RELATIVE NEOCORTEX SIZE AND ITS CORRELATES IN DOLPHINS: COMPARISONS WITH HUMANS AND IMPLICATIONS FOR MENTAL EVOLUTION.

by

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Preface

The research described in this thesis was undertaken at the University of Natal, South Africa, between January 1996 and October 1998, under the supervision of Dr Michael Budek and the co-supervision of Dr Vic Peddemors of the Natal Sharks Board.

The design and execution of the studies on which this thesis is based represent my original and unassisted work, unless otherwise indicated and acknowledged in the text. No part of this thesis has been submitted for any other degree at any university.

Alain J-P.C. Tschudin

Dedication

Mothers play a crucial role in the successful development of their young, although their efforts often appear to pass as unnoticed or unacknowledged. This thesis is dedicated to two of the greatest mothers one could ever wish for, my mother Marcelle, and my grandmother, Isabel. Without your constant love, faith, hope (and prayers!), this work and I would not have been possible.

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Abstract

The superior neocortex ratios in primates and their distinctive relationship with sociality among terrestrial mammals are well documented. However, there has been an absence of research into relative neocortex size, its evolution and correlates in marine mammals, such as cetaceans (dolphins, porpoises and whales). This study uses the advanced radiological techniques of computed tomography and magnetic resonance imaging to establish neocortex ratios in dolphins and to re-assess these values for humans. It was found that freezing and defrosting did not significantly alter the neocortex raitos of dolphins and thus extra material as included in the analysis. Furthermore, equations for the estimation of neocortex ratios from CT and MRI have been applied to the cranial volumes calculated for 19 toothed whale species, in order to extend the range of analysis.

Using these techniques, it appears that dolphin neocortex ratios are higher than those of other mammals, except for primates. A notable finding is that dolphin values lie between human and other primates and are closer to human ratios at 4.1, than to non-human ratios reaching 3.22 (Dunbar, 1992). The highest delphinid neocortex ratio from MRI was 3.94 for common dolphins, while the highest estimated neocortex ratio was at 3.95 for killer whales. To establish the correlates of such high neocortex ratios in dolphins, their scores were related to variables representing foraging ecology, sound and sociality.

Although delphinid neocortex ratios do not appear to be related to foraging variables, they are significantly related with sound and sociality variables. Of these relationships, the most substantial finding exists with respect to the relationship of delphinid neocortex ratios and their mean group size. The capacity to predict group size from relative neocortex size has not been noted in non-primate species, and has formed the basis for current theories of social intelligence and mental evolution. The findings of this study are therefore of considerable interest and may have substantial implications. These may impact on current theories of primate-human mental evolution and therefore it is strongly recommended that the mental capacities of other mammals, such as dolphins, be examined in greater detail to support or refute these claims.

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Appendix: Table of selected abbreviations

Chapter 1. Brain size and the correlates of mental evolution in mammals

1. Introduction

The quest for knowledge concerning the evolution of mind and intelligence is of long standing and continues with increasing interest. Scholars of this topic are drawn from diverse backgrounds and often promote complementary or contrasting perspectives. The mainstream of evolutionary research widely accepts the notion of the continuous physical evolution of humans from earlier communal primate-ape clade ancestors (Darwin, 1871). However, a contrasting scenario prevails with respect to the evolution of human cognitive capacities. The present consensus is that this process is discontinuous and thus dissimilar to that in other animals (Corballis, 1991; Povinelli, 1993).

The theory of discontinuous mental evolution implies that the nature of the human mind and intellect is not merely quantitatively different to other mammals and primates, but also qualitatively different. The premise of distinctly unique human intelligence has been supported by a large base of literature, although the concept of intelligence is problematic in its own right (Byrne, 1995).

Within this context of qualitative difference, researchers have attempted to discern what distinguishes human mental and intellectual evolution from that of other species. Originally it was proposed that the large brains of humans and primates, in absolute terms, might be the significant difference when these were compared to other animals (Passingham, 1982). However, when certain megaherbivore and cetacean species such as elephants and whales were considered, this approach rapidly lost favour, as it became apparent that absolute brain size (ABS) favoured larger animals (Passingham, 1982).

During the 1970s, it was suggested that the degree of relative brain size (RBS) might be the hallmark of primate brain evolution (Jerison, 1973). The encephalisation quotient (EQ) was built on the cephalisation co-efficient of von

Bonin (1937) and provided the ratio of observed to expected brain weight over body mass of the animal (Jerison, 1973). According to this measure, humans were significantly more encephalised than other primates (Passingham, 1982). Megaherbivores were eliminated from contention using the EQ. However, the superior scores of dolphins among the cetaceans (Ridgway, 1990) and of cetaceans in relation to primates (Jerison, 1982b; Marino, 1997, 1998; Worthy and Hickie, 1986) are problematic and continue to confound the theory of discontinuous human cognitive evolution.

Although the EQ (Jerison, 1973) and its derivatives (Clutton-Brock and Harvey, 1980; Eisenberg, 1981; Marino, 1996, 1997; Passingham; 1982; Worthy and Hickie, 1986) have been in use since the 1970s, criticism has been drawn from several different perspectives. For example, evolutionary changes in body size may not necessarily have accompanying alterations in brain size (Deacon, 1990b). It has been suggested that body size is thus a confounding variable and should be excluded from analysis (Barton and Dunbar, 1996). Furthermore, relative changes in regional brain areas such as the neocortex may occur fairly independently of body size (Dunbar and Bever, 1997). However, in spite of the drawbacks of the EQ, the cautionary comment directed at it and the development of more appropriate brain size measures, it continues to be utilised in current research (see Marino, 1995, 1996, 1997, 1998).

More apparently appropriate indices of RBS are thought to include processing capacity relative to cortical surface area (Jerison, 1982a), the relative size of the neocortex (Sawaguchi and Kudo, 1990) and the neocortex ratio (Dunbar, 1992). These measures are used to study the brain in relation to itself, insofar as neuroanatomical regions are examined in relation to each other. Such ratios are believed to provide a more adequate reflection of relative brain size than ratios such as the EQ, which express brain size in relation to non-brain variables.

However, the above investigations share common ground, in that they have not merely sought to establish the size of the brain, its degree of encephalisation or even the relative size of areas such as the neocortex. They have also attempted to establish what factors are related to an expanded brain or enlarged neocortex, in order to ascertain what might be related to intellectual evolution.

