

# Comparative studies of sex differences in the song-control system of songbirds

Scott A. MacDougall-Shackleton and Gregory F. Ball

**Songbirds exhibit some of the most extreme sex differences in the brain of all vertebrates. Understanding the function of these sex differences has relied on making interspecies comparisons. In some species, females sing rarely or not at all, and the brain nuclei that control song are many times larger in volume in males than in females. In other species, males and females sing approximately equally, and the sizes of the brain nuclei that control song are approximately equal between the sexes. This article reviews sex differences in the song-control system of songbirds, and introduces statistical comparative methods developed by evolutionary biologists. These methods control for phylogenetic effects while comparing the co-evolution of traits. The extreme sex differences in song seem to have co-evolved with the extreme sex differences in singing behavior in songbird species.**

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IN MOST ANIMAL SPECIES, differences exist between the sexes in their behavior, morphology and physiology. Although sex differences in many aspects of reproductive behavior and physiology have been studied throughout the history of the biological sciences, it is only relatively recently that researchers have begun to explore sex differences in the brain. The mechanisms that regulate sex differences in behavior were initially studied by behavioral endocrinologists. Early views focused on the idea that sex differences in behavior were controlled by sex differences in steroid-hormone secretion<sup>1</sup>. It later became apparent that the mechanisms that mediated differences in behavior between adult males and adult females were due not only to differences in hormone secretion but also to the differing responses of male and female brains to steroid hormones<sup>2</sup>. This suggested that at some level male and female brains must be different.

A revolution in the study of sex differences in brain and behavior occurred in 1976 when Nottebohm and Arnold reported on qualitative sex differences in the volumes of the brain regions controlling singing behavior in males and females of two songbird species: zebra finches (*Taeniopygia guttata*) and canaries (*Serinus canaria*)<sup>3</sup>. Prior to this, it had generally been assumed that the neural bases of sex differences in behavior would involve somewhat subtler differences. For example, initial studies of neural sex differences had focused on synaptic morphology and related factors<sup>4</sup>. Thus, there was genuine surprise in the neuroscience community when Nottebohm and Arnold discovered that the volume of the telencephalic nuclei involved in song behavior exhibited extreme sex differences. Nuclei such as the HVC (sometimes called the high vocal center) and the robust nucleus of the archistriatum (RA) were found to be approximately five times larger in volume in male zebra finches than in females and three times larger in male canaries than in females. Another nucleus, a subdivision of the corpus striatum, called 'area X' by Nottebohm, because its function was poorly understood, was found to be nearly four times larger in volume in male canaries than in females. Area X is a large, well-delineated nucleus in male zebra finches, but

is not discernible in female zebra finches. At that time, lesion studies had indicated that HVC and RA were necessary for song production<sup>5</sup>, and area X was thought to be involved in song behavior because of the massive projection it received from HVC. Further comparative studies revealed that nuclei such as HVC, RA and area X were not present in closely related non-songbird species that did not learn or produce complex vocalizations<sup>6</sup>. Nottebohm and Arnold's discovery provided an opportunity to explore sex differences in the brain in a truly comparative sense. The fact that sex differences were more pronounced in zebra finches than in canaries was related to the variation in vocal behavior between the species. Among zebra finches only males produce courtship song (although both sexes produce calls). In canaries both males and females can produce courtship song, although males sing far more often and with more complexity. Thus, the initial description of these marked sex differences in the brain relied on a species comparison to make functional sense of the brain dimorphism.

Subsequent to this discovery of such large sex differences in morphology of the songbird brain, similar observations were made in many vertebrates, including species from several different mammalian orders, non-songbird avian orders, and in reptiles and amphibians<sup>7,8</sup>. Among songbirds, subsequent studies have focused on at least three major areas of investigation. One has been the study of the neuroendocrine mechanisms mediating the ontogeny of sex differences in songbird brains. Such work will not be the focus of this article, but these studies suggest that sex differences in the song-control system do not develop via the neuroendocrine mechanisms that govern the development of sex differences in the brains of mammals or birds other than songbirds. In particular, these neural sex differences appear to develop independently of gonadal steroid hormones<sup>9,10</sup>. A second area of research has involved the further characterization of exactly which neural characteristics of the song-control system differ between the sexes. Sex differences in neuron number, somata size, dendritic length and the incidence of androgen target cells in HVC have all been documented in the song system of zebra finches

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TABLE 1. Sex differences in brain and behavior among songbird species

