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Cetacean Brain Evolution

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Cetaceans (whales, dolphins and porpoises) are a group of aquatic mammals consisting of baleen whales and toothed whales. While the brain size relative to body size of the earliest cetaceans was not particularly large, this significantly increased in toothed whales around 34 million years ago. The increase in relative brain size involved a considerable decrease in body size and a more modest increase in absolute brain size. Nowadays, the relative brain size of cetaceans is exceptionally large; in some toothed whales this is second only to humans. A significant amount of energy is required to grow and maintain such large brains, so why have they evolved? This question has sparked considerable debate among researchers. Several drivers of cetacean brain enlargement have been suggested, including a need to cope with social and/or environmental challenges. Other researchers suggest that a global decline in oceanic temperatures during cetacean evolution drove their brain expansion. However, this hypothesis has received considerable criticism. As well as the drivers of their brain enlargement, fascination surrounds the cognitive abilities and behaviours such brains may engender for cetaceans, among both researchers and the general public. Studying such behaviours has wider implications for how intelligent these animals are perceived to be, which has challenged traditional views of the intellectual status of non-human animals.

Abstract

Cetaceans (whales, dolphins and porpoises) are aquatic mammals of the order Cetacea, which comprises two extant suborders, Mysticeti (baleen whales) and Odontoceti (toothed whales). Cetaceans diverged from terrestrial ancestors approximately 53 million years ago. The brain size relative to body size of the earliest cetaceans was not particularly large, although this significantly increased in odontocetes at the time of the Eocene-Oligocene transition around 34 million years ago. The increase in relative brain size was characterised by a considerable reduction in body size and a more modest increase in absolute brain size. The relative brain size of modern cetaceans is exceptionally large; in some odontocetes this is second only to humans. Growing and maintaining such large brains is metabolically expensive, so why have they evolved? Various drivers of cetacean brain expansion have been proposed, including the necessity to cope with social and/or ecological challenges. A more controversial hypothesis posits that declining global oceanic temperatures during cetacean evolution drove their brain expansion. In addition to the drivers of their exceptionally large brains, fascination surrounds the cognitive abilities and behaviours such brains may engender for cetaceans. Studying such behaviours has impacted how these animals are perceived in terms of their intellectual status, which has challenged traditional views of the intelligence of non-human animals.

Background

Cetaceans (whales, dolphins and porpoises) are aquatic mammals of the order Cetacea, which comprises two extant suborders, Mysticeti (baleen whales) and Odontoceti (toothed whales). Cetaceans diverged from terrestrial ancestors approximately 53 million years ago (Marino, 2004). The brain size relative to body size of the earliest cetaceans was not particularly large, although this significantly increased in odontocetes during the Eocene-Oligocene transition around 34 million years ago (Marino *et al.,* 2007). This increase was characterised by a considerable reduction in body size and a more modest increase in absolute brain size. The relative brain size of modern cetaceans is exceptionally large, second only to humans in some odontocetes (Marino, 2004). Growing and maintaining such large brains is metabolically expensive, so why have they evolved? This question has become a contentious topic, giving rise to theories regarding the factors and selection pressures shaping the evolution of large cetacean brains, and the cognitive abilities such brains engender.

The social brain hypothesis

The social brain hypothesis (SBH) posits that large brains evolved to cope with challenges of group living, including communication and cooperation (Dunbar, 1998). Without the ability to recognise group members and communicate about their behaviours, individuals may be exploited by cheaters. Cheaters reap the benefits of cooperative behaviours of others in the group, while themselves avoiding participation in them. Thus, cheaters reduce the fitness of other group members, necessitating methods for individuals to detect and avoid cheaters. The SBH is well-supported in primates. Within this highly-encephalised group, mean social group size significantly correlates with neocortex ratio (neocortex size relative to the rest of the brain) (Barton, 1996). The neocortex is a brain region governing higher-order functions including decision making (Bennett, 2019). Striking similarities exist between primates and cetaceans. The highest encephalisation quotient (EQ) values among animals are found within both groups. EQ is a measure of actual brain size relative to brain size predicted from various reference species (Marino, 1996). Behavioural similarities between primates and cetaceans include alliance formation and alloparenting (parenting of non-descendent young) (Marino, 2002). Such similarities provide a putative case of convergent evolution (Marino, 2002), resulting in the SBH being extended to cetaceans.