One of the more recently notable measures has been the neocortex ratio (C_R), which is a measure of the neocortex volume relative to the volume of the rest of the brain (Aiello and Dunbar, 1993; Dunbar, 1992, 1995; Dunbar and Bever, 1997). This is an apparently better measure, as the neocortex is accepted as being responsible for complex cognitive functioning, although this assumes that intellectual functions are localised in the cortex (Byrne, 1995). Hence the neocortex ratio is considered to be an important indicator of intellectual capacity. According to this reasoning, an animal with a high volumetric ratio of neocortex relative to the rest of the brain has more potential for intellect than an animal with a low C_R. As humans are conventionally conceived of as being the most intelligent species, it is not surprising to find that they obtain the highest C_R at 4.1, followed by chimpanzees at 3.22 and other primates from 2.67 downwards (Dunbar, 1992).

To interpret the significance of high C_R values in humans, Dunbar (1992) initially studied the C_R of primates in relation to different behavioural ecology variables. These included social complexity, crudely represented by mean cohesive group size, and the complexity of foraging ecology, in the form of home range and dietary composition. He found that in the older strepsirhine primates, C_R was related with foraging ecology, but not with sociality (Dunbar, 1992). The C_R only appeared to be related to sociality in the more recently evolved haplorhine primates, a finding that has subsequently been confirmed (Dunbar, 1995). When applied to other orders of terrestrial mammals, the C_R did not appear to relate to sociality. For example, in insectivores, the C_R was related to foraging ecology, but was unrelated to sociality (Dunbar and Bever, 1997). Recently, however, a significant relationship between C_R and sociality has been presented for carnivores (Dunbar 1992; Dunbar and Bever, 1997).

The observation of the relatedness of C_R and sociality apparently exclusively in the more recently evolved primates until the study by Dunbar and Bever (1997) has had several substantial implications. Dunbar (1992) argued that the availability of neocortex constrained the capacity to sustain social relationships. An evolutionary solution enabling animals to live in larger cohesive social groups would entail expanding the relative size of the neocortex relative to the rest of the brain. Thus, although the total cranial volume of modern humans may be smaller than that of their ancestral hominids and australopithecines, their neocortex ratio, or relative neocortical volume, is higher (Aiello and Dunbar, 1993).

In short, the neocortex is believed to be intricately related with the capacity for intelligent behaviour. In most of the literature, large neocortices appear to be exclusively restricted to primates, reaching a zenith in humans (Dunbar, 1992). Relative neocortex size in other orders of mammals is primarily related to foraging ecology, in contrast to the relationship with sociality in primates and carnivores. It has previously been argued that the difference in primate and human intelligence is that it is more geared towards social complexity than to feeding or ecological complexity (Dunbar, 1992, 1995), although Byrne (1995) considers such distinctions to be artificial.

Additional supporting evidence for the exclusivity of primate social intelligence has been drawn from the fields of social anthropology, evolutionary psychology and primatology. For example, Cosmides and Tooby (1993) have indicated that the human brain is better geared towards solving social problems in comparison with logico-mathematical problems. Cheney and Seyfarth (1990) considered that intentionality, an important attribute of social intelligence, was not present in other primates, with the possible exception of certain great apes. Whiten and Byrne (1988) coined the term "Machiavellian Intelligence" to describe the intelligence employed by primates, noting that the origins of human strategic intelligence are evident in our primate relatives.

Within this paradigm, the implication is that as social intelligence is a recent evolutionary phenomenon, it is logically solely represented in the primate domain. Even more "sensible" is the assertion that humans, as the most recently evolved primates, should possess the largest relative neocortices, in addition to demonstrating the greatest degree of social intelligence. This can be summed up in a recent statement by Povinelli (1993) who does not consider it possible that another species could have a mind "as replete with social intelligence as our own".

Although the concepts of discontinuous mental evolution or distinctive primate-human social intelligence might be enticing, there is a problem. The reasoning from which these conclusions are drawn is based on a potentially faulted premise. A certain highly adapted order of mammals has been omitted from comparative studies of the brain and its correlates. This omission might not seem immediately obvious nor pertinent. The reader will note that other orders of terrestrial mammals such as carnivores and insectivores have been examined, without any evidence of a relationship between neocortex and sociality. Yet, the significance of the omission may become apparent when one considers the excluded order of interest.

The order in question is that of *Cetacea*, whose members include species of dolphins, whales and porpoises. Although theories describing the evolution of cetaceans have been largely speculative (see Rothausen, 1985), recent paleaontological findings indicate that the terrestrial order *Condylarthra* were the forebears of the archaeocetes at the end of the Palaeocene (Barnes, 1984; Evans, 1987; Gingerich, Wells, Rusell and Shah, 1983; West, 1980). Test results of cetacean DNA divergence correspond closely with the documented data on their phylogenetic relationships (Arnason, 1974; Gretarsdottir and Arnason, 1992), except for the sperm whales, who are thought to have diverged long before their extant relatives (Douzery, 1993).

Within this classification, the study is primarily concerned with members of the family *Delphinidae* (delphinids). The delphinids are of relative recency (Table 1.1), as is evidenced by fossils from the Late Miocene (Evans, 1987; Sylvestre, 1995).

Although speculation remains as to the origin of placental mammals, the proposals range from the beginning of the Cretaceous (140Ma) onwards into the Cenozoic era, also referred to as the 'Age of Mammals' (Hildebrand, 1995; Martin, 1990). The ancestral primate stock is said to have diverged from the general stock of placental mammals 90-100Ma (Martin, 1990). This possibly represents the last plausible time that a common ancestor was shared between the modern primates and cetaceans (see Table 1.1).

While the cetaceans were evolving in the water, largely isolated from terrestrial life, highly significant evolutionary adaptations were occurring on land, as is evident in Table 1.1. Whereas dolphins represent the most recent product of the significant evolutionary changes in water, the terrestrial equivalent is the current sub-species of humans, *Homo sapiens sapiens*, who have only been in existence for 250,000 years (Martin, 1990; Passingham, 1982). Accelerated hominid evolution is said to have been made possible by cultural innovation (Donald, 1993).

