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Mind the gap: why neurological plasticity may explain seasonal interruption in humpback whale song

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*Much is unknown about humpback whale (*Megaptera novaeangliae*) song. The behaviour is limited almost exclusively to males, occurs almost exclusively on the calving grounds and is identical within a population, although it changes periodically throughout the season. Much of current thinking associates humpback whale song with breeding, although it is not clear if it is intended to attract a mate, fend off challengers, or a combination of the two. There is, however, very little information on the internal biology of these large, sea-going mammals, so the majority of hypotheses have not considered much in the way of physiological mechanisms. Nonetheless, we believe that there is enough information available to infer that a seasonal process of neurological development and atrophy similar to that found in other animals may be present in humpback whales. We believe this explains why humpback whale song is not produced between breeding seasons and also why it does not vary between seasons, while it does so within a season. It also adds additional weight to the idea that humpback whale song is an honest signal of fitness to a potential mate or competitor.*

Keywords: humpback whale, song, brain, neurology, reproductive behaviour

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INTRODUCTION

Parsons *et al.* (2008) recently reviewed the available literature on humpback whale (*Megaptera novaeangliae*) song. First, they reviewed humpback whale behaviour, ecology and population structure in general. Then, they summarized numerous studies, reviewed the various current theories on the reasons that humpback whales sing, and offered a few new ideas for behavioural and cultural mechanisms that might be involved, as well as its evolutionary origins. In short, humpback whales generally migrate from high-latitude summer feeding grounds to low-latitude winter breeding grounds. Male humpback whales produce some quite complex songs on these breeding grounds, as well as on the migration routes to a lesser extent. These appear to play a role in male–male competition, but may also be involved in female selection of a male. However, there are various arguments for and against these main ideas for the use of song by humpbacks. There are also a number of other generally less-favoured proposals that have yet to be refuted completely. It is quite possible that a combination of uses and origins are needed to explain current singing behaviour.

While breeding populations of humpbacks around the world may have different songs (although geographically neighbouring regions may share various elements), all the individuals within a population sing the same song. This song may change several times throughout the breeding season and the changes are quickly adopted by all the singers within the population. Despite this, the song structure and components at the beginning of any given breeding season are the same as those observed at the end of the previous season, when singing recommences. Among the many mysteries that surround humpback whale song remain the reasons for the changes in song, the reasons why all the males sing the same song, and why the changes occur within breeding seasons, but not between them. (For further details about humpback whale migrations and behaviour, as well as the various exceptions to each, the acoustic properties of humpback song, the various ideas for its use and origins, and the many arguments for and against each of those, see Parsons *et al.*, 2008, and references therein.)

Despite their quite thorough review, Parsons *et al.* (2008) did not consider much in the way of physiological mechanisms, upon which behavioural ones might be based. We realize that this is mostly because there is very little information on the internal biology of these large, sea-going mammals. Nonetheless, we believe that there is indeed enough information available to infer that a seasonal process of neurological development and atrophy similar to that found in other animals across various taxa (including mammals; see Tramontin & Brenowitz, 2000) may be present in humpback whales.

SEASONAL PLASTICITY IN SONGBIRDS

Such seasonal plasticity in the adult brain has been highly studied in songbirds. Each year, during early stages of seasonal

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reproductive development, the volume of certain areas of the brain associated with song learning and production in various songbird increases (sometimes dramatically), along with the number, size and spacing of neurons (see review by Tramontin & Brenowitz, 2000 and references there in). Stimulated primarily by increasing levels of testosterone in the blood (possibly through the direct action of one or more of its metabolites; see Tramontin *et al.*, 2003), but also affected by lengthening days, thyroid hormones and other factors, this occurs several weeks before the actual onset of breeding, at the same time as (or even a little before) gonadal recrudescence (i.e. the redevelopment of the testes) and the reappearance of secondary sexual characteristics (see Tramontin & Brenowitz, 2000; Tramontin *et al.*, 2001; Brenowitz & Lent, 2002).

These changes do not affect the memory of previously learned songs. Song sparrows (*Melospiza melodia*), a species whose ability to learn new songs is age-limited (i.e. they do not learn to produce new songs as adults), obviously retain the songs learned when young, despite the seasonal reduction in size of the neurological song control system. Similarly, the same seasonal changes in the song control system do not necessarily affect the ability of song sparrows to make difficult song discriminations—although it may in other species (Reeves *et al.*, 2003). This would allow them to discriminate and respond appropriately to all other con-specific and environmental sounds equally well throughout the year.

