitive  
25  
26 93 ability in five different tasks (motor learning, associative learning, reversal learning,  
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28 94 spatial learning, and impulse inhibition) was not correlated with song repertoire size,  
29  
30 95 vocal performance, or a measure of song learning accuracy (i.e. how representative  
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32 96 the song of an individual is within its population; DuBois et al. 2018). Positive, negative,  
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34 97 and lack of correlations between spatial memory and song repertoire size/complexity in  
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36 98 European starlings (*Sturnus vulgaris*) and song sparrows have also been reported  
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38 99 (Farrell et al. 2011; Sewall et al. 2013; Anderson et al. 2017). Note that Sewall et al.  
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40 100 (2013) and Anderson et al. (2017) both tested the song sparrows using similar  
41  
42 101 experimental designs yet reported different results, which suggests that species  
43  
44 102 differences alone do not explain some of these conflicting results. Still, these  
45  
46 103 inconsistencies do not necessarily invalidate the hypothesis that song functions to  
47  
48 104 advertise cognitive ability, but rather necessitate: 1) a closer look at how learning is  
49  
50 105 determined; 2) attempts to link song characteristics with cognitive abilities that are  
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52 106 expected to be functionally related to song learning and production.  
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108 Learning strategies: an overlooked component to cognitive ability

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4 109 Differences in methods of testing **cognitive ability** may produce conflicting findings,  
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6 110 especially when strategies that can be used to solve the task are not controlled or  
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8 111 measured. For instance, developmental stress affects **song learning accuracy and**  
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10 112 **complexity and the song nucleus HVC** (Nowicki et al. 2002; Spencer et al. 2003;  
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12 113 **Buchanan et al. 2004)** and the structure and function of the hippocampus (a region  
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14 114 **important for spatial learning/memory**; Pravosudov et al. 2005), yet researchers have  
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16 115 failed to find concordant relationships between song **learning** and spatial memory in  
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18 116 song sparrows and European starlings (Farrell et al. 2011; Sewall et al. 2013;  
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20 117 Anderson et al. 2017). These differences could result from different strategies used to  
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22 118 solve the task, as these studies did not use methods that were previously shown to  
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24 119 directly assess **a hippocampus-dependent** spatial learning strategy, so test subjects  
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26 120 could have used strategies that do not rely primarily on hippocampus. **Memory of a**  
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28 121 **sequence of movements and cues about when to change movement trajectory are**  
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30 122 **characteristic of egocentric spatial learning strategies while memory for the location of**  
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32 123 **landmarks relative to each other are characteristic of allocentric spatial learning**  
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34 124 **strategies. The former is highly dependent on the striatum while the latter is highly**  
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36 125 **dependent on the hippocampus** (O'Keefe & Nadel 1978; White & MacDonald 2002;  
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38 126 **Vorhees & Williams 2014)**. Developmentally-stressed zebra finches were impaired in a  
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40 127 spatial memory task that required usage of a hippocampus-based strategy, yet were  
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42 128 quicker than controls to learned a spatial association task where they could use any  
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44 129 strategy (Kriengwatana et al. 2015). This suggests that developmental stress-induced  
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46 130 changes in hippocampus-dependent spatial memory may be masked in spatial  
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48 131 memory tasks where other spatial learning strategies can be employed.  
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55 133 This perspective is supported by findings from human and rodent studies, where stress  
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57 134 **in adulthood** appears to shift individuals away from using hippocampus-dependent  
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59 135 learning strategies (Schwabe 2013; Goldfarb & Phelps 2017). **Additionally**, human  
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4 136 adults that experienced prenatal stress were more likely to use spatial navigation  
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6 137 strategies that required the dorsal striatum over hippocampus-dependent strategies  
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8 138 (Schwabe et al. 2012). In an instrumental learning task where participants learn to  
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10 139 exhibit a particular behaviour through reinforcement and/or punishment, adults that  
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12 140 experienced postnatal stress showed greater reliance on striatum-dependent learning  
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14 141 strategies than hippocampus-dependent strategies (Patterson et al. 2013).  