It appears as if dolphins have interacted significantly enough with humans to be well documented in culture and language (Lockyer, 1990). This is evident from cultural artefacts dating from approximately 1600 BC to 2000 BC (Lockley, 1979; Lockyer, 1990). Literary accounts support the proposal that dolphins and humans have interacted through antiquity (Guerber, 1944; Lockley, 1979; Stenuit, 1971; Sylvestre, 1995).

However, although a substantial amount of popular interest has been invested in dolphins and whales, a paucity of scientific knowledge exists with respect to these mammals in relation to other mammals, such as primates. Although the scientific study of cetaceans began with Aristotle, little progress was made until 1551, when Pierre Belon du Mans comprehensively described dolphins. The next notable scientific investigation of cetaceans was conducted by Linnaeus (1735), who included them as mammals in his classification of the animal kingdom. Although cetology is currently in its infancy, contemporary research aims to broaden our understanding of these animals.

A study pertaining to the neocortical evolution of dolphins and humans is considered to be important, as it may provide more insight into general mammalian mental evolution and possible convergent evolution between different orders.

Table 1.1: The evolution of cetaceans and primates.

Time period	Cetaceans	Primates
Jurassic (210-140 Ma)	Earliest mammals	
Early Cretaceous (140 Ma)	Placental mammals	
Late Cretaceous (98-80Ma)	Possible last common ancestor	
Late Cretaceous to Early Palaeocene (80-66 Ma)	Artiodactyls	Ancestral Primates
Palaeocene (65-55 Ma)	Condylarths	Lemurs, Tarsiers
Eocene (54-35Ma)	Archaeocetes (ancestral whales)	New World monkeys, Old World monkeys
Late Oligocene to Early Miocene (28Ma-21Ma)	Odontocetes: sperm whales and beaked whales	lesser apes
Middle Miocene (21-17Ma)	-	great apes: orangutan
Late Miocene (16-12Ma)	delphinids	-
Pliocene (11-3Ma)	-	great apes: gorilla and chimpanzee
Pleistocene (2Ma)	-	hominid ancestors
250,000 Ya	-	Homo sapiens

Note: Ma= Million years ago; Ya= Years ago. Sources. Barnes, 1984; Benton, 1990; Evans, 1987; Hildebrand, 1995; Leatherwood and Reeves, 1983; Marino, 1996; Martin, 1990; Passingham, 1982; Sylvestre, 1995.

Dolphins and whales are genetically related to humans and other terrestrial mammals, albeit distantly (Deacon, 1990). The order *Cetacea* is also considered to be consequential for comparative analysis, as it is the only mammalian order that has engaged in a complete secondary return to permanent existence in water (Kesarev, 1971). This, in its own right, makes dolphins interesting for research. However, the degree to which dolphins have successfully adapted to life in a complex, three-dimensional aquatic medium, radically different to land, is perhaps equally significant (Deacon, 1990; Finlay and Darlington, 1995). This is possibly evidenced by several features of cetacean brains, which require discussion in relation to other mammals.

It was mentioned above that certain cetacean species have the largest absolute brain size (along with elephants) and the greatest EQ of all species. In addition, members of this order also possess the most convoluted brains and greatest cortical surface area of all animals (Elias and Schwartz, 1969; Ridgway and Brownson, 1984). Several brain size findings have been reported where dolphins score above humans (Elias and Schwartz, 1971; Jerison, 1982a; Ridgway, 1986a) or below humans, but above other primates (Haug, 1970; Hofman, 1982a; Jerison, 1973; Martin, 1990, 1982, 1981; Ridgway 1986a; Ridgway, Flanigan and McCormick, 1966).

The cortex and cytoarchitectonics of the dolphin brain have been investigated; however, the relative size of the neocortex, specifically the neocortex ratio, has not been previously documented in dolphins. This is addressed in the current study.

If one considers that the C_R has not been examined in dolphins, it follows that the correlates of relative neocortex size have also not been studied in these animals. Although a positive relationship between the large encephalisation of dolphins and their sociality has been described by Marino (1996, 1997), it is suggested that neocortical evolution may follow a radically different route from that of encephalisation. The C_R could plausibly have some entirely different or unanticipated correlates to those of delphinid EQ. However, although Marino's efforts are based on the EQ, they may provide preliminary support for the relationship of neocortex and sociality in dolphins.

A positive association between neocortex and sociality or communication in dolphins would have several implications. These may potentially affect theories of social intelligence, primatology and cognitive evolution, as discussed in subsequent chapters.

2. Study Aims and Hypotheses

In the light of the published data on dolphin brains and following the above overview, the following hypotheses are investigated in this study:-

-that dolphins have high neocortex ratios;

-that dolphin neocortex ratios fall at least within the primate range of neocortex;

-that dolphin neocortical ratios are more closely linked to social and communicative complexity than to the demands of foraging ecology.

Previous studies have remarked at the encephalisation and extraordinary brain development of dolphins and the documented literature indicates that dolphins lie between humans and other primates in terms of EQ (Marino, 1997). However, as brains are energetically expensive, it is unlikely that a relatively large delphinid neocortex would have evolved without serving some notable functional purpose. To investigate the correlates of C_R in dolphins, it is necessary to pay attention to their life history parameters. Dolphins reside in a complicated visuo-spatial environment, described as the "sensory periphery" (Finlay and Darlington, 1995). Although dolphins display a complex variety of foraging ecology, perhaps more impressive is their range of fluid and advanced social organisation, as well as their elaborate sound production. The above hypotheses are therefore tested for various groups of *Cetacea*, from a category including three dolphin species exhibiting varied life histories and social structure, to a sample representing the wider family *delphinidae* through to the order *Odontoceti*.

Sociality variables incorporate gestation, lactation, intercalf interval, mean group size and maximum aggregate size. Acoustic variables include the minimum, maximum and range values of sound frequency, sound energy and signal duration, as well as the number of sound types produced. Foraging ecology variables comprise foraging depth, number of total, fish and cephalopod prey species, the ratio of total prey items to fish items or cephalopod items, the ratio of fish to cephalopod species and the Shannon-Wiener Index of dietary diversity (Sekiguchi, Klages and Best, 1992).