The SBH is currently the most widely accepted explanation for the evolution of large cetacean brains. Cetaceans are highly social; common bottlenose dolphins (*Tursiops truncatus*) and humpback whales (*Megaptera novaeangliae*) reside in fission-fusion societies, whereby group size and composition constantly change. Complex cognition is required to continually form alliances and track dynamic group properties (Pearson, 2011). These social structures have been observed in bottlenose dolphins in

Shark Bay in Australia, with alliances occurring between males to monopolise females and between females to reduce predation risk (Pearson, 2011). Social behaviours within humpback whales include cooperative hunting (Jurasz & Jurasz, 1979) and the transfer of hunting techniques between individuals (Allen *et al.,* 2013). Cetacean cooperation is not purely intraspecific; dolphins have been observed cooperatively fishing with humans (Pryor & Lindbergh, 1990). Empirical evidence also supports the SBH in cetaceans; across many cetacean species, encephalisation predicts the extent of social behaviours (Figure 1) (Fox *et al.,* 2017).

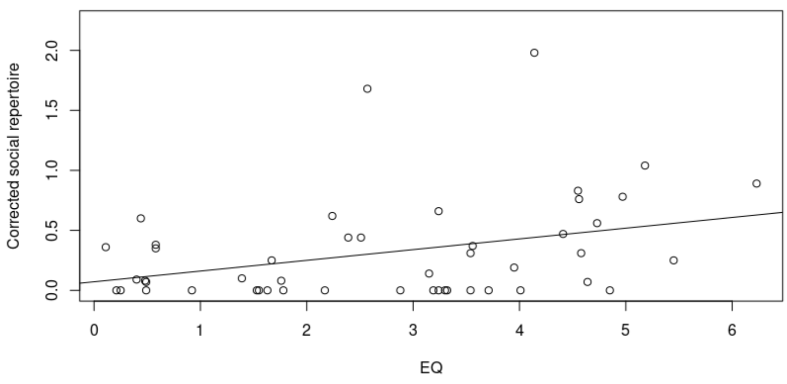

Figure 1. The relationship between corrected social repertoire size and encephalisation quotient (EQ) across 48 cetacean species. Corrected social repertoire scores measure the breadth of sophisticated social and cultural behaviours for each species (e.g. interspecific cooperation or alloparenting) identified from literature searches. Data taken from Fox *et al.* (2017).

The ecological intelligence hypothesis

The ecological intelligence hypothesis posits that cetacean brain expansion was driven by the need to overcome ecological challenges (Pearson, 2011), stemming from factors such as geographical range and dietary richness (Fox *et al.,* 2017). Greater cognitive abilities may be required to map greater spatial ranges and/or adapt to different environments. Increased dietary richness may require complex cognition to implement different foraging strategies. Fox *et al.* (2017) found that both latitudinal range and dietary richness were positively associated with cetacean relative brain size, but also found significant associations between sociality indices and relative brain size. Further statistical analyses attempting to disentangle cause from impact led them to conclude that cetacean brain expansion is best explained by the need to overcome social rather than ecological challenges (Fox *et al.,* 2017). Muller and Montgomery (2019) conducted a further test of the ecological intelligence hypothesis. Across cetaceans, dietary richness was significantly associated with both cerebrum and cerebellum mass, although latitudinal range was not. These results somewhat support the ecological intelligence hypothesis but should be treated with caution due to the small sample sizes in the study.