Species	F/M HVC volume	F/M RA volume	F/M song repertoire	F:M song output <sup>a</sup>	Refs
<b>Family Corvidae</b>					
Slate-colored boubou ( <i>Laniarius funebris</i> )	0.556	0.5	0.978	5	12
<b>Family Muscicapidae</b>					
White-browed robin-chat ( <i>Cossypha heuglini</i> )	0.341	0.427	0.075	4	14,18
<b>Family Sturnidae</b>					
European starling ( <i>Sturnus vulgaris</i> )	0.625	0.588	0.517	2	19,20
<b>Family Certhiidae</b>					
Marsh wren ( <i>Cistothorus palustris</i> )	0.076	0.169	0	1	21
Buff-breasted wren ( <i>Thryothorus leucotis</i> )	0.769	0.667	0.9	5	13,14 <sup>b</sup>
Carolina wren ( <i>Thryothorus ludovicianus</i> )	0	0	0	1	22
Bay wren ( <i>Thryothorus nigricapillus</i> )	0.667	0.909	0.921	5	15,23
Rufous-and-white wren ( <i>Thryothorus rufalbus</i> )	0.455	0.588	0.429	4	13,15 <sup>b</sup>
<b>Family Passeridae</b>					
Orange bishop ( <i>Euplectes franciscanus</i> )	0	0.034	0	1	24
Domestic Bengalese finch ( <i>Lonchura striata domestica</i> )	0	0	0	1	25
Zebra finch ( <i>Taeniopygia guttata</i> )	0.137	0.133	0	1	3,12
Red-cheeked cordonbleu ( <i>Uraeginthus bengalus</i> )	0.667	0.714	0.923	4	26,27
<b>Family Fringillidae</b>					
Red-winged blackbird ( <i>Agelaius phoeniceus</i> )	0.312	0.213	0.5	2	28,29
Dark-eyed junco ( <i>Junco hyemalis</i> )	0.26	0.314	0	1	30
Domestic canary ( <i>Serinus canaria</i> )	0.33–0.27	0.23–0.37	~0.5	2	3,12,31
White-throated sparrow ( <i>Zonotrichia albicollis</i> )	0.546	0.577	1	4	32,33
White-crowned sparrow ( <i>Zonotrichia leucophrys</i> )	0.27	0.417	1 <sup>c</sup>	3	16,17
Bay-winged cowbird ( <i>Molothrus badius</i> )	0.386	n.d.	n.d.	2	34
Screaming cowbird ( <i>Molothrus rufoaxillaris</i> )	0.387	n.d.	0	1	34
Shiny cowbird ( <i>Molothrus bonariensis</i> )	0.144	n.d.	0	1	34

Taxonomy and nomenclature from Refs 35,36.

<sup>a</sup>Scoring system: 1, females never observed to sing; 2, females rarely sing; 3, females sing, but much less often than males; 4, females commonly sing; 5, females and males duet.

<sup>b</sup>Data also from S.M. Farabaugh, PhD thesis, University of Maryland, 1983.

<sup>c</sup>Females often sing short or incomplete songs.

Abbreviations: F, female; HVC is sometimes called high vocal center; M, male; n.d., not determined; RA, robust nucleus of the archistriatum.

(see Ref. 10 for a review). A third area of research (the focus of this article) concerns further comparative approaches to the study of sex differences in the songbird brain. Nearly half of the more than 9000 living species of birds are songbirds (suborder Passeri). Thus, there are many opportunities to relate the variation between species in the degree of sex differences in vocal behavior to the degree of sex differences in the morphology of the song-control system.