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16 142 Experiencing very low lifetime stress also reduced adult participants' performance on a  
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18 143 striatum-dependent learning, but not hippocampus-dependent learning, multi-cued  
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20 144 visual search task (Goldfarb et al. 2017). Early-life stress may facilitate striatum-  
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22 145 dependent learning over hippocampus-dependent learning through the effects of  
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24 146 glucocorticoids on the brain, as infusion of corticosterone into the rat dorsal striatum  
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26 147 enhanced striatum-dependent spatial memory (Packard & Knowlton 2002). The  
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28 148 possibility that early-life stress could produce similar effects on spatial learning  
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30 149 strategies in songbirds is currently speculative, but is nevertheless supported by data  
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32 150 from a few relevant studies. Specifically, Area X is a song nucleus located in the  
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34 151 striatum that expresses glucocorticoid receptors (Suzuki et al. 2011) but its volume was  
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36 152 not significantly affected by developmental stress (either by food restriction or  
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38 153 glucocorticoid administration; MacDonald et al. 2006; Schmidt et al. 2013). This  
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40 154 suggests that early-life stress may not adversely affect behaviours that are highly  
41  
42 155 reliant on the striatum. In line with this expectation, the same study found that song  
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44 156 stereotypy – a feature of song that Area X is critically involved in (Scharff & Nottebohm  
45  
46 157 1991; Sohrabji et al. 1990) – was not affected by early-life stress (Schmidt et al. 2013).  
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48 158 Thus, much work is needed to clarify whether early-life stress leaves striatum-  
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50 159 dependent learning intact, or perhaps even enhanced in situations where the stress  
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52 160 response system is activated.  
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4 162 The idea that developmental stress may not necessarily impair **cognitive abilities**  
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6 163 **globally**, but rather encourage (or depress) the development or deployment of  
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8 164 particular learning strategies is part of an on-going debate about whether early-life  
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10 165 stress is aversive or adaptive (Monaghan 2008; Frankenhuis & de Weerth 2013).  
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12 166 According to the latter perspective, harsh developmental conditions may lead an  
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14 167 individual to develop phenotypic characteristics that enable them to survive better in  
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16 168 harsh conditions later on in life; that is, they develop **specialised** phenotypes for coping  
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18 169 with harsh environments (Frankenhuis et al. 2016; Ellis et al. 2017). **It has received**  
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20 170 **some support in birds (Crino & Bruener 2015) but still remains far from conclusive (see**  
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22 171 **Uller et al. 2013). For example, MacDougall-Shackleton (2015) suggests that early-life**  
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24 172 **stress modifications of song are unlikely adaptive phenotypic changes because**  
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26 173 **songbirds are mobile, long-lived, and seasonal breeders so their early-life**  
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28 174 **environments are probably poor predictors of later life environments. Nonetheless it**  
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30 175 **may be useful to outline the results we might expect according to an adaptive**  
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32 176 **perspective.** Under this view, songs may potentially advertise a singer's cognitive  
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34 177 biases and/or **learning ability** in certain environments. Predictions arising from this  
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36 178 hypothesis include: 1) song characteristics are associated with a particular **learning**  
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38 179 strategy that is used consistently across different environmental conditions (i.e. song  
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40 180 **characteristics** signal a particular cognitive bias); 2) song characteristics are positively  
41  
42 181 associated with **learning** in conditions that match developmental environments and  
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44 182 negatively associated with **learning** in conditions that do not match (i.e. song  
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46 183 **characteristics** signal cognitive specialisation for developmental environments).  
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48 184 **Moreover, if songs carry information about cognitive biases or specialization, females**  
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50 185 **could use it during mate choice. This has not yet been directly tested, although it is**  
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52 186 **possible that females are choosing a mate with cognitive specialisations for his**  
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54 187 **developmental environment because zebra finch females preferred songs of males**  
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4 188 with a similar developmental history (i.e. from experimentally enlarged or reduced  
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6 189 broods; Holveck & Riebel (2009)).  
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10 191 To use spatial learning strategies as an example to illustrate the hypotheses, the first  
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12 192 prediction might be that song characteristics affected by early-life stress are correlated  
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14 193 with striatum-dependent learning strategies (e.g. birds with less complex song are  
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16 194 more likely to use striatum-dependent strategies). Specifically, developmentally  
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18 195 stressed birds might show a preference for striatum-dependent over hippocampus-  
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20 196 dependent learning strategies because the former requires less cognitive resources  
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22 197 (such as working memory; White & McDonald 2002), which allows individuals to keep  
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24 198 monitoring their environment for threats and/or opportunities – an conceivable  
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26 199 adaptation for living in harsh environments. This strategy preference would be evident  
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28 200 in both matching and mismatching adult environments (matching environments would  
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30 201 be if corticosterone administration in early-life and adult life, for example). The second  
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32 202 prediction is that spatial learning (but not strategy preference) of developmentally  
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34 203 stressed birds is enhanced in matching adult conditions because acute stress-induced  
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36 204 increases in corticosterone improve striatum-dependent learning. In mismatching adult  
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38 205 conditions, there might be no difference between learning of control and  
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40 206 developmentally stressed birds if they are allowed to choose which strategy to use.  