3. Overview of study animals and methods

Several difficulties have possibly precluded detailed work with cetaceans. While some populations are heavily depleted by commercial fishing, a scarcity of specimens is available for scientific research. If one considers that the dolphins used for research are rare finds, then the value of their cortical matter becomes appreciable. With the co-operation of the Natal Sharks Board (NSB), access to dolphin specimens was made possible. The NSB is the local scientific body responsible for installing and maintaining anti-shark netting along the KwaZulu-Natal coast, South Africa. The majority of dolphin specimens were incidental catches who had asphyxiated in the nets deployed to protect bathers from shark attacks. Other dolphin specimens were provided by Durban Seaworld and the KwaZulu-Natal Stranding Network. All of the dolphin subjects were deceased on examination and therefore no vivisection was performed. The human subjects were all volunteers, who provided their informed consent. The cetacean crania were provided by the Port Elizabeth Museum.

As delphinid crania are valuable for taxonomic and morphometric investigation, they may not be damaged by physically extracting brains for analysis. Although the use of sophisticated imaging technology to study such brains has been possible for some time, the prohibitive costs involved are probably responsible for the use of such techniques in very few studies.

The current study utilises the latest neuroradiological techniques of computed tomography (CT) and magnetic resonance imaging (MRI) to provide a non-invasive and harmless method of investigating dolphin and human brains, with a focus on the neocortex. In addition to scanning freshly obtained dolphin subjects, the brains of several subjects were frozen, defrosted and re-scanned to ascertain whether or not defrosted material could be reliably scanned to increase the sample size.

The specimen data have been studied in relation to broader population parameters established using cranial volume analysis (CVA). This has been done in order to address any concerns about the representativeness of the neuroimaging sample. CVA has also been used to extend the application of the neuroimaging findings to a wider spectrum of species and also serves as a comparison with the MRI findings.

If the data in the present study are supportive of the hypothesis that large dolphin neocortex ratios are related to sociality to a greater extent than to foraging ecology, several implications arise. The notion that primate and human neocortical evolution share a unique relationship with sociality can be refuted. This in turn leads one to question the premise that social intelligence is the sole domain of humans, with its beginnings in primate relatives.

4. Structure of thesis

This thesis assesses the relative neocortex size of dolphins and the correlates thereof in comparison with the findings for humans and other primates. The implications of the study for the theory of social intelligence and mental evolution are also discussed.

CHAPTER 2 provides an assessment of brain size and relative neocortex size in dolphins and humans using the neuroimaging techniques of CT and MRI. The brain volume relationships in dolphins from CT and MRI are documented. The effect of specimen condition on the MRI process is described. The relationship between CT and MRI is also documented. Finally, human MRI neuroanatomical data are provided.

CHAPTER 3 discusses the use of cranial volume analysis (CVA) to verify the suitability of the sample used for neuroimaging in terms of representing the wider population. The relationship between cranial volume and neuroanatomical data from neuroimaging is also used to estimate the neuroanatomical values for CVA subjects. This provides an extension of the study to other delphinid and odontocete species.

CHAPTER 4 considers the relationship of foraging ecology and relative neocortex size in dolphins. The ecological theory and variables relevant to dolphins are reviewed, prior to the presentation and discussion of the results and the implications thereof.

CHAPTER 5 describes the relationship of relative neocortex size and acoustics in dolphins. Dolphin sound production and sonar are reviewed prior to providing the results and their illustration.

CHAPTER 6 investigates the relationship of sociality and relative neocortex size in dolphins. The social organisation of the study species and the selected variables are described, following which, the findings of neocortex in relation to sociality are presented and discussed.

CHAPTER 7 serves as a general discussion of the findings and a summary of the thesis. Concluding comments are made regarding the implications of the study, its limitations and future directions for research.

The format of the thesis follows the publication manual of the American Psychological Association (4th Ed.), in accordance with the guidelines specified by the School of Psychology, at the University of Natal, Pietermaritzburg. For ease of reference, a table of abbreviations has been included as an appendix to the study.

Chapter 2: An assessment of brain size and relative neocortex volume in dolphins and humans using neuroimaging

1. Introduction

Since classical times, a wealth of investigations have been conducted into the anatomy of the brain and its evolution, often in relation to its increasing size or organisational complexity (Klinowska, 1994). The initial drive behind studies of brain size, such as that of Dubois (1897), pertained to the comparative assessment of animal "intelligence", which was inferred from the greater interactions associated with larger brains (Armstrong, 1985; Radinsky, 1982). Potential selective mechanisms related to the evolution of large or complex brains have formed the focal point of many such enquiries. Some of the key issues in this research are largely addressed by comparative analysis. From this perspective, an overview of evolutionary neuroanatomy and brain size in mammals is provided, prior to reviewing the use of neuroimaging technology to engage in such studies.

1.1. Evolutionary neuroanatomy and brain size in mammals

Comparative analysis allows for the distinction of and appreciation of the adaptive benefits of similar and different cognitive capacities (Povinelli, 1993; Tschudin, 1998). From an evolutionary perspective, comparative analysis is enabled through phylogenetic reconstruction, which in turn relies on evolutionary neuroanatomy. This specifically involves the study of comparative anatomy, embryology, ontogenesis and palaeontology. Within evolutionary neuroanatomy, correlative neuroanatomy is of interest, as it relates the structural organisation of the brain to its functioning. Researchers have either developed absolute or relative measures of brain size from this frame of reference (Dunbar, 1992; Jerison, 1973; Passingham, 1982; Sawaguchi and Kudo, 1990; von Bonin, 1937). The current section discusses neuroanatomy and measures of relative brain size (RBS) in primates, other terrestrial mammals and cetaceans. The advantages and limitations of these studies are subsequently assessed in chapter 7 (section 7.2).

Increasing interest has been shown in evolutionary analysis, from which evolutionary neuroanatomy has arisen (Kesarev, 1971). Within the paradigm of evolution, Haeckel's triad is considered important for any attempts at phylogenetically reconstructing brain development (Kesarev, 1971), as it proposes that the findings of comparative anatomy, embryology, ontogeny and palaeontology be synthesised. The final element of the triad (ontogeny and palaeontology) is not evident with respect to the brain. For this reason, it is essential to compare the human cortex to the cortices of other related and unrelated species to understand brain evolution (Kesarev, 1971; Tschudin, 1998).

It is in the light of the above literature on comparative neuroanatomy and theories of brain evolution that attempts have been made at measuring dimensions of the brain and its regions. A brief overview of investigations into brain size for primates and dolphins is provided.