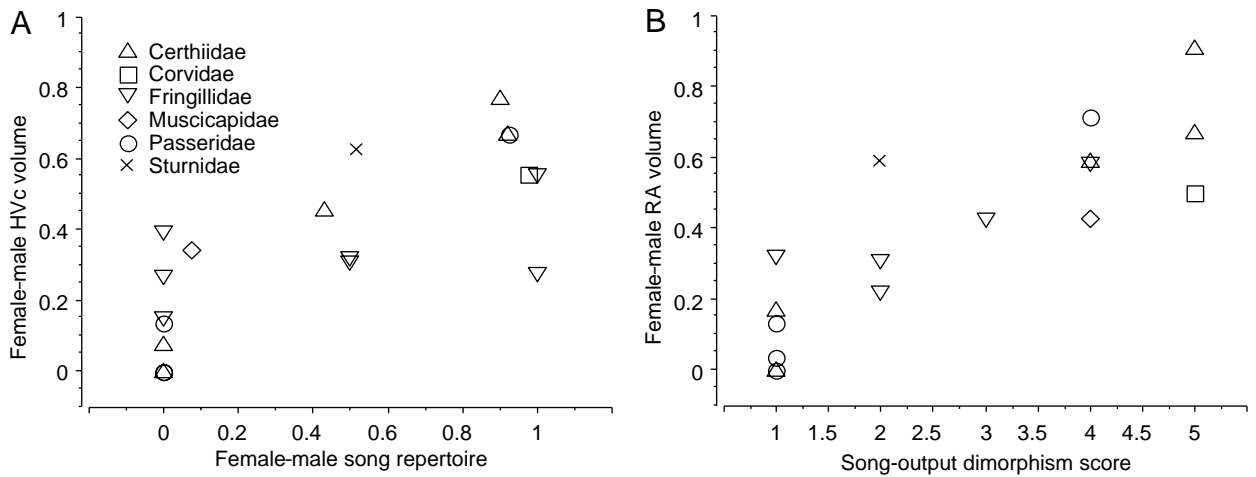
As more and more species have been investigated it has become clear that a systematic approach to the problem of comparison must be adopted. Several researchers have claimed that, in general, there is a good correlation between the degree of sex difference in vocal behavior and the degree of sex difference in the volume (or some other morphological measure) of the song-control nuclei<sup>7,11</sup>. However, others have questioned the validity of this claim and have suggested that statistical analyses of these sex differences do not reveal a good correlation between brain variation and behavioral variation<sup>12</sup>. Interspecies comparisons are fraught with potential problems: for example, should a comparison between two very closely related species (such as in the same genus) be treated the same as a comparison between two distantly related species (such as in different families)? If they are not going to be treated in the same way, which method should be applied in order to compare them appropriately? This article introduces and applies comparative methodology developed by evolutionary biologists to explore the co-evolution of sex dif-

ferences in the brain and sex differences in behavior among songbird species.

### Cross-species comparisons

Following the discovery of pronounced sex differences in the brains of zebra finches and canaries, neurobiologists began to examine other species that exhibit different patterns of male and female courtship singing. For example, bay wrens (*Thryothorus ludovicianus*) and buff-breasted wrens (*Thryothorus leucotis*) sing antiphonal song duets, with both sexes singing equally often and with similar song complexity<sup>13</sup>. Brenowitz and co-workers discovered that males and females of these species have similar-sized song-control nuclei<sup>14,15</sup>. In other species, sex differences exist in song behavior that fall between the extreme of zebra finches (where females never sing) and the wren species mentioned above (where males and females duet). In these species intermediate sex differences in the brain also exist. For example, female white-crowned sparrows (*Zonotrichia leucophrys*) sing, although much less often than males<sup>16</sup>. In this species, male HVC volume is about three times that of the female<sup>17</sup>. Thus, variation in HVC volume dimorphism appears to match variation in singing behavior in these species.

Since the earliest observations of a relationship between dimorphism in the brain and dimorphism in behavior, data have accumulated for several other songbirds. Table 1 presents a summary of such data for 20 songbird species from six different families. Data for



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**Fig. 1. Relationship between sex differences in songbird brains and sex differences in song behavior.** Each point represents data from a single species (see Table 1) and species from different taxonomic families are plotted with different symbols. (A) Sex differences in HVC volume are compared with sex differences in song-repertoire size. (B) Sex differences in RA volume are compared with sex differences in song-output scores. Statistically significant correlations exist between HVC size and song-repertoire size sex differences and between RA size and song-output sex differences for two of the three songbird families for which there are data from more than a single species (Certhiidae: HVC repertoire  $r = 0.98$ ,  $P < 0.05$ ; RA output  $r = 0.96$ ,  $P < 0.05$ . Passeridae: HVC repertoire  $r = 0.97$ ,  $P < 0.05$ ; RA output  $r = 0.98$ ,  $P < 0.05$ . Fringillidae: HVC repertoire  $r = 0.55$ ,  $P > 0.05$ ; RA output  $r = 0.83$ ,  $P > 0.05$ ). Abbreviations: HVC is sometimes called the high vocal center; RA, robust nucleus of the archistriatum.