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42 207 Therefore, impaired learning in the developmentally stressed individuals would be  
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44 208 observed if they were tested in mismatching adult conditions in a task that forced them  
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46 209 to use hippocampus-dependent learning strategies. Falsifying these predictions  
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48 210 requires testing spatial learning in the same individual repeatedly under both matching  
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50 211 and mismatching conditions – something, which to the best of my knowledge, no  
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52 212 studies so far have done. As learning can take place with repeated testing and  
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54 213 influence behaviours on later tests, different extra-maze cues could be used because  
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56 214 birds will have previously learned to orient according to the cues used in the first test.  
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4 215 Additionally, we would expect that birds that use a different strategy in later tests would  
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6 216 take longer to learn than birds using the same strategy in all tests.  
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10 218 In summary, depending on which learning strategy is being tested or how vigorously  
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12 219 experimenters have controlled for the use of different learning strategies in their  
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14 220 design, the effects of developmental stress on learning ability may vary, and  
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16 221 subsequently their relation to song characteristics may also vary from study to study.  
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18 222 Quantifying learning strategies may therefore be the key for clarifying links between  
19  
20 223 song learning and cognitive ability, as speed of learning – the most frequently used  
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22 224 proxy of cognitive performance – does not necessarily measure what is being learned  
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24 225 and is also often confounded by non-cognitive factors such as motivation (despite our  
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26 226 best efforts to control for these factors when possible; see Rowe & Healy 2014). The  
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28 227 development of well-validated tasks is a crucial step towards making sure that  
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30 228 individual differences in learning ability are not obscured by individual differences in  
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32 229 learning strategy (or that these two factors can be teased apart). Furthermore,  
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34 230 investigations into learning strategies may reveal whether song learning signals  
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36 231 cognitive ability in general or in a more limited context. In this paper I outline methods  
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38 232 that could be used to help uncover what strategies birds are exploiting when  
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40 233 performing discrimination learning and spatial learning/memory experiments.  
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46 235 **Discrimination learning.** A commonly used test of cognition in songbirds involves  
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48 236 discriminating between stimuli that differ in shape or colour and learning to associate  
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50 237 the feature with (food) reward (e.g. Isden et al. 2013; van Horik et al. 2017; Boogert et  
51  
52 238 al. 2011). Learning speed is taken as a measure of cognitive ability yet further  
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54 239 examination of what is learned is not usually conducted. For example, if a bird learned  
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56 240 to peck green squares and not red squares for food, did it learn by associating the  
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58 241 features of the stimulus with reward or by abstracting and applying rules? Feature-  
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4 242 based associative learning is thought to occur when animals link physical features of a  
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6 243 stimulus with an outcome; hence the ability of animals to generalise information  
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8 244 acquired in this way is stimulus specific (Rescola & Wagner 1987; Pearce 1987, 1994).  
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10 245 On the other hand, rule learning occurs when animals link regularities related to the  
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12 246 stimulus (rather than stimulus-specific features) with an outcome. These rules can be  
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14 247 subsequently applied to other stimuli that do not share physical features with the  
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16 248 stimulus the animal used to learn the rule in the first place.  
