

Reviews

Brain space for a learned task: strong intraspecific evidence for neural correlates of singing behavior in songbirds

László Zsolt Garamszegi, Marcel Eens*

Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610, Wilrijk, Belgium

Accepted 18 December 2003

Abstract

There is a controversial issue in neuroscience whether the expansion of neural network space permits the development of more complex behavior. One of the best-known model systems for studying the relationship between brain space and behavior is song production and the associated song control system in songbirds. Although the neuroanatomical background of song production is well established, the direct link between song nuclei volumes and song traits remains puzzling. Analyses within species have provided conflicting results regarding the association between song nuclei volumes and measures of song complexity and song length. Based on a meta-analysis, we present here the results of the first synthetic review, in which we test for overall intraspecific patterns in relation to bird song and the size of associated neural tissues. We found significant positive relationships between the volume of two important song nuclei (HVC and RA) and repertoire size and song length. We assessed the importance of absolute and relative volumes, and found that a control for the covariation with the telencephalon may be important. By estimating the adequate sample size that would be needed to reach sufficient statistical power in particular studies, we conclude that previous studies finding non-significant associations between song and volumes of brain nuclei were of weak power. When we factored out the covariation between song length and repertoire size, we found that these traits may explain independently significant amount of variations in the relative volume of HVC, but not of RA. The link between the volumes of song nuclei and song features has important theoretical implications with regard to the neurobiology and evolution of bird song.

© 2004 Elsevier B.V. All rights reserved.

Theme: Neural basis of behavior

Topic: Neuroethology

Keywords: Bird song; Brain space; HVC; Meta-analysis; RA; Repertoire size; Song system

Contents

1. Introduction	187
2. Methods	188
3. Results and discussion	190
Acknowledgements	192
References	192

1. Introduction

Determining relations between brain structure and function is a principal focus in neurobiology. Bird song is one of

the few systems in which complex behavior has been successfully linked to anatomically defined brain structures [11,33,37,43]. Anatomical and gene-expression studies revealed that considerable amount of neurons and greater synaptic and dendritic development in specialized areas of the brain are required for the auditory and motor government of sound production [18,43]. For example, the descending motor control pathway includes the forebrain vocal areas HVC (nucleus HVC of the nidopallium) and RA

* Corresponding author. Tel.: +32-3-820-22-84; fax: +32-3-820-22-71.

E-mail addresses: laszlo.garamszegi@ua.ac.be (L.Z. Garamszegi), marcel.eens@ua.ac.be (M. Eens).

(nucleus robustus archistriatalis), which are necessary for the production of learned vocalizations [26]. HVC might also be involved in the modulation of singing activity [1,41], and may play an important role in song perception [35]. Electrophysiological work in the zebra finch *Taeniopygia guttata* suggests a hierarchical organization of the song system with HVC activity coding for motor unit sequences, such as syllables, and RA activity coding for subsyllable components [45]. RA probably connects the forebrain song system to further motor systems that are active during singing, such as beak, tongue and larynx control circuits [43].

There is extensive variation in singing behavior both among and within songbird species [13,38], and various researchers have examined whether the expansion of neural network space permits the development of more complex acoustic behavior [6]. However, available studies testing the scenario have provided conflicting results. First, researches examining individual male variation in song in relation to the size of several song nuclei revealed that the size of HVC is positively correlated with repertoire size (e.g., Refs. [3,37]), although the evidence is often contradictory (e.g., Ref. [24]). For instance, in male zebra finches, a significant positive relationship between HVC volume and repertoire size has been described in one study [3] but not in others [32,42]. Second, comparisons between sexes revealed that inter-sexual variation in the size of song related nuclei, such as HVC and RA is associated with inter-sexual variation in singing activity and complexity [31]. However, examples at conflict with this observation have also been reported [21]. Finally, comparative analyses based on phylogenetically independent contrast have showed positive interspecific correlations between HVC volume and repertoire size across species [17,40]. In some species it has been demonstrated that seasonal changes in singing behavior is accompanied by parallel changes in HVC size [41], but in others this pattern was not detected [29].