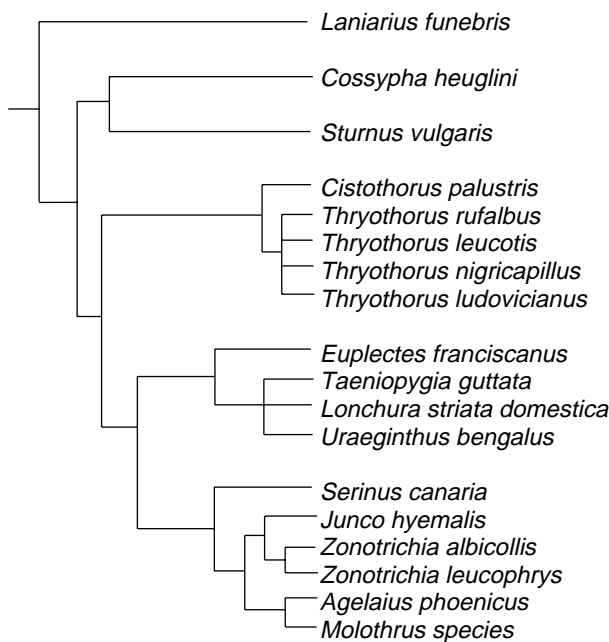
dimorphism in two song-control nuclei, HVC and RA, are presented as the proportion of the female nucleus volume compared with male nucleus volume. Data for dimorphism in song complexity are presented as the proportion of female song repertoire size compared with male song repertoire size. Sex differences in song output that are independent of song complexity have also been estimated, and each species has been assigned a score on a scale of 1–5. In estimating these sex differences in song output, we took into account how often females sang in relation to males of the same species, regardless of how complex female song was in comparison with the male song. These two song variables have both been

included because sex differences in these two aspects of song might vary independently among species.

A cursory examination of the data in Table 1 suggests that the proposed correlation between sex differences in the brain and sex differences in behavior is general across many species. A problem with this inferred correlation, however, is that it is confounded by phylogenetic effects. The species with the most-extreme sex differences in brain and behavior are almost all members of the family Passeridae. Conversely, duetting species with little or no sex differences in brain and behavior tend to be in the family Certhiidae (subfamily Troglodytinae). Because species are the endpoints of a branching lineage, they cannot be treated as statistically independent data. Thus, to test rigorously for a relationship among species between sex differences in the brain and sex differences in behavior, a comparative method that accounts for phylogeny must be used.

**Comparative methods**

The problem of comparing data statistically between species has long been a fundamental issue in evolutionary biology. It is now well accepted that cross-species comparisons must take into account the potential effects of phylogeny, and a range of statistical techniques has been developed to do this<sup>37,38</sup>. An important feature that is common to all such techniques is the use of an established phylogeny to control somehow for phylogenetic effects while examining relationships among phenotypic traits across species. Although the application of such techniques is now standard operating procedure in evolutionary biology research, they have been less widely applied in cross-species comparisons in fields such as comparative psychology, comparative physiology and comparative neuroethology. In many studies, interspecies data are compared nonstatistically without considering potential phylogenetic effects<sup>7,11</sup>. Moreover, in some cases, parametric statistics are applied to non-independent data in order to draw inferences about interspecies variation. For example, Gahr *et al.* compared data from 14 different songbird species in order to examine the relationship between sex differences in the



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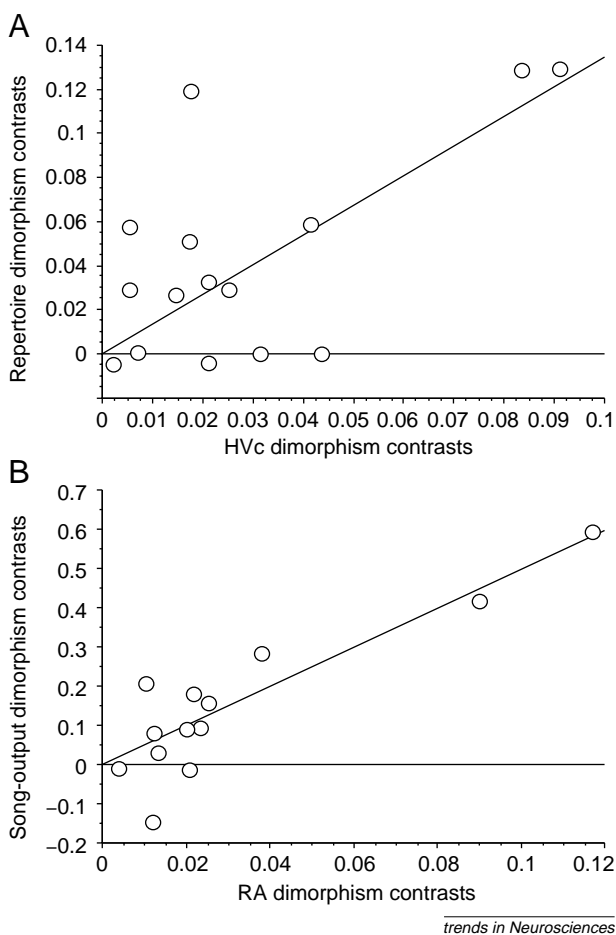
**Fig. 2. Phylogenetic relationships among the species used in the comparative analyses.** (Common names are listed in Table 1.) The branching pattern was obtained from DNA–DNA hybridization studies<sup>35</sup>. Branch lengths have been drawn for clarity and are not exactly proportional to time since divergence.