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21 250 One way to dissociate these two ways of learning is to see how the bird generalises  
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23 251 what it learned to novel stimuli. If performance was achieved through feature-based  
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25 252 associative learning then animals would generalise and perform well if faced with novel  
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27 253 stimuli that shared superficial physical features with the familiar stimuli. However if rule  
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29 254 learning took place then animals could transfer the rule to novel stimuli that did not  
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31 255 share any physical features with the familiar stimuli. In human studies the Shanks-  
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33 256 Darby task (Shanks & Darby 1998) is a popular method used to tease apart feature-  
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35 257 based learning and rule learning. To achieve high accuracy in this task, participants  
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37 258 must learn to discriminate two patterns (a negative and positive pattern) that together  
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39 259 form an “opposites” rule. In negative patterning, individual elements (A and B) predict  
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41 260 an outcome (X) but the combination of these elements (AB) predicts a different  
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43 261 outcome (not X). Specifically,  $A = X$ ,  $B = X$ ,  $AB = \text{not } X$ . In positive patterning, it is  
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45 262 reversed:  $C = \text{not } X$ ,  $D = \text{not } X$ ,  $CD = X$ . Thus, the opposites rule is that individual  
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47 263 elements predict opposite outcomes from their compounds. To use the Cinderella story  
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49 264 as an example of positive and negative patterning, let the outcome X be Cinderella  
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51 265 attending the ball and A, B, C, and D stand for the fairy godmother, pumpkin,  
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53 266 stepmother, and stepsisters, respectively. In positive patterning, Cinderella cannot go  
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55 267 to the ball (X) when only fairy godmother (A) or only pumpkin (B) are present ( $A = \text{not}$   
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57 268  $X$ ,  $B = \text{not } X$ ), but she can when they are present together ( $AB = X$ ). In negative  
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4 269 patterning, Cinderella can go to the ball if only stepmother (C) is present or stepsisters  
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6 270 (D) are present ( $C = X$ ,  $D = X$ ) but cannot go if both stepmother and stepsisters are  
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8 271 present to try and stop her ( $CD = \text{not } X$ ). It is important to note that positive and  
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10 272 negative patterns themselves can be learned as features or rules; it is how subjects  
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12 273 treat novel stimuli that will reveal what type of learning strategy has been used.

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17 275 To determine whether participants used feature-based or rule learning to predict the  
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19 276 outcome X, Shanks and Darby showed them incomplete patterns and tested their  
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21 277 response to individual and compound stimuli: for example, they are shown  $E = X$ ,  $F =$   
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23 278  $X$ , and  $GH = \text{not } X$  and tested on  $EF$ ,  $G$ , and  $H$ . Thus, participants can only accurately  
24  
25 279 classify test stimuli if they have learned and applied the opposites rule. If participants  
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27 280 have associated stimuli with outcomes based on features they will respond incorrectly  
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29 281 to test stimuli (e.g. predicting  $EF = X$  instead of  $\text{not } X$ ) because they will have formed  
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31 282 associations with stimulus features that contradict the rule (e.g.  $E = X$  and  $F = X$ ).

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36 284 The Shanks-Darby task may be useful for investigating learning strategies in songbird  
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38 285 discrimination learning for several reasons. First, prior work shows that various  
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40 286 animals, including birds, are capable of learning positive and negative patterning (e.g.  
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42 287 honeybees, Desig et al. 2001; pigeons, Broadbent et al. 1999; rats, Harris et al. 2009).  
43  
44 288 Second, specific neural regions have been implicated in these two types of learning  
45  
46 289 (see Ashby et al. 1998; Milton et al. 2016). In humans, rule learning requires working  
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48 290 memory and is more effortful compared to feature-based associative learning (Wills et  
49  
50 291 al. 2011). As a result, brain-imaging studies often find that the prefrontal cortex is  
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52 292 recruited to a greater degree in rule learning (e.g. Ashby & Maddox 2011; Milton et al.  
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54 293 2016; Cao et al. 2016; Strange et al. 2001). In songbirds, the HVC – a neural region  
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56 294 crucial for song learning and production – is situated in the nidopallium caudolaterale  
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58 295 (NCL), which is the avian “prefrontal cortex” (Güntürkün 2005). Given that early-life

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4 296 stress negatively impacts the mammalian prefrontal cortex (Arnsten 2009), early-life  
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6 297 stress in songbirds may conceivably reduce overall NCL volume, with HVC being one  
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8 298 of the regions in NCL showing this reduction (e.g. Buchanan et al. 2004). If this is the  
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10 299 case then there is a neural basis for hypothesising that poorer song learners would  
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12 300 also be poorer rule learners. Additionally, rule-based generalisation in the Shanks-  
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14 301 Darby task is correlated with intelligence in humans (Maes et al. 2017). If the same  
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16 302 relationship exists in songbirds then the Shanks-Darby task could reveal potential links  
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18 303 between general intelligence and strategy use in songbirds (for discussions of a  
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20 304 general intelligence factor in birds see Boogert et al. 2011 and Farrell et al. 2015).  
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22 305 Third, the Shanks-Darby task is versatile and can be easily modified to test reversal  
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24 306 learning and discrimination learning with other sensory modalities (e.g. auditory  
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26 307 discrimination learning).  
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30 309 Existing work on rule learning in songbirds frequently uses artificial grammar learning  
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32 310 experiments, which similar to the Shanks-Darby task, involves learning to discriminate  
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34 311 patterns (such as XXY and YXX) and generalising this behaviour to novel stimuli (e.g.  