In general, supporting studies may suggest a functional relationship between song behavior and brain space that is needed for learning and storing large repertoires [6]. However, this conclusion might be immature due to the list of inconsistent results, and evidence for a direct relationship between male brain structure and song behavior thus remains controversial [23]. The mixture of significant positive, non-significant and even negative associations between measures of song complexity and song nuclei volumes has led to intense discussion and narrative reviews [5], but a synthetic revision using statistical approaches would be needed for making clear-cut conclusions about the link between brain space and song repertoires or other measures of song complexity.

The objective of this study was to determine whether variations in the size of two important song nuclei, HVC and RA, were associated with repertoire size and song length within species, which is the key assumption of the hypothesis that brain space is needed for learning songs

[37]. Based on available correlative studies investigating the relationship between the volumes of song nuclei and song features, we applied a meta-analytic approach to determine the overall intraspecific pattern of such associations. Meta-analytical techniques offer quantitative and objective methods to summarize a body of research by examining the magnitude and the generality of a predicted relationship, while taking sample size into account [15,25,39,44]. Therefore, we regard our analysis as a fundamental test that has a potential to reveal a general intraspecific role for the volumes of HVC and RA to be significantly related to repertoire size and song length.

2. Methods

The purpose of our meta-analysis was to provide estimates of true effect sizes based on available studies for the intraspecific relationship between the volume of song nuclei in the brain and song features in birds. To obtain these estimates, different test statistics or significance levels should be transformed into a common currency termed effect size. After necessary transformations, overall effects size may be calculated for the relationship in focus, and the general significance of the studied phenomenon can be tested [15,39]. We collected published results of studies investigating correlatively the intraspecific association between male repertoire size and/or song length and the size of HVC and/or RA. Hence, we did not include studies that investigated seasonal variation in RA and HVC volumes and song by sampling males in different seasons, or compared groups of birds experiencing different tutoring regimes or originating from different populations. We applied a careful and systematic electronic search using PubMed (<http://www.ncbi.nlm.nih.gov/PubMed>) and Web of Science (<http://www.isi1.isiknowledge.com>). We also asked three experts of the topic to check whether our selection covers all relevant studies. We used one unpublished study that was also available, because this may reduce the risk of committing problems arising from publication bias (see below). However, when we excluded this study from our analysis the results and conclusions remained very similar. We included analyses based on Pearson's correlations (two-tailed), or other equivalent statistics testing the null hypothesis that males with higher repertoire size or longer songs have similar size for their HVC or RA than males with smaller repertoire size or shorter songs. For studies that simultaneously reported neural associations for repertoire size and song length together with the covariation between these song traits, we computed partial correlations between brain nuclei and a given song feature, while holding the other constant. Different effect size correlations were entered in a meta-analysis in which we tested for the overall effect in focus being significantly different from zero. We performed this analysis for the entire data and also for different subsets testing for the effect corresponding to the relationship

between specific song features and song nuclei. First, we calculated overall effect sizes for associations that were based on Pearson's correlations that neglect the covariation between song traits. Second, we repeated these analysis with a smaller sample, for which we could calculate partial correlation coefficients, and tested for overall effects when the covariation between song repertoire size and song length was controlled. As some studies distinguished between the absolute and relative volumes of brain nuclei by taking or not the covariation with telencephalon into account, we also estimated effect sizes for absolute and relative volumes of

the HVC and RA. In some cases when correlations were not given by the original source, we calculated correlation coefficients for the relationships of interest based on the raw individual data if available. Based on the estimated overall effect sizes we calculated the adequate sample size that would be needed in particular studies to detect the relationship of interest with the power of 80% [14]. Using tests of heterogeneity, we checked whether the dispersion of the effect sizes from study to study can be attributed to random variation. The list of studies used in the meta-analysis and the calculated effect sizes are given in Table 1.