The absolute size of the brain (ABS) is not adequate for comparative analysis, as it favours larger animals, who require bigger organs to permit efficient functioning (Passingham, 1982). Given this, it is not surprising that large megaherbivores and cetaceans possess the largest absolute brain size. As a result of this shortcoming, it was suggested that interspecific comparison could be achieved by employing a simply derived ratio, relating brain size to body size (brain weight over body weight), although this ratio has been argued to favour smaller animals (Stephan, Bauchot and Andy, 1970). Passingham (1982) noted that the larger animals have smaller brain/body ratios, as an increase in brain size is relatively smaller than an increase in body size. Such a relative increase only allows valid comparisons between similar sized species.

To overcome the difficulties inherent in absolute brain size, it has been suggested that the brain size and body weight of a species group be studied in relation to each other (Jerison, 1973). From logarithmic transformations of these variables, the best line of fit between brain and body size for the group can be derived. This permits interspecific analysis of brain size based solely on body weight (Passingham, 1982).

Von Bonin (1937) formulated the cephalisation coefficient, an equation correlating body weight and brain weight. He concluded that brain weight increased as the 0.655th power of body weight, with interspecific variation in the coefficient. Based on this measure, Jerison (1973) derived the EQ, which consists of scaling the observed brain size of each species to the expected brain size of an average mammal, similar in body weight. As the original slope of the EQ has been held to overestimate brain size in large mammals and underestimate it in small mammals, the equation has been refined several times (Clutton-Brock and Harvey, 1980; Eisenberg, 1981; Martin, 1990).

Using the EQ, human brain size may be compared to a “hypothetical relative”, by reading the brain size predicted for a hypothetical primate of similar body weight from the regression line. According to this measure, human brain size is three times larger than expected for a primate of similar size (Passingham, 1982).

Several mammalian groups can be differentiated into three classes of EQ. These include insectivores and rodents, who have small brains relative to weight; ungulates, carnivores and prosimians with moderately sized brains; and finally simians and humans, who have large brains. Thus although the absolute brain size of the elephant is greater than that of primates, its EQ is within the range of ungulates and carnivores (Passingham, 1982). The data of Jerison (1973) indicate that only 3 out of 25 ungulates and 2 out of 15 carnivores hold an EQ within the range of 48 simian primates.

While a fair amount of encephalisation research has been undertaken with primates (Clutton-Brock and Harvey, 1980; Gould, 1975; Jerison, 1973, 1979; Jungers and Olson, 1985; Martin, 1990), less work has been conducted with insectivores and bats (Stephan, 1985), carnivores and ungulates (Gittleman, 1986; Martin, 1981; Pirlot, Jiao and Xie, 1985). Similarly, a relative shortage of research exists concerning the encephalisation of non-terrestrial mammals, especially with respect to sirenians (Kamiya, Pirlot and Hasegawa, 1985) and cetaceans (Marino, 1996, 1997, 1998; Worthy and Hickie,1986).

The comparative lack of dolphin studies is surprising if one considers that their neuroanatomical features have intrigued researchers from the time of Belon, in 1551, to the present (Kruger, 1966). Cetaceans, along with certain megaherbivores such as the elephant, possess the largest absolute brain size (Passingham, 1982). The Delphinidae family includes species such as the bottlenose dolphin, which hold the greatest brain to body size ratios amongst cetaceans (Ridgway, 1990). According to Jerison (1982b), certain cetaceans, in common with humans, possess the highest relative brain size to body weight ratio.

In opposition to Count (1947), the findings of Elias and Schwartz (1969) suggested that cetaceans have the most convoluted brains of all species. Certain dolphins have the largest cortical surface area. For example, the average bottlenose surface area was calculated as 3745cm^2 (Ridgway and Brownson, 1984), as opposed to the human average at 2275cm^2 (Elias and Schwartz, 1969). Several cetaceans also have longer gyri as a function of brain size than humans (Elias and Schwartz, 1971; Jerison, 1982a; Ridgway, 1986b).

In spite of the interesting proposals that have been made by researchers within the above frame of reference, there are complications with brain size *per se.* For example, Stephan, Frahm and Baron (1981) proposed that considerations of size might lead to the determination of the functional significance of cerebral areas in different species. Although their suggestion has drawn support, their method of relating brain size to body weight for interspecific comparison via allometric scaling has been criticised. Although allometry, as "the study of the relationship between size and adaptation", appears to be the method of choice for such investigations (Fleagle, 1985:1), it is subject to several considerable limitations.

Allometric scaling that relates brain size to body size depends on a power relationship between the two variables, which requires that the species points fall on a straight line (Byrne, 1995). Although logarithmic plots provide straight lines for species groups, Deacon (1990) suggests that the relationship may be a curvilinear function. In addition, Martin (1990) notes that allometry is based on the premise that some standard allometric value applies to all species under comparison and that an appropriate baseline is chosen to compare species.

From the description of EQ above, it was reported that the residuals (deviations from the line of best fit) were important. An animal placed above the line was more encephalised than expected and, conversely, one below the line was less encephalised than expected. However, Byrne (1995) argues that there is no theoretical basis for the above reasoning, suggesting that this type of scaling makes a strong assumption about the functioning of neural tissue, namely that more is better. Although the brain does cope with sensorimotor inputs and outputs, it also has additional processing capacity for computational intelligence, something that has been marginalised in allometric studies (Byrne, 1995).

Although the general method used in the above gross brain size studies appears not to be as satisfactory as once believed, the criticism of these studies can be extended to their specific measures, such as the EQ. Several limiting factors exist with respect to the interpretation of EQ values. The EQ relies on body weight, which is considered to be a confounding variable (Barton and

Dunbar, 1996), as changes in body size need not be accompanied by changes in brain size (Deacon, 1990b). It follows that specific changes within the brain, for example, in neocortex, occur fairly independently of body size, which diminishes the usefulness of the EQ (Dunbar and Bever, 1997).

Without establishing a certain degree of maturation, it is very difficult to determine an accurate EQ. The inability to determine the exact age of cetacean specimens is therefore problematic. A related issue is that immature animals have larger relative brain sizes than mature individuals (Count, 1947) and it has been suggested that EQ decreases as body length increases (Ridgway, 1986a; Ridgway and Brownson, 1984). Nevertheless, in spite of these reservations, contemporary studies of dolphin brain size have continued to use the EQ (Marino, 1996, 1997).