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36 312 AAB and ABA; Spierings & ten Cate 2016; Chen et al. 2015). These studies, however,  
37  
38 313 indicate that there is currently insufficient evidence of definite rule learning in songbirds  
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40 314 tested so far (see ten Cate 2018), which is problematic for application of the Shanks-  
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42 315 Darby task. To the best of my knowledge, no studies have tested songbirds in the  
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44 316 Shanks-Darby task, although Maes et al. (2015) tested pigeons in the task and found  
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46 317 that none of their subjects used rules. Task difficulty could be a cause of this result  
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48 318 because increasing task difficulty increases the tendency to use feature-based  
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50 319 judgments (Wills et al. 2011), and rule acquisition in the Shanks-Darby task is difficult  
51  
52 320 even for humans – in some experiments only about half of the participants use rules  
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54 321 (e.g. Maes et al. 2017). Thus it remains possible that some pigeons used rules but that  
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56 322 an easier version of the Shanks-Darby task was needed reveal individual differences in  
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4 323 strategy use. For researchers interested in linking song characteristics and learning  
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6 324 strategies, it might be sufficient to train birds with either the positive or negative  
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8 325 patterning (instead of both) before testing their generalisation of the “opposites” rule  
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10 326 with novel stimuli (e.g. train A = X, B = X, AB = not X, C = X, D = X, EF = not X and test  
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12 327 CD, E, F).

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17 329 **Spatial learning & memory.** As early-life stress impacts both spatial learning/memory  
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19 330 and hippocampus, it makes sense to investigate whether hippocampus-dependent  
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21 331 spatial learning (and not other forms of spatial learning) is specifically affected. The  
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23 332 Morris water maze, one of the most widely used methods for testing spatial learning  
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25 333 and memory, is ideal for this investigation. In the original version designed for rodents  
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27 334 (Morris 1981), rats are placed in a circular pool of cloudy water and swim in the pool  
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29 335 until they find a platform that they can climb onto to escape out of the water. The  
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31 336 platform could be visible or invisible (i.e. submerged under water) and could be in a  
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33 337 stable location across trials or change locations on each trial. If the platform was  
34  
35 338 visible, rats could find it by using it as a landmark (*cue strategy*), regardless of whether  
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37 339 its location in the pool remained stable or not. However, if the platform was submerged  
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39 340 and remained in a stable location, rats had to rely on a *place strategy*, which involves  
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41 341 learning about the location of the platform in relation to objects in the experimental  
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43 342 room (objects in the room such as the door, window, cabinet were visible from the  
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45 343 maze). Compared to cue strategies, place strategies rely much more heavily on the  
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47 344 hippocampus (e.g. Morris et al. 1982). On each trial, rats started their search at  
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49 345 different points in the maze so that they could not swim to the platform by simply  
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51 346 remembering a sequence of movements. To test spatial learning and strategy, the  
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53 347 platform is subsequently removed and the amount of time subjects spend searching in  
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55 348 different areas of the maze is recorded. If subjects have learned the location of the  
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57 349 platform they should spend more time swimming in the area where the platform once  
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4 350 was. Specifically, removal of the platform should disrupt subjects' search if they used a  
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6 351 cue strategy but not if they used a place strategy (as objects in the experimental room  
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8 352 do not change). Thus, the Morris water maze can measure whether subjects have  
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10 353 learned the location of the platform (i.e. where they spend time searching during test  
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12 354 trials) as well as whether they are using a hippocampus-based place strategy or a cue  
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14 355 strategy (depending on platform visibility and position consistency).  
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19 357 Watanabe & Bischof (2001, 2004) adapted the maze for use with zebra finches, calling  
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21 358 it the "dry version" of the Morris water maze (see Mayer et al. 2013 for a detailed  
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23 359 description and illustration of the maze). Instead of escaping onto a platform in a pool  
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25 360 of water, the dry version uses a large rectangular free-flight aviary where birds can  
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27 361 navigate by flying or hopping to search for food in four identical feeders (only one of  
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29 362 which is baited). These feeders remain in fixed positions throughout the experiment.  
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31 363 Similar to the original Morris water maze, objects in the experimental room (e.g.  