volume of specific song-control nuclei and sex differences in song behavior<sup>12</sup>. They concluded that, other than differences between species in which females never sing and species in which females do sing, there was no correlation between sex differences in the song-control system and sex differences in behavior. However, these authors treated species as independent data points, even though in some cases the species were very closely related (for example, congeneric or in the same subfamily) and in other cases they were more distantly related. One of the goals of this article is to demonstrate how comparative methods developed by evolutionary biologists can be used to examine brain-behavior relationships between species.

The first step in comparing data across species is to consider the phylogenetic relationships between those species. The data in Table 1 have been arranged by taxonomic family, where each family represents a monophyletic group within the songbird order. One simple way to control for phylogeny is to compare species within families rather than across families. Figure 1 compares sex differences in HVC volume to sex differences in song-repertoire size, and sex differences in RA volume to sex differences in song output within taxonomic families. Within two of the three families for which there are data from more than a single species, statistically significant correlations exist between HVC size and song-repertoire size sex differences and between RA size and song-output sex differences. Because data are available for so few species at this time, these tests are limited in their statistical power. However, in controlling for the differences between Certhiidae and Passeridae songbirds outlined above, a positive relationship between sex differences in the brain and sex differences in behavior across species appears to hold.

A problem with the simple approach used above is that even for species within families the data are not independent. A rigorous comparative method should control for phylogenetic relationships at the species level. There are several statistical techniques available that control for phylogenetic effects in order to produce statistically independent data from different species. Recently, one of these techniques<sup>39</sup> has been used to examine the relationship between HVC volume and song-repertoire size in a variety of songbird species<sup>40,41</sup>. In simple terms, this method calculates the amount of change (a contrast score) between nodes on a phylogenetic tree. Contrast scores are calculated by determining ancestral values for the traits in question at each node in the phylogeny. These ancestral values are means of the derived values, weighted by branch length. Although the values of character states at various nodes are not independent data points, the amount of change between nodes is independent from branch to branch. Thus, contrast scores for different traits can be compared using standard regression analyses. A positive correlation between contrast scores for two characters indicates that a positive change of evolutionary history in one trait has been associated with a positive change in the other trait.

This method of independent contrasts was used to assess whether variation in sex differences in the brain has co-evolved with sex differences in behavior in songbird species. Analyses were performed using the CAIC software package<sup>39</sup>. Use of this method requires a detailed phylogeny of the species in question. Phylogenetic relationships and branch lengths used were based on data



**Fig. 3. Regression of the contrast scores produced by the comparative analyses for sex differences in the brain and sex differences in behavior.** (A) Plots of contrast scores for song-repertoire size sex differences versus contrast scores for HVC size sex differences ( $r^2 = 0.67$ ,  $P < 0.05$ ). (B) Plots of contrast scores for song-output sex differences versus contrast scores for RA size sex differences ( $r^2 = 0.87$ ,  $P < 0.05$ ). Abbreviations: HVC is sometimes called the high vocal center; RA, robust nucleus of the archistriatum.

from DNA-DNA hybridization studies (Fig. 2)<sup>35</sup>. Where branch-length data were unavailable, the phylogenetic distance between nodes was made equal. Once contrast scores had been calculated, the scores for brain and behavior sex differences were compared using simple linear regression forced through the origin<sup>39</sup>.