Measures that focus either solely on the absolute size of the brain, or even on the size of the brain relative to the body are considered simplistic, as they do not take the differentiation within the brain into account. Bearing these limitations in mind, the discussion focuses on the brain in its own right and considers more appropriate measures of relative brain size and the importance of the neocortex.

The first precursor of modern variables to take account of this variation in relative brain size may have been the measurement of brain size relative to spinal cord by Warden (1951). He proposed that a relative ratio, such as brain weight to spinal cord, might allow for a standard of comparative intelligence across mammals. Following this method, Ridgway *et al.* (1966) found that whereas fish have a brain weight less than the cord, horses score approximately 2.5:1, cats 4 or 5:1, apes 8:1 and humans 50:1; the average brain-spine weight ratio for bottlenose dolphins is 40:1. The importance of this study appears to lie in the ranking of the odontocetes between humans and the apes, as subsequent studies have verified this as being a common pattern for cetacean and primate comparisons (Marino, 1996, 1997).

The brain is divided into three basic areas, namely the hindbrain or rhombencephalon, midbrain or mesencephalon and forebrain or telencephalon (Nauta and Feirtag, 1986). In general terms, the hindbrain houses the cerebellum, which is covered with cerebellar cortex. The base of the forebrain houses the thalamus, with thalamic nuclei relaying sensory information to the neocortex.

Brain size could therefore be more directly related to a measure of brain input and output, such as medulla size, which would provide an indication of the additional brain tissue not required for sensory analysis or directed movement (Passingham, 1982). However, the problem with this technique has been the absence of such area measurements for different species (Passingham, 1982).

To be more specific in terms of interspecific brain differences, an interesting pattern is evident from comparative indices of different brain parts. While the human pons and medulla are of an expected size for a primate of our size, there is a fair enlargement of the midbrain (mesencephalon), interbrain (diencephalon) and the striatum (in the telencephalon) compared to other primates (Passingham, 1982). The greatest difference occurs in cortical areas that diminish, such as the piriform cortex (palaeocortex), hippocampal cortex (archicortex) and cerebellar cortex and those that expand, such as the neocortex (Nauta and Feirtag, 1986).

Jerison (1982a) realised the significance of the cortex and related its surface area to possible processing capacity. Each square centimetre of cortex is said to contain, on average, 2000 processing units or modules. According to this study, a mouse with a $4cm^2$ cortex possesses 8000 modules, a chimpanzee with $800cm^2$ has 1.6 million modules and a human with $2000cm^2$ cortex has the highest capacity at 4 million modules (Jerison, 1982a).

Following the method of Jerison (1982a), the dolphin, with a 3000cm^2 cortex, would obtain the highest result of all mammals, at 6 million processing units. However, in spite of this large cortical area, dolphins display half the cortical thickness of humans (Kesarev, 1971; Ridgway and Brownson, 1982). Whereas the dolphin has a larger cortical surface area than the human brain, it has only 80% of the average human cortical volume, according to an estimate from Ridgway (1986a). This led him to verify the finding of Haug (1970), that *Tursiops* scores below humans and above terrestrial mammals with high encephalisation. However, data cited in this regard must be treated with caution, as Ridgway's estimate was drawn from an immature specimen.

Remaining with the cerebral cortex, the neocortex (often vaguely referred to as cortex) covers the cerebral hemispheres (Passingham, 1982). The cerebral hemispheres range from being small in lower vertebrates to large in higher mammals (Nauta and Feirtag, 1986). The main cerebral areas of the human brain may be defined as follows: neocortex (new cortex), archicortex (old cortex), intermediate cortex, palaeocortex (primitive cortex) and peripalaeocortex (Kesarev, 1971; Nauta and Feirtag, 1986). Contrasting features are traced between the oldest cortex (palaeocortex) and youngest differentiated formations (neocortex). While the palaeocortex regresses during evolution, the neocortex is the most recent to appear and the last to conclude its development in humans (Kesarev, 1971; Nauta and Feirtag, 1986).

Joseph (1996) notes that the brainstem, which has retained its specialisation for receiving information from the immediate environment, can be contrasted with the forebrain, which is associated with cognition, emotion, memory and the evolution of the neocortex. The evolution of primary, association and tertiary neocortex therefore conferred a considerable advantage to mammals, who could "engage in multimodal sensory analysis and information storage" and outwit the competition (Joseph, 1996:30).

Different neocortical areas perform specialised functions (Martin, J.H., 1981). Sensory cortex receives sensory information via the thalamus, from motor areas controlling movement and from association areas which appear essential to learning (Johnson, 1997). Crude divisions exist between three types of areas; koniocortex in the sensory areas, agranular cortex in the motor and premotor areas and eulaminate cortex in the association areas. Although the human brain has the expected amount of sensory cortex, it is distinguished by the extent of the agranular cortex and the association areas. For example, the premotor cortex is especially large in humans (Johnson, 1997; Passingham, 1982). The importance of the neocortex is apparent. As it can be distinguished from other types of cerebral cortex and as its importance in higher functions has been recognised, the neocortex forms the centre for interspecific comparison (Passingham, 1982).

Two recent measures have taken cognisance of the relevance of the neocortex and have been specifically aimed at its structure. These are the relative size of neocortex (Sawaguchi and Kudo, 1990) and the neocortex ratio (Dunbar, 1992, 1995).

The relative size of the neocortex (RSN) was initially measured by Sawaguchi and Kudo (1990), to assess the degree of neocortical development in each superfamily of primates. RSN is based on the allometric relationship between neocortex volume and brain weight for each superfamily. Using regression analysis to obtain the equation for each superfamily, Sawaguchi and Kudo reported that RSN, for a congeneric group, appears independent of the effects of brain and body size. However, this research used a very broad level of analysis, namely the superfamily, rather than the more particular genus or species.

The final measure of RBS and the most important one for the purposes of this study is the neocortex ratio (Dunbar, 1992). This ratio relates neocortex volume to the rest of the brain at the genus level and serves to separate the rather loosely defined volume of neocortex from the rest of the brain, or hindbrain (Dunbar, 1992). In terms of the importance of the neocortex (Passingham, 1982), this method was considered to be the most appropriate for a true indication of relative neocortical importance at the more distinctive genus level.