The thermogenesis hypothesis

The thermogenesis hypothesis offers an alternative explanation for the evolution of large cetacean brains. During the Eocene-Oligocene transition, global oceanic temperatures cooled, corresponding with an expansion in cetacean brain size. Manger (2006) suggests these declining temperatures drove an increase in thermogenic glia (non-neuronal cells) within cetacean brains, resulting in whole brain expansion. He argues this change allowed cetacean brains to function as thermogenic organs, generating heat via non-shivering thermogenesis in glial cells and thus counteracting heat loss to ambient waters. Non-shivering thermogenesis involves uncoupling proteins (mitochondrial inner membrane proteins) that generate heat via the dissipation of the proton gradient in cellular respiration (Manger *et al.,* 2021). Modern cetacean neocortices have a high ratio of glia to neurones, which Manger claims supports his theory. However, the hypothesis has received considerable criticism. Substantial evidence suggests odontocete body size decreased during the Eocene-Oligocene transition, consequentially increasing relative brain size. Maximino (2009) argues this contradicts Manger's hypothesis; rather than decrease, body sizes generally increase as climate cools (Hawkins, 1996), reducing the animal's surface-area-to-volume ratio and thus heat loss. Furthermore, across 20 odontocetes, Maximino (2009) found no significant difference between environmental temperature and relative brain mass, nor in relative brain masses between clades. Marino *et al.* (2008) also dispute the thermogenesis hypothesis. They refute Manger's claim that cetaceans lack complex cognition, citing the large volume of evidence to the contrary.

Complex cognition in cetaceans

Relative brain expansion could potentially enhance cognitive ability. Laboratory-based studies of bottlenose dolphins suggest they have multidimensional intellectual abilities, which include understanding how things function (procedural knowledge); understanding behaviours and identities of other individuals (social knowledge); and an awareness of their own self (self-knowledge), as reviewed by Herman (2006). The enhanced cognitive abilities of cetaceans appear to translate into observable behaviours, such as imitation, one of the most advanced forms of social learning (Rendell & Whitehead, 2001). Behavioural imitation requires the ability to not only mentally perceive another's actions, but then map that representation onto one's own body. Various cetaceans including killer whales (*Orcinus orca*) are capable of vocal imitation (Abramson *et al.,* 2018), while dolphins can exhibit both vocal and behavioural imitation, making them the only known mammal (excluding humans) capable of this (Marino *et al.,* 2007). Other indicators of complex communication in cetaceans include regional pod-specific dialects in killer whales (Ford, 1991) and personalised whistles in dolphins (Tyack, 1997). Cetacean play behaviour has also been extensively documented. Examples include dolphins riding waves into the shore, repeatedly throwing and hitting prey with their tails, and playing ball toss with humans (Paulos *et al.,* 2010). However, identifying play behaviours is difficult, as they can occur in other non-recreational contexts including mating or foraging. Observing wild cetaceans is usually restricted to surface-level behaviours, further compounding this issue (Paulos *et al.,* 2010). Cetacean tool use has also been reported; at Shark Bay, some female bottlenose dolphins carry sponges on their rostra (beaks), which is assumed to prevent abrasions when foraging on the sea floor (Smolker *et al.,* 1997). However, evidence of cetacean tool use is limited compared to extensive examples documented in primates.

Arguments against complex cognition in cetaceans

While widely accepted that the behaviours described above imply high cognitive abilities, not all researchers agree. Manger (2013) argues that 'sponging' is not indicative of complex cognition. He disagrees that the sponges are used for protection, claiming the sand-bottom foraging habitats would not necessitate their use. According to Mann *et al.* (2008), dolphins with sponges spend an additional 11.36% of the day foraging than those without. Thus, Manger (2013) concluded that 'sponging' was actually maladaptive. Patzke *et al.* (2015) also challenge cetaceans' intellectual abilities in their study of the hippocampus, a brain structure associated with complex cognition. They found that hippocampus volume was 8-20% of that predicted from brain size in four cetacean species. Patzke *et al. (*2015) suggest this explains the results of previous studies, where cetaceans scored lower in an object permanence task than other mammals and birds (Mitchell & Hoban, 2010; Jaakkola *et al.,* 2009). Such tasks require an understanding that objects exist even when hidden, hence rely on spatial memory, which is associated with the hippocampus. Thus, Patzke *et al.* (2015) claim that these studies, along with their own findings**,** suggest cetaceans may lack complex cognition.

Concluding remarks

Although not universally agreed upon, the general consensus is that cetaceans evolved relatively large brains to cope with challenges of social living, and as such, are widely viewed as highly intellectual. The extent of their cognitive abilities remains contentious. Some researchers argue cetaceans are no more cognitively complex than the average mammal, while others believe they are so intelligent they should be granted a special status within the animal kingdom. Currently, the debate shows no sign of ceasing, but may be resolved in future as new evidence emerges.

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