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33 364 posters) are visible and serve as extra-maze cues, and subjects are released into the  
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35 365 maze from one of four positions on each trial. Successful learning is evidenced by a  
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37 366 reduction in the number of visits to incorrect feeders and latency to search in the baited  
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39 367 feeder over learning trials. During test trials, individuals that have used a hippocampus-  
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41 368 based place strategy should exhibit an increase in search errors if prevented from  
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43 369 seeing extra-maze cues. Memory of spatial locations can also be tested by introducing  
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45 370 a retention interval and measuring changes in search accuracy and/or latency.  
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50 372 Several studies have shown that hippocampus is recruited while navigating this maze.  
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52 373 Hippocampus lesions significantly disrupted zebra finches' ability to learn and  
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54 374 remember the location of the baited feeder, and neural activation was found in the  
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56 375 hippocampus of zebra finches that successfully learned the location of the baited cup  
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58 376 (Bischof et al. 2006; Watanabe & Bischof 2004; Mayer et al. 2010). Additionally, when  
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4 377 zebra finches could use a spatial place-strategy or a non-spatial pattern strategy (i.e.  
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6 378 the baited feeder had unique pattern that was from the other three feeders), individuals  
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8 379 that used a spatial strategy showed significant immediate early gene activity in the  
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10 380 hippocampus while those that used a non-spatial strategy did not (Mayer & Bischof  
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12 381 2012). Although the authors did not look at differences in learning speed of birds using  
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14 382 spatial and non-spatial strategies, it is interesting to note that the number of birds that  
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16 383 used spatial and non-spatial strategies was almost equal (8 and 9 birds, respectively).  
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18 384 As early-life stress is expected to impair hippocampus function, early-life stressed birds  
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20 385 may preferentially use a non-spatial strategy but still learn the location of the baited cup  
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22 386 just as fast as control birds using a spatial strategy. Thus, the dry version of the Morris  
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24 387 water maze may be an optimal solution for examining the influence of early-life stress  
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26 388 on hippocampus-dependent spatial learning/memory strategies.  
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#### 390 Songs as potential indicators of social cognition and motivation

391 Song learning and production is essentially a social process, as songs are learned  
392 from conspecifics and intended for communication with conspecifics. A number of  
393 studies have shown that altering social cues affects neural regions regulating song and  
394 song production behaviours, and that manipulating song-related neural regions also  
395 affects social behaviours. For instance, providing male white-crowned sparrows  
396 (*Zonotrichia leucophrys gambelii*) with access to females, but not other males,  
397 increases the size of song-related brain regions (Tramontin et al. 1999). Lesions to a  
398 neural region of the social behaviour network (a network of neural regions controlling  
399 social behaviour) in European starlings diminished song output and song bout length (a  
400 proxy for song complexity in this species) and decreased markers of neural activity in  
401 the song control nuclei (Alger et al. 2009). Lesions to song control nuclei in female  
402 brown-headed cowbirds (*Molothrus ater*) altered their behaviours towards males,  
403 leading to changes in the larger social network (Maguire et al. 2013). Moreover,

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4 404 administration of nonapeptide hormones, which play important roles in vertebrate  
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6 405 social behaviour, affect songbird vocal behaviour (Maney et al. 1997; Goodson 1998;  
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8 406 Goodson et al. 2004). In zebra finches, singing directed at females also increased  
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10 407 nonapeptide mRNA in regions of the social behaviour network [which includes the](#)  
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12 408 paraventricular nucleus of the hypothalamus (PVN) and the bed nucleus of the stria  
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14 409 terminalis (BSTm); Lowrey & Tomaszycki 2014). Nonapeptides could exert their effect  
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16 410 on song indirectly by modifying social attention, or may act directly on the song control  
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18 411 system, as nonapeptide binding sites have been reported in song-related areas in the  
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20 412 white-throated sparrow and zebra finch brain (Leung et al. 2009).  
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25 414 These findings combined with the observation that singing is a social act that fulfills  
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27 415 important social functions indicates that song learning, production and perception and  
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29 416 social [learning \(i.e. the motivation and ability to learn from others\) are strongly related](#)  
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31 417 [at functional and neural levels](#). This in turn implies that early-life factors that affect song  
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33 418 learning [noticeably impact social behaviours](#). In fact, the influence of developmental  
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35 419 stress on social cognition and behaviour may underlie, or at least partially explain,  
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37 420 many of the effects of developmental stress on song [learning](#). That is, early-life stress-  
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39 421 induced reductions in song imitation accuracy, complexity and repertoire size may be  
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41 422 caused to a certain extent by decreased attention and motivation for song acquisition,  
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43 423 and/or reduced ability to learn from others. These changes in social behaviours may be  
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45 424 limited to stressful periods experienced during development (including song acquisition  
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47 425 periods) or persist throughout life due to developmental programming of [the social](#)  
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49 426 [behaviour network in the](#) brain.  