Although this measure is not subject to the same allometric critique as other brain size indices, it may have potentially problematic definitional issues. Aside from the inconsistent usage of the term neocortex, the definition of specific brain regions is problematic. For example Dunbar (1992) includes the mesencephalon and diencephalon as parts of the hindbrain, whereas these regions are thought to lie in the midbrain and forebrain respectively (Kolb and Whishaw, 1990). Although the neocortex ratio is considered to be more accurate as a measure of the brain than its brain size-body size counterparts, such as the EQ, it still relies on the assumption that intelligence is localised in the neocortex (Byrne, 1995).

The neocortex ratio has been documented for many mammalian genera representing several orders (primates: Dunbar 1992, 1995; hominids: Aiello and Dunbar, 1993; insectivores and carnivores: Dunbar and Bever, 1997). From this comparative research, primates appear to be distinguishable from other orders of mammals on the basis of their large neocortex ratios. As the relative importance of the neocortex has been noted above, the consequences of possessing large neocortices become highly consequential in relation to ecological, communicative, social and intellectual functioning (refer to Chapters 4-7).

It is therefore surprising that there is an absence of dolphin neocortex data comparable to primates. This is particularly the case if one considers that Kruger (1966) observed the most striking feature of the cetacean brain as being the size of the cerebral cortex and the large extent of its fissurization. This was of comparative importance, as the cerebral cortex is thought to be related to intelligence (Kruger, 1966). Yet, although absolute brain size values have been obtained and dolphin encephalisation studied, no examination of relative neocortical importance has been conducted with these animals.

One reason for this omission may be the scarcity of cetacean subjects in scientific studies, something that is especially apparent with respect to brain research. For example, in a recent article, Ridgway (1986a) had to rely on secondary sources for data (Kojima,1951; Pilleri and Gihr, 1971; Ridgway and Brownson, 1984). Furthermore, large interspecific variation in delphinid brain size was reported by Ridgway and Brownson (1984).

This chapter therefore aims to provide the first study of relative neocortex size in dolphins, with a special emphasis on establishing neocortex ratios for members of the delphinid family.

1.2. The use of neuroimaging in behavioural, psychological and neuroanatomical research.

The above section has addressed the content of what this chapter aims to study, while the current section reviews the method to be used in the investigation of the brain. A brief review of the use of neuroimaging in behavioural, psychological and neuroanatomical research is provided in order to provide the methodological context of the current study.

Neuroimaging techniques, specifically computerised tomography (CT) scanning and magnetic resonance imaging (MRI), have developed into powerful sources of investigation in several disciplines. Aside from the utility and value of the standard application of CT and MRI to medical studies of pathology and surgery, several alternate applications are possible. These alternatives hold much potential for inter-disciplinary investigations. The use of neuroimagery in behavioural, psychological and neuroanatomical research encompasses diverse disciplines such as psychiatry, psychology, anatomy and histology, physiology, pharmacology, biology, veterinary science and biomedical research. From the literature, it is apparent that these techniques are under-utilised for research, in spite of their great scientific potential.

Computed tomography and nuclear magnetic resonance (the forerunner of MRI) were pioneered during the 1970s by Allan Cormack and Godfrey Hounsfield (see Cormack, 1980; Hounsfield, 1980). As an enhanced form of x-ray tomography, CT has been an important innovation in the medical field for over the past two decades and has served to assist in increasing the efficiency of radiology (McCort, 1987). Although surgical and pathological applications are not the focus of this topic, it is important to note that CT permits the most accurate diagnosis of all imaging methods in head, spinal and pelvic injuries and allows for faster surgical intervention and reduced fatalities (McCort, 1987). For these reasons, the popularity of CT scanning increased throughout the 1980s, (Evens and Mettler, 1985; Steinberg, Anderson and Steinwachs, 1987). As the more recent and enhanced technique of MRI has similar clinical applications to CT, it may be reasonable to expect a related increase in MRI units by the year 2000.

In a similar vein to the popularity of CT, the demand for MRI is steadily increasing (Evens and Evens, 1991). For example, MRI referrals in the U.S.A are twice as high as in an economically comparable country such as Japan, even though Japanese fees are substantially lower (Hisashige, 1994). From this, it appears as if neuroimaging techniques are potentially overutilised for medical referrals in some countries, when they could be more appropriately shared and invested in research applications.

From an examination of the literature, it was found that CT and MRI were almost exclusively used for the detection and diagnosis of pathology, injuries or in the assistance of surgical treatment. Only a handful of articles pertained to behaviour or psychology and these dealt with psychological reactions when confronted with MRI. Almost all of the behavioural articles related to organic disorders, pre-, intra- and post-operative findings. No topics related to behaviour *per se,* in terms of motor responses, and no cognitive or perceptual applications were found.

Investigations of human social behaviour using CT and MRI, from their inception to current times, all appear to relate to psychiatric disorders and psychopathology. Searches of the mainstream neuroimaging literature therefore indicate that CT and MRI have not been used extensively in behavioural and psychological research. However the literature examined excluded fMRI, or functional MRI, which is gaining popularity for a wide spectrum of research.

All the documented cases of animal behaviour research using CT relate either to pharmacological, neurophysiological or neuropsychological effects on animals. For the past decade, MRI investigations in this area have all related to lesions, surgical observations and chemical experimentation. Only one documented case exists relating to actual animal behaviour. Repeated open-field and passive avoidance tests were administered to rats by Ossenkopp, Innis, Prato and Sestini (1986), who concluded that there was no evidence for short or long term behavioural alteration in animals exposed to MRI.

Whereas the above section has focused on behavioural applications of neuroimaging, the following discussion studies the use of such techniques in comparative neuroanatomical research.

Although research in this area is scarce, it may hold potential for future comparative studies. Ruff (1989) suggests that comparative image analysis, including computerised tomography, provides important information on structural evolution. An example stems from the use of high-resolution CT scanning for the examination of the vestibular system of certain extant and extinct primates (Spoor and Zonneveld, 1995; Spoor, Wood and Zonneveld, 1994). From this research, the earliest species reflecting modern human morphology appears to be *Homo erectus,* in contrast with southern African crania, attributed to *Australopithecus* and *Paranthropus,* that relate more closely to the contemporary great apes (Spoor, Wood and Zonneveld, 1994). This illustrates the value of neuroimaging techniques such as CT and supports the introduction, albeit cautiously, of imaging workstations into the field of computer-aided primatology (Vannier and Conroy, 1989).