Table 1

Studies involved in the meta-analysis to investigate the intraspecific relationship between the size of song nuclei and song features in birds based on effect size correlations (r) [14]

Species	Relationship	N	r	Reference [first author (date)]
<i>Acrocephalus schoenobaenus</i>	Rep–relHVC	13	0.649	Airey (2000) [2]
	CMPX–relHVC	13	0.514	Airey (2000) [2]
	Length–relHVC	13	0.507	Airey (2000) [2]
	Rep–Length	13	0.380	Airey (2000) [2]
<i>Agelaius phoeniceus</i>	Rep–HVC	12	0.080	Kim (1989) [27]
	Rep–RA	12	0.120	Kim (1989) [27]
<i>Cistothorus palustris</i>	Rep–RA	7	0.860	Brenowitz (1995) [10]
	Rep–RA	7	0.250	Brenowitz (1995) [10]
	Rep–HVC	8	0.240	Brenowitz (1995) [10]
	Rep–HVC	8	0.630	Brenowitz (1995) [10]
	Rep–HVC	10	0.600	Canady (1984) [12]
	Rep–HVC	7	0.718	Canady (1984) [12]
<i>Molothrus ater</i>	Rep–HVC	14	–0.217	Hamilton (1998) [24]
<i>Parus caeruleus</i>	Rep–HVC	11	0.610	M. Eens unpublished
	Rep–RA	10	0.374	M. Eens unpublished
<i>Pipilo erythrophthalmus</i>	Rep–HVC	9	0.060	Brenowitz (1991) [9]
	Rep–HVC	10	0.130	Brenowitz (1991) [9]
	Rep–RA	9	0.260	Brenowitz (1991) [9]
	Rep–RA	10	–0.230	Brenowitz (1991) [9]
<i>Serinus canaria</i>	Rep–HVC	25	0.449	Nottebohm (1981) [37]
	Rep–RA	25	0.380	Nottebohm (1981) [37]
<i>Sturnus vulgaris</i>	Rep–RA	9	0.460	Bernard (1996) [4]
	Rep–HVC	9	0.200	Bernard (1996) [4]
	Length–HVC	9	0.690	Bernard (1996) [4]
	Length–RA	9	0.700	Bernard (1996) [4]
	Rep–Length	9	0.490	Bernard (1996) [4]
	<i>Taeniopygia guttata</i>	Length–RA	21	0.143
Length–relHVC		21	0.674	Airey (2000) [3]
Length–relRA		21	0.155	Airey (2000) [3]
Rep–HVC		21	0.337	Airey (2000) [3]
Rep–RA		21	0.016	Airey (2000) [3]
Rep–relHVC		21	0.501	Airey (2000) [3]
Rep–relRA		21	0.129	Airey (2000) [3]
Length–HVC		21	0.528	Airey (2000) [3]
Rep–Length		22	0.551	Airey (2000) [3]
Rep–relRA		16	0.360	MacDougall-Shackleton (1998) [32]
Rep–relHVC		16	0.480	MacDougall-Shackleton (1998) [32]
Rep–RA		16	0.210	MacDougall-Shackleton (1998) [32]
Rep–HVC		16	0.420	MacDougall-Shackleton (1998) [32]
Length–relRA		16	0.420	MacDougall-Shackleton (1998) [32]
Length–relHVC		16	0.340	MacDougall-Shackleton (1998) [32]
Length–HVC		16	0.250	MacDougall-Shackleton (1998) [32]
Length–RA		16	0.160	MacDougall-Shackleton (1998) [32]
Rep–Length		16	0.670	MacDougall-Shackleton (1998) [32]
Rep–HVC		12	0.177	Ward (1998) [42]

Rep: repertoire size, Length: song length, CMPX: a measure of song complexity, HVC: absolute volume of the HVC, RA: absolute volume of the RA, relHVC and relRA are relative values (i.e., corrected for the volume of the telencephalon).