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54 428 In songbirds, studies examining the effects of early-life stress on [the social behaviour](#)  
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56 429 [network](#) are only slowly beginning to accumulate, although a wealth of research  
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58 430 demonstrates that early-life stress has profound effects on social behaviour in rodents  
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4 431 (Sandi & Haller 2015; van der Kooij & Sandi 2012). The few existing studies in  
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6 432 songbirds provide preliminary support for the possibility that song advertises aspects of  
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8 433 social cognition, and that developmental stress alters both variables. In zebra finches,  
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10 434 developmentally-stressed juveniles had weaker associations to their parents in a social  
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12 435 network (Boogert et al. 2014) and stronger associations with unrelated adults (which  
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14 436 they were more inclined to learn from; Farine et al. 2015). Almost all studies on  
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16 437 developmental stress and song using zebra finches have housed families separately,  
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18 438 preventing developmentally-stressed juveniles from potentially learning songs from  
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20 439 unrelated males. Consequently, reports of reduced song complexity and imitation  
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22 440 accuracy in zebra finches (Spencer et al. 2003; Holveck et al. 2008; Zann & Cash  
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24 441 2008; Brumm et al. 2009) may arise, not necessarily from reduced ability to learn  
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26 442 songs, but rather reduced motivation to learn their father's songs. Recent findings by  
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28 443 Boogert et al. (2018) support this idea. They raised birds in free-flying aviaries and  
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30 444 found that that half of the early-life stressed juvenile males in their experiment (i.e. 6  
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32 445 out of 12 birds) sang songs that were more similar to brothers or unrelated individuals  
33  
34 446 than fathers (note that only 2 out of 8 control males demonstrated this behaviour). For  
35  
36 447 both control and stressed birds, father-son song similarity was positively correlated with  
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38 448 the feeding together, suggesting that accurate father's song imitation is related to the  
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40 449 motivation to be social with their fathers (and hence to learn from them). The stress-  
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42 450 induced switch in social learning strategy (i.e. who to learn from) also suggests that  
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44 451 developmental stress may affect social behaviours in a context-dependent manner –  
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46 452 that is, depending on who they are with – rather than affecting social behaviours  
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48 453 globally. These observations are also supported in cases of song: Woodgate et al.  
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50 454 (2010) found that developmentally-stressed female zebra finches were less likely to  
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52 455 engage with males but not other females. In addition, injections of a nonapeptide  
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54 456 antagonist (i.e. arginine vasotocin, the avian homolog of mammalian arginine  
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56 457 vasopressin) in early-life reduced song production rate and imitation accuracy in zebra  
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4 458 finches compared to controls (Baran et al. 2016; 2017). Song similarity was also found  
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6 459 to correlate with the preference to be near other conspecifics (i.e. social motivation;  
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8 460 Baran et al. 2017), although concurrent changes in the song control system and social  
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10 461 behaviour network were not investigated.  
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15 463 In sum, attempts to understand whether song characteristics can signal cognitive  
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17 464 abilities have so far focused on linking song with cognitive abilities that are weakly  
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19 465 functionally related (e.g. spatial memory, controlling impulsive behaviour, and colour  
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21 466 discrimination learning), in the sense that these other cognitive abilities likely have little  
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23 467 involvement in song learning and production (e.g. having good spatial memory does  
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25 468 not help a bird learn better songs). However, it may be useful to first firmly establish  
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27 469 whether song learning is even predictive of a type of learning that it should be  
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29 470 functionally related to, i.e. social learning. This is because their functional relationship  
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31 471 means that they engage or are connected to some of the same neural structures, and  
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33 472 we have a good understanding of the neural structures involved in song learning and  
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35 473 social behaviour. Glucocorticoids may explain how early-life stress produces links  
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37 474 between song learning and social behaviour because (i) the brain regions for these two  
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39 475 types of behaviours express glucocorticoid receptors and (ii) glucocorticoids can  
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41 476 modulate the effects of nonapeptides in the brain and vice versa (Engelmann et al.  
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43 477 1999; Patchev et al. 1993; Watters et al. 1996; Neumann 2007). By understanding the  
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45 478 mechanisms by which song learning is related to social behaviour, we may be able to  
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47 479 extrapolate these principles to link song learning with other more distant cognitive  
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49 480 processes.  