Results of the above comparative analysis indicate that sex differences in the song-control system have co-evolved with sex differences in singing behavior. Contrast scores for HVC volume dimorphism were significantly associated with contrast scores for song-repertoire dimorphism (Fig. 3A). In addition, contrast scores for RA-volume dimorphism were significantly associated with contrast scores for song-output dimorphism (Fig. 3B). Thus, in general, it appears that extreme sex differences in the song-control system have co-evolved with extreme sex differences in singing behavior in a variety of songbird species, as was previously proposed<sup>7,11</sup>.

### Concluding remarks

The above analyses illustrate how comparative methods can be used in neuroscience to validate inferences drawn regarding cross-species comparisons. In this case, it appears that extreme sex differences in the song-control system have co-evolved with extreme sex differences in singing behavior. That is, in species where females sing little or not at all, evolution has produced

females with very small or nonexistent song-control nuclei. Comparative methods might be very useful in other cases where one wants to make brain-behavior correlations between a large number of related species.

The above results pose many interesting questions for future research. For example, in some songbird species, females appear to lack completely the song-control nuclei that are present in male birds. In these cases, standard staining procedures, such as Nissl stain or cytochrome-oxidase histochemistry, that delineate the nuclei in male birds fail to show any similar structure in female birds. Is this apparent lack of a nucleus qualitatively different from a female having a very small nucleus? The properties of these nuclei within the song-control neural circuit could be very relevant. For example, female zebra finches have no apparent area X, and afferents that project from HVC to RA and to the (nonexistent) area X are qualitatively different from other species in which females do have an area X (Ref. 42). Other questions raised by this study concern the function of these very small nuclei in female birds. For example, female zebra finches have a very small HVC, never sing and do not appear to need an intact HVC in order to perceive song normally<sup>43</sup>, as appears to be the case in other species<sup>44</sup>. Does the HVC in female zebra finches have some other function, or could it be merely sexually vestigial, such as nipples in male mammals? In order to answer such questions, a comparative approach will probably prove most useful.

Sex differences in morphology are often discussed in terms of 'costs and benefits'. One of the challenges for the future is to ascertain how one can coherently measure and assess the costs of maintaining brain areas of particular sizes. Is there a cost to males of maintaining a large HVC? If so, what is it? It is possible that the cost is not related to the brain area itself but rather to the regulatory system that maintains it. If high testosterone is required to maintain a large HVC, perhaps the cost that needs to be avoided is the high concentration of testosterone in the plasma and not the large brain nucleus itself. Thus, integrating neurobiological techniques with an evolutionary biological approach should continue to be fruitful.

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## LETTERS TO THE EDITOR

### Time to decrease the weight attached to looming?

Rind and Simmons<sup>1</sup> have provided an excellent description of how neurones respond to looming stimuli. Unfortunately, however, their article missed some of the recent trends in the story of how humans judge time to contact (ttc). In particular, recent work suggests that previous accounts of human timing behaviour might have exaggerated the role of looming and neglected the part of binocular information.

Hoyle<sup>2</sup> described originally how ttc information could be obtained from the rate of expansion of an approaching object (the ratio between retinal image size and the

rate of change of expansion). Lee<sup>3</sup> championed this cue as a timing variable and dubbed it  $\tau$ . Although, in principle  $\tau$  can provide ttc information (with specific limitations<sup>4</sup>), it is a different issue as to whether animals actually use this cue. In fact, a number of studies have purported to show that  $\tau$  is the timing variable used by animals (including humans) for a number of actions<sup>1</sup>. For example, Lee and Reddish apparently provided evidence that diving gannets fold their wings at a particular value of  $\tau$  (Ref. 1). A number of subsequent studies have also proposed the use of  $\tau$  in animal timing behaviour<sup>6,7</sup>. Wann<sup>8</sup>

has recently analysed all of these studies, however, and has shown that these data do not support the  $\tau$  hypothesis. Most notably, he demonstrated that the gannets used by Lee and Reddish<sup>5</sup> were flying too low (most below 50 cm above the water) to allow any conclusions regarding the use of  $\tau$  to be drawn from these data (a better explanation for the results is that the birds use a strategy based on height-above-water rather than  $\tau$ ).

It appears, therefore, that caution is required when interpreting some of the behavioural evidence that suggests  $\tau$  is a sufficient source of ttc information. Indeed, it can be shown a priori that  $\tau$  cannot provide precise enough information to explain timing behaviour in humans<sup>4</sup>. Instead, Tresilian<sup>4</sup> has proposed a general solution to the