In meta-analytical approaches, it is necessary to assess whether the non-balanced set of publication of significant results introduces publication bias in the data [34]. Publication bias refers to phenomena arising from bias in submitting, reviewing, accepting and publishing scientific results. We assumed that publication bias did not confound our analysis, because in our sample both significant and non-significant relationships were present with similar frequencies. Additionally, one recommended method for detecting publication bias is to construct a funnel plot by plotting the effect size against the corresponding sample size [30]. The funnel plot has an underlying assumption that the effect size is independent of sample size. Publication bias may be suspected if a correlation exists between the effect size and the sample size, which was not the case in our data ($r = -0.173$, $P = 0.280$, $N = 41$).

3. Results and discussion

In general, although half of the available studies reported non-significant patterns, we found strong evidence for song traits being related to the volumes of the song nuclei in the brain. When we included all analyses we found that the mean effect size was 0.356 (S.E. = 0.047) that was highly significant ($P < 0.001$, $N = 577$ from 41 studies). The mean effect sizes for different relationships are given in Tables 2 and 3.

When we used absolute volumes of the song nuclei, and the calculations were based on simple Pearson's correlation coefficients (Table 2), the overall effect sizes indicated significant positive relationships between HVC size and, respectively, repertoire size ($r = 0.328$) and song length ($r = 0.472$). The calculated sample size that would be required for sufficient power (80%) in intraspecific tests was larger than any of the particular studies involved (Table 2). This suggests that non-significant associations between absolute HVC size and song traits in published studies might have appeared because of high probability of committing type II error. Hence, the previously found non-

significant relationships often were the result of insufficient power, and in the majority of cases the alternative hypothesis that the volumes of song nuclei are related to song production cannot be rejected.

Although the signs of the mean effects sizes for the relationship between the absolute size of the RA and song traits were in the expected direction, the general pattern was weaker. The mean effect size for repertoire size ($r = 0.253$) was significant, but for song length ($r = 0.261$), it was not. Note that the sample size that guarantees sufficient statistical power was higher than in the pooled sample for both song traits (Table 2). This also applies to all particular studies, which have thus low potential to find statistically significant associations between song length and RA.

When we selected studies that used relative volumes of the song nuclei by correcting for the volume of the telencephalon, we found similar patterns as above (Table 2). Indeed the relationship between HVC size and song traits appeared to be stronger ($r > 0.500$), and the adequate sample sizes for sufficient power become smaller and thus reachable for particular studies. However, the associations between relative RA volume and song length and repertoire size were similar to those found for absolute volumes. We would like to emphasize again that the available sample size was much smaller than a powerful test would require.

Combining effect sizes from individual studies (see Table 1), the overall correlation coefficient calculated between repertoire size and song length was robust (overall effect size: 0.548 (S.E. = 0.144), $P < 0.001$, $N = 60$ from 4 studies; test for heterogeneity: $P = 0.802$). This may be a general phenomenon among passerine birds, as revealed by an interspecific comparison [22]. When we controlled for this covariation by using partial correlation coefficients, the relationship between repertoire size, song length and the size of the brain nuclei appeared to be weakened (Table 3). Although the available sample size was smaller, the most obvious pattern was that the significant positive correlations between repertoire size and the absolute volumes of the brain nuclei disappeared. However, both repertoire size and

Table 2

Relationships between the absolute and relative size of song nuclei (HVC, RA) and song repertoire size and song length as revealed by the meta-analysis