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## 53 54 482 Conclusions

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56 483 Delineating relationships between song characteristics and cognitive ability in  
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58 484 songbirds takes a unique direction in understanding why birdsongs are sexually  
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4 485 selected traits (i.e. are songs an honest indicator of an individual's ability to withstand  
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6 486 early-life stress?). In this paper I have discussed two subjects that will help to advance  
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8 487 research on this topic. The first is the need to assess learning strategies in addition to  
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10 488 learning ability. I have described a pattern discrimination learning task (Shanks-Darby  
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12 489 task) and spatial learning/memory task (dry version of the Morris water maze) that are  
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14 490 routinely used in humans and rodent studies and allow quantification of learning  
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16 491 strategies. These tasks recruit brain regions that are sensitive to early-life conditions  
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18 492 and are differentially involved in song learning. Rule-learning strategies in the pattern  
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20 493 discrimination task is expected to recruit the NCM (the avian "prefrontal cortex") which  
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22 494 contains the song nucleus HVC. Place strategies in the spatial learning task recruit the  
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24 495 hippocampus, which is negatively affected by early-life stress but not involved in song  
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26 496 learning. Thus, song characteristics may be positively correlated with rule strategy use  
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28 497 and place strategy use, even though only one of these strategies relies on brain  
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30 498 regions involved in song learning. This is related to the second issue, which is the need  
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32 499 for experiments that link song learning with social behaviours, which will subsequently  
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34 500 allow the study the mechanism by which early-life conditions produce correlations  
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36 501 between song learning and cognitive abilities. Because song learning and production  
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38 502 are social behaviours, song most likely correlates with other forms of social behaviours  
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40 503 as well (particularly social learning). Early-life conditions may influence song learning  
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42 504 and social learning through the direct actions of glucocorticoids or indirect actions of  
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44 505 glucocorticoids via nonapeptides on song control nuclei and social behaviour network  
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46 506 in the brain.

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508 If song learning and other cognitive abilities are correlated because they overlap in  
509 developmental timescales and share or compete for resources (Spencer &  
510 MacDougall-Shackleton 2011), glucocorticoids are a prime candidate for  
511 mechanistically linking song learning and cognitive abilities. A popular explanation has

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4 512 focused on the role of glucocorticoids in energy allocation. The idea is that  
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6 513 glucocorticoids divert resources away from the brain during stressful periods of  
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8 514 development, thereby restricting neural growth and resulting in smaller neural volumes  
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10 515 and compromised song learning and cognitive abilities (e.g. in the song control system,  
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12 516 Buchanan et al. 2003; in the hippocampus, Pravosudov et al. 2005). Another  
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14 517 potentially co-occurring mechanism that has received less attention is neural damage  
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16 518 caused by glucocorticoid-induced increase in oxidative stress (Costantini et al. 2011;  
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18 519 Hausmann & Marchetto 2010). Oxidative stress occurs when reactive oxygen species  
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20 520 (ROS) generated primarily during energy production in the mitochondria are not  
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22 521 completely neutralized by the antioxidant system (Monaghan et al. 2009). As ROS  
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24 522 damage cellular proteins, lipids, and DNA, oxidative stress has been linked to various  
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26 523 health disorders, degenerative diseases and survival in wild animal populations (e.g.  
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28 524 Costantini 2008; Herborn et al. 2016). The developing brain is particularly susceptible  
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30 525 oxidative stress because of its high energy requirements and immature antioxidant  
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32 526 system, among others (Ikonomidou & Kaindl 2011). von Schantz et al. (1999) have  
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34 527 proposed that sexual ornaments act as conspicuous signals of oxidative stress, and  
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36 528 there are studies on song activity that support this notion (i.e. amount of singing is  
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38 529 positively associated with dietary antioxidants and negatively associated with oxidative  
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40 530 damage; Casagrande et al. 2014; Costantini et al. 2015; Van Hout et al. 2011).  
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42 531 Similarly, Hill (2014) suggests that sexual ornaments reveal mitochondrial function,  
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44 532 specifically, the balance between ATP and ROS production in the mitochondria, such  
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46 533 that song learning and other cognitive abilities are connected because the integrity and  
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48 534 survival of neural tissue – whether for song learning or for cognitive abilities such as  
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50 535 spatial memory – rely on a common pathway (i.e. cellular respiration). As connections  
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52 536 between oxidative stress/mitochondrial function, song learning and cognitive ability  
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54 537 have yet to be made, future studies are needed to verify this potential mechanism.  
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