SEASONAL PLASTICITY IN HUMPBACK WHALES

We propose that similar changes occur seasonally within the brains of humpback whales: certain parts of the humpback whale brain increase in size (or 'hypertrophy') as breeding season approaches, allowing and/or promoting song-related behaviour, before again shrinking in size once breeding is over. Indeed, Piersma & Lindstrom (1997) noted that the performance of a seasonally predictable behavioural task is often preceded by hypertrophy of the organs or tissues that are required for that task in many species. Furthermore, there is some evidence that, as in birds, humpback whale testis change in size seasonally, being larger on the breeding grounds (e.g. Chittleborough, 1955; Symons & Weston, 1958). This is in line with changes observed in the size of testis of other baleen whales (e.g. grey whale, *Eschrichtius robustus*, Rice & Wolman, 1971; minke whale, *Balaenoptera* sp., Best, 1982; but see discussion of *B. acutorostrata* subsp. and *B. bonaerensis* in Rice, 1998; Reilly *et al.*, 2008a, b). It has also been suggested that such seasonal changes in testis size will occur in any baleen whale species that exhibit seasonal reproductive cycles (Brownell & Ralls, 1986). Additional weight is thus added to the empirical evidence, as humpback whales tend to migrate annually, as briefly mentioned above (see review by Clapham, 1996, for additional details; but also see Mikhalev, 1997). We therefore submit that this hypothesis addresses many of the outstanding issues related to humpback whale song behaviour, as we shall now demonstrate.

Firstly, it would be reasonable to assume that, as in birds, the reduction in size of the neurological song control system in humpback whales during the non-breeding season would decrease the frequency of singing, perhaps to the point that no singing occurs at all. The advantage of this to the whale would be a reduction in metabolic costs, as the maintenance of any hypertrophied organ systems or tissues is thought to be energetically expensive, thus probably making such hypertrophy common to many vertebrates that live in variable environments (Jacobs, 1996; Piersma & Lindstrom, 1997).

These increased metabolic costs may also add weight to the idea that the song is an honest signal of reproductive fitness (as discussed by Parsons *et al.*, 2008). The metabolic costs of rebuilding and maintaining the song control system each year would be in addition to the handicap conferred by the song production itself, indicating fitness to a potential mate or competitor.

Although this hypothesis does not explain why humpback whale song changes continuously throughout the season (or why others adopt the new song) it may explain why it does *not* change between breeding seasons (e.g. Payne *et al.*, 1983). The ability to learn new song elements would not be required during the non-breeding season and thus the area of the brain responsible for song change could also be included in the song control system reduced during this period.

Similarly, if the neurological song control system in humpback whales increases in size prior to the onset of migration in a similar manner to the neurological changes seen in birds, then singing males could be expected on the feeding grounds just prior to their migration to the breeding grounds, as well as perhaps also immediately upon their return. In fact, there is increasing evidence that this may indeed be the case (e.g. Clark & Clapham, 2004; Vu *et al.*, 2009). This may also offer a mechanism for transfer of song components from one breeding population to another, as foraging populations may contain individuals from different breeding populations, and vice versa.

Finally, neurological changes may also explain why songs can be detected, on occasion, out-of-season (e.g. Charif *et al.*, 2001). The males of various bird species produce songs more frequently (and with less song-to-song variability) during the breeding season, but do not cease entirely during the non-breeding season (see Tramontin & Brenowitz, 2000). It may be that it is normal for certain elements to remain in the humpback repertoire out-of-season in a similar way, although they might be largely indefinable as song components. Alternatively (and perhaps more likely), it might be possible for certain disease-related conditions to circumvent the inhibition of song through the reduction in size of the song control centre. For example, the seasonal development of the song control system in song sparrows appears to occur at sub-maximal levels of circulating testosterone (Tramontin *et al.*, 2001) and can be artificially induced (to some extent) in Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*) through the experimental application of testosterone (Brenowitz & Lent, 2002). This suggests that physiological conditions resulting in unusually high levels of testosterone might be able to induce at least some parts of the song control system to hypertrophy, possibly resulting in out-of-season and/or female song production.

CONCLUSIONS

This hypothesis does not address the underlying reason for the initial production of novel song component, the reasons why all whales adopt the same song, or even hint at the largest question of all: why do humpback whales sing? (see Parsons *et al.*, 2008, for discussions of these issues). However, it does provide a physiological mechanism underlying the behaviour processes that has been missing to date and offers a possible avenue for research into this elusive species. This idea may also be testable through the use of stranding and by-catch data in humpbacks or other cetacean species. And, should it turn out that the songs are used to attract a mate, it may confirm the possibility offered in closing by Parsons *et al.* (2008), that 'humpback whales really are attracted to their mates for their minds'.

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