Relationship	Effect size (\pm S.E.)	No. of studies	Total sample size	P for effect size	Sample size needed for 80% power	P for heterogeneity
<i>Absolute volumes</i>						
HVC–Repertoire size	0.328 (\pm 0.088)	14	172	<0.001	68	0.704
HVC–Song length	0.472 (\pm 0.164)	3	46	0.002	30	0.442
RA–Repertoire size	0.253 (\pm 0.102)	10	126	0.011	117	0.520
RA–Song length	0.261 (\pm 0.164)	3	46	0.104	110	0.275
<i>Relative volumes</i>						
HVC–Repertoire size	0.534 (\pm 0.156)	3	50	<0.001	22	0.810
HVC–Song length	0.542 (\pm 0.156)	3	50	<0.001	21	0.437
RA–Repertoire size	0.229 (\pm 0.180)	2	37	0.194	144	0.497
RA–Song length	0.271 (\pm 0.180)	2	37	0.121	102	0.422

Results based on fixed effects are presented, as tests for homogeneity revealed homogenous patterns. Random effect models showed very similar results.

Table 3

Relationships between the absolute and relative size of song nuclei (HVC, RA) and song repertoire size and song length when the covariation between song length and repertoire size has been factored out

Relationship	Effect size (\pm S.E.)	No. of studies	Total sample size	<i>P</i> for effect size	<i>P</i> for heterogeneity
<i>Absolute volumes</i>					
HVC–Repertoire size	0.124 (\pm 0.164)	3	46	0.449	0.461
HVC–Song length	0.336 (\pm 0.164)	3	46	0.034	0.148
RA–Repertoire size	0.043 (\pm 0.164)	3	46	0.792	0.775
RA–Song length	0.201 (\pm 0.164)	3	46	0.214	0.368
<i>Relative volumes</i>					
HVC–Repertoire size	0.356 (\pm 0.156)	3	50	0.017	0.541
HVC–Song length	0.359 (\pm 0.156)	3	50	0.016	0.266
RA–Repertoire size	0.080 (\pm 0.180)	2	37	0.657	0.861
RA–Song length	0.168 (\pm 0.180)	2	37	0.345	0.655

Results of the meta-analyses in which partial correlation coefficients were used. Fixed effects are presented, as tests of heterogeneity revealed homogenous patterns. Random effect models showed very similar results.

song length independently explained a significant amount of variance in the relative volume of HVC (12.67% and 12.89%, respectively). No relationship reached the significance level in association with the volume of RA. These results indicate that the non-independence of different song features is important. Hence, an apparent significant association between a song trait and the volume of a song nucleus may be due to real mechanistic linkage between the two or/and due to a covariation with another song variable. Since both repertoire size and song length were related to the volume of the HVC independently of each other, the neural government of song complexity and song duration may involve substantially different mechanisms that may require independent brain space.

In summary, our results thus provide strong intraspecific evidence for repertoire size and song length being related to the volume of song areas in the brain. Although, the relationship was stronger for HVC than RA, an adequate sample size has the potential to reveal significant associations between RA size and song traits as well. We were able to demonstrate that both relative and absolute volumes of the song nuclei—having different biological meaning—were positively correlated with repertoire size and song length. We also showed that the storage of song length and repertoire size in the brain may involve independent roles. The strongest relationships were found for the relative volume of HVC. Our calculations suggest that studies testing the hypothesis concerning the link between song and neural space should investigate the relative size of the HVC in association with song by using a sample of at least 20 birds. On the other hand, if the volume of RA is in focus of particular interest, a correlative approach would require studying more than a hundred birds. Given that experimental approaches are likely to be more powerful to reveal significant associations among traits that are considered, and that sample size may be limited for neuroanatomical studies, we suggest conducting directed experiments when studying the relationship between neural space and song instead of correlative approaches.

Previously, three explanations have been proposed for the failure of some studies to detect an association between repertoire size and the size of the song control nuclei [6]. First, the lack of a functional relationship between brain space and song complexity may account for the negative findings. Second, species for which non-significant associations were reported may be different in the degree to which the amount of song learned is reflected in measurements of total repertoire size [36]. Third, non-relevant measures of song complexity in some species due to methodological differences in quantifying repertoire size may have led to heterogeneous patterns. In addition, one may argue that possible methodological differences related to volume measurements in the brain may raise heterogeneous associations. For example, different techniques used to visualize the borders of song nuclei may lead to different findings (Refs. [19,20], but see also Ref. [41]), but differences in the criteria used to delimit neuronal groups may have an impact as well. However, we suspect that these possibilities are not applicable for the data at hand, as we have provided strong evidence for the relationship between song features and brain nuclei, and in our analysis none of the tests for heterogeneity was significant (Table 2). This provides clear statistical evidence that the relationship between brain space and song is present, and is homogeneous among different species and studies that were available. We believe that the insufficient statistical power may have been the main reason for the lack of significant relationship in previous intraspecific studies.

On the other hand, we are cautious with making general validations for songbirds. The insufficient statistical power may be applied to the heterogeneity tests in our meta-analysis. Therefore, it remains plausible that the available sample was small to uncover differences in the neuroanatomical determination of repertoire size and song length, and we cannot exclude a role for heterogeneity in terms of methodology. For example, all studies involved in the meta-analysis used Nissl staining techniques, thus it was not possible to test statistically whether other approaches (see

Ref. [20]) would lead to different patterns. The vast interspecific variation in song organization and complexity may result in that a measure of song complexity (song type or syllable repertoire) in one species does not match with the same biological phenomenon in another [28]. It follows that methodological differences in quantifying repertoire size across species may exist that can cause some variation in the potential association with neural structures. We suggest that behavioral assays should be used to determine which aspects of song have the most relevance to the species under study.

In this study, we have used a correlative approach to unravel the relationship between brain space and song behavior. However, correlative methods do not have the potential to determine causal mechanisms. At this moment, the exact mechanism that generates the observed relationship between repertoire size and the volumes of brain nuclei is not evident. It may be that: (i) the number of songs learned by a bird determines the size of the song nuclei; (ii) the size of the song nuclei determines the number of songs that a bird learns, or (iii) other factors determine both the size of the song nuclei and the repertoire [7,8,37]. An experimental study in the marsh wren *Cistothorus palustris* revealed that the number of songs learned did not determine the size of the song nuclei [10]. We clearly need further experimental evidence to understand the causal relationship.

Our results raise important theoretical implications with regard to the neurobiology and evolution of bird song [16]. If larger brain space is needed for larger repertoires, substantial neural constraints may act during the development and maintenance of songs and the associated neural tissues. The tradeoffs in brain space devoted to song and other functions may determine the neural cost of the production of complex songs, which may affect the outcome of sexual selection [2].

Acknowledgements

G. Ball, J. Balthazart and two anonymous referees provided constructive comments. We thank A.P. Møller for his help with the meta-analysis. L. Z. Garamszegi and M. Eens were supported by the FWO-Flanders (Belgium).

References

- [1] P. Absil, R. Pinxten, J. Balthazart, M. Eens, Effect of age and testosterone on autumnal neurogenesis in male European starlings (*Sturnus vulgaris*), *Behav. Brain Res.* 143 (2003) 15–30.
- [2] D.C. Airey, K.L. Buchanan, T. Székely, C.K. Catchpole, T.J. DeVoogd, Song, sexual selection, and song control nucleus (HVC) in the brains of European sedge warblers, *J. Neurobiol.* 44 (2000) 1–6.
- [3] D.C. Airey, T.J. DeVoogd, Greater song complexity is associated with augmented song system in zebra finches, *NeuroReport* 11 (2000) 2339–2344.
- [4] D.J. Bernard, M. Eens, G.F. Ball, Age- and behavior-related variation in volumes of song control nuclei in male European starlings, *J. Neurobiol.* 30 (1996) 329–339.
- [5] J.J. Bolhuis, E.M. Macphail, A critique of the neuroecology of learning and memory, *Trends Cognit. Sci.* 5 (2001) 426–433.
- [6] E.A. Brenowitz, Comparative approaches to the avian song system, *J. Neurobiol.* 33 (1997) 517–531.
- [7] E.A. Brenowitz, A.P. Arnold, Interspecific comparisons of the size of neural song control regions and song complexity in duetting birds: evolutionary implications, *J. Neurosci.* 6 (1986) 2875–2879.
- [8] E.A. Brenowitz, D.E. Kroodsma, The neuroethology of birdsong, in: D.E. Kroodsma, E.H. Miller (Eds.), *Ecology and Evolution of Acoustic Communication in Birds*, Cornell Univ. Press, Ithaca, 1996, pp. 285–305.
- [9] E.A. Brenowitz, B. Nalls, J.C. Wingfield, D.E. Kroodsma, Seasonal changes in avian song nuclei without seasonal changes in song repertoire, *J. Neurosci.* 11 (1991) 1367–1374.
- [10] E.A. Brenowitz, K. Lent, D.E. Kroodsma, Brain space for learned song in birds develops independently of song learning, *J. Neurosci.* 15 (1995) 6281–6286.
- [11] E.A. Brenowitz, D. Margoliash, K.W. Nordeen, An introduction to birdsong and the avian song system, *J. Neurobiol.* 33 (1997) 495–500.
- [12] R.A. Canady, D.E. Kroodsma, F. Nottebohm, Population differences in complexity of a learned skill are correlated with the brain space involved, *Proc. Natl. Acad. Sci. U. S. A.* 81 (1984) 6232–6234.
- [13] C.K. Catchpole, P.J.B. Slater, *Bird Song: Biological Themes and Variations*, Cambridge Univ. Press, Cambridge, 1995.
- [14] J. Cohen, *Statistical Power Analysis for the Behavioural Sciences*, Lawrence Erlbaum Associates, Hillsdale, 1988.
- [15] H. Cooper, V. Hedges, *The Handbook of Research Synthesis*, Russell Sage Foundation, New York, 1994.
- [16] T.J. DeVoogd, T. Székely, Causes of avian song: using neurobiology to integrate proximate and ultimate levels of analysis, in: I. Pepperberg, A. Kamil, R. Balda (Eds.), *A Synthetic Approach to Studying Animal Cognition*, Academic Press, New York, 1998, pp. 337–380.
- [17] T.J. DeVoogd, J.R. Krebs, S.D. Healy, A. Purvis, Relations between song repertoire size and the volume of brain nuclei related to song-comparative evolutionary analyses amongst oscine birds, *Proc. R. Soc. Lond. B* 254 (1993) 75–82.
- [18] M.A. Farries, The oscine song system considered in the context of the avian brain: lessons learned from comparative neurobiology, *Brain, Behav. Evol.* 58 (2001) 80–100.
- [19] M. Gahr, Delineation of a brain nucleus: comparisons of cytochemical, hodological, and cytoarchitectural views of the song control nucleus HVC of the adult canary, *J. Comp. Neurol.* 294 (1990) 30–36.
- [20] M. Gahr, How should brain nuclei be delineated? Consequences for developmental mechanisms and for correlations of area size, neuron numbers and functions of brain nuclei, *Trends Neurosci.* 20 (1997) 58–62.
- [21] M. Gahr, E. Sonnenschein, W. Wickler, Sex difference in the size of the neural song control regions in a duetting songbird with similar song repertoire size of males and females, *J. Neurosci.* 18 (1998) 1124–1131.
- [22] L.Z. Garamszegi, A.P. Møller, Extra-pair paternity and the evolution of bird song, *Behav. Ecol.* (2004) (in press).
- [23] D. Gil, M. Gahr, The honesty of bird song: multiple constraints for multiple traits, *Trends Ecol. Evol.* 17 (2002) 133–141.
- [24] K.S. Hamilton, A.P. King, D.R. Sengelaub, M.J. West, Visual and song nuclei correlate with courtship skills in brown-headed cowbirds, *Anim. Behav.* 56 (1998) 973–982.
- [25] L.V. Hedges, I. Olkin, *Statistical Methods for Meta-Analysis*, Academic Press, London, 1985.
- [26] E.D. Jarvis, F. Nottebohm, Motor-driven gene expression, *Proc. Natl. Acad. Sci. U. S. A.* 94 (1997) 4097–4102.
- [27] J.R. Kim, R.P. Clower, D.E. Kroodsma, T.J. DeVoogd, Song-related

- brain regions in the red winged blackbird are affected by sex and season but not repertoire size, *J. Neurobiol.* 20 (1989) 139–163.
- [28] D.E. Kroodsma, Song repertoires: problems in their definition and use, in: D.E. Kroodsma, E.H. Miller (Eds.), *Acoustic Communication in Birds*, Academic Press, New York, 1982, pp. 125–146.
- [29] S. Leitner, C. Voigt, L.M. Garcia-Segura, T. Van't Hof, M. Gahr, Seasonal activation and inactivation of song motor memories in wild canaries is not reflected in neuroanatomical changes of forebrain song areas, *Horm. Behav.* 40 (2001) 160–168.
- [30] R.J. Light, D.B. Pillemer, *Summing Up*, Harvard Univ. Press, Cambridge, 1984.
- [31] S.A. MacDougall-Shackleton, G.F. Ball, Comparative studies of sex differences in the song-control system of songbirds, *Trends Neurosci.* 22 (1999) 432–436.
- [32] S.A. MacDougall-Shackleton, S.H. Hulse, G.F. Ball, Neural correlates of singing behavior in male zebra finches (*Taeniopygia guttata*), *J. Neurobiol.* 36 (1998) 421–430.
- [33] P. Marler, A.J. Doupe, Singing in the brain, *Proc. Natl. Acad. Sci. U. S. A.* 97 (2000) 2965–2967.
- [34] A.P. Møller, M.D. Jennions, Testing and adjusting for publication bias, *Trends Ecol. Evol.* 16 (2001) 580–586.
- [35] R. Mooney, M.J. Rosen, C.B. Sturdy, A bird's eye view: top down intracellular analyses of auditory selectivity for learned vocalizations, *J. Comp. Physiol.* 188 (2002) 879–895.
- [36] K.W. Nordeen, E.J. Nordeen, Anatomical and synaptic substrates for avian song learning, *J. Neurobiol.* 33 (1997) 532–548.
- [37] F. Nottebohm, S. Kasparian, C. Pandazis, Brain space for learned task, *Brain Res.* 213 (1981) 99–109.
- [38] A.F. Read, D.M. Weary, The evolution of bird song: comparative analyses, *Philos. Trans. R. Soc. Lond. B* 338 (1992) 165–187.
- [39] R. Rosenthal, *Meta-Analytic Procedures for Social Research*, Sage Publications, Thousand Oaks, 1991.
- [40] T. Székely, C.K. Catchpole, A. DeVoogd, Z. Marchl, T. DeVoogd, Evolutionary changes in a song control area of the brain (HVC) are associated with evolutionary changes in song repertoire among European warblers (Sylviidae), *Proc. R. Soc. Lond. B.* 263 (1996) 607–610.
- [41] A.D. Tramontin, E.A. Brenowitz, Seasonal plasticity in the adult brain, *Trends Neurosci.* 23 (2000) 251–258.
- [42] B.C. Ward, E.J. Nordeen, K.W. Nordeen, Individual variation in neuron number predicts differences in the propensity for avian vocal imitation, *Proc. Natl. Acad. Sci. U. S. A.* 95 (1998) 1277–1282.
- [43] J.M. Wild, Neural pathways for the control of bird song production, *J. Neurobiol.* 33 (1997) 653–670.
- [44] D.B. Wilson, M.W. Lipsey, *Practical Meta-Analysis*, Sage Publications, Thousand Oaks, 2000.
- [45] A.C. Yu, D. Margoliash, Temporal hierarchical control of singing in birds, *Science* 273 (1996) 1871–1875.