Documented primate MRI research has related predominantly to the visual cortex (Engel *et al.,* 1994; Rizzo, Nawrot, Blake and Damasio, 1992). As with CT in this field, MRI studies relating to behaviour or anatomy are extremely rare.

A large amount of research related to the current field of interest is documented in the discipline of veterinary science. Although the majority of the articles pertain to surgical treatment and the diagnosis of pathology, some articles relate directly to neuroanatomy. Examples from CT include the *in vivo* cephalic scanning of the chimpanzee (Saban *et al.,* 1985) and the neurology of small animals (Lang, Huber and Vandevelde, 1988). Principles of CT and MRI usage in such areas have been proposed by Wortman (1986) and the interpretation of relevant images is discussed by Stickle and Hathcock (1993).

Neuroimaging applications are far more scarce for marine mammals than for terrestrial mammals. With the exception of Sebes, Langston, Gavant and Rothschild (1991), all studies have been anatomical. The first use of CT with delphinids was to observe acoustic structural anatomy in the forehead of spinner dolphins (Cranford, 1988). CT was also used in the determination of airsacs in the dolphin species *Lagenorhynchus albirostris* (Brouwers, Kaminga, Klooswijk and Terry, 1990) and the acoustics of *Delphinus delphis* (Aroyan, Cranford, Kent and Norris, 1992). Cranford, Amundin and Norris (1996) used CT and MRI to study the odontocete nasal complex in relation to biosonar signal production.

In spite of a lack of general information about comparative neuroanatomical studies using CT or MRI, a search was made for the more specific study of the cerebral cortex and neocortex using these techniques. None of the investigations relating to mammalian cerebral cortex in general, nor particularly to primates and dolphins had been conducted using CT or MRI. It therefore appears reasonable to conclude that a minority of studies into comparative neuroanatomy have been carried out using neuroimaging techniques. However, an example of such a study is the volumetric measurement of the amygdala and hippocampus using MRI (Watson, Andermann, Gloor and Jones-Gotman, 1992). Using the MRI technique, it was found that the volume of the amygdala and 90-95% of the hippocampal volume could be reliably measured. Guidelines obtained from studies such as the above are not only useful for understanding pathogenesis, but also indicate the accuracy of MRI in volumetric analyses.

An important potential of neuroimaging techniques lies in their ability to broaden our understanding of structural evolution. In terms of animal research, MRI is a more favourable application than CT, as it does not expose the animal to radiological effects. As MRI is non-invasive and non-lethal, it should be considered ahead of other potentially inhumane research methods.

MRI has increased rapidly in its popularity and applicability during the last decade and along with CT holds much potential for future research. A shortage exists in the behavioural, psychological and neuroanatomical applications of structural CT and MRI, although functional MRI (fMRI) is a highly efficient research tool. Very few studies have been conducted into social and animal behaviour using structural neuroimaging methods.

The current study aims to harness the techniques of CT and MRI to provide the first documented data, using neuroimaging, on cranial capacity, brain volume, neocortical volume, brainstem volume and cerebellar volume in dolphins. In addition, the suitability of frozen and defrosted brain material for neuroimaging analysis was assessed. Neocortex ratios were also calculated for humans using neuroimaging to permit comparison with the existing literature (Dunbar, 1992; Dunbar, 1995).

2. Method

2.1. Study location

This study was conducted along the coastline of the province of KwaZulu-Natal, South Africa. The coast measures approximately 560 kilometres, running from the boundary of Mozambique (26°52'S/32°54'E) to the border of the Eastern Cape Province (31°05'S/30°11'E) (Figure 2.1).

Martin and Fleming (1988) describe the coastal belt of southern Africa as having formed during the splitting off of the continents, beginning during the Jurassic and Early Cretaceous Periods. The narrow continental shelf off the KwaZulu-Natal coast is the result of shearing off from the Falkland plateau. The warm, southward flowing Agulhas current runs off this shelf, influencing the composition of the coastal waters, physically and biologically (Fleming and Hay, 1988; Schumann, 1988a). The water temperature ranges from approximately 22°C in winter to 26°C in summer (Heydorn *et al.*, 1978; Schumann, 1988a). The KwaZulu-Natal coastline has a semi-diurnal tidal cycle, ranging from 1m at neap to 2m at spring tide, while experiencing vastly changeable surf conditions and large swells (South African Navy Hydrographer).

The climate of KwaZulu-Natal's coastal belt is humid and subtropical (Schumann, 1988b), with most of the province's rain falling during the summer months, from November to March (Hunter, 1988). The surface salinity of the Agulhas current ranges from 35,2 to 35,4 $^{0}/_{00}$, and averages 35,3$^{0}/_{00}$, although inshore salinity is affected by river run-off, with this decreasing after the summer rains (Pearce, 1973; Van Der Elst and Fennessy, 1990). Inshore turbidity is also heightened during the summer, as the rains transport silt from the rivers into estuaries and the inshore zone (Martin, 1987). Heydorn *et al.* (1978) propose that coastal low pressure systems cause a current reversal, during which the Agulhas current switches to a northerly flow and then reverts to its usual course.

However, Schumann (1988b) suggests that wind force and potential shelf waves may cause this phenomenon. Such changes in shelf water movements are believed to be a major factor in determining faunal movements in local waters (Heydorn *et al.,* 1978).

The ichthyofauna of KwaZulu-Natal mainly comprises tropical Indo-Pacific species, occurring seasonally, with tropical species more evident in summer, while winter species are both endemic and migratory (Van Der Elst, 1988). Winter migrants from the Cape head north to spawn in sub 21°C waters, bringing with them predatory sharks, dolphins and game fish (Van Der Elst, 1988). This initiates the most popular event on the local fishing calendar, colloquially termed the annual “sardine run”.

During the 1950s, a series of shark attacks along the KwaZulu-Natal coastline resulted in the installation of anti-shark netting at Durban and at selected beaches along the coast (Davies, 1964; Davis, Cliff and Dudley, 1989). The gillnets used in the fishery of sharks protect bathers by decreasing the number of human-shark interactions (Dudley and Cliff, 1993), which stems from the diminished prevalence of larger sharks off popular bathing areas (Van Der Elst, 1979). The 1960s and 1970s witnessed a sharp escalation in the number of netted areas (Cliff, Dudley and Davis, 1988) and a dramatic decline in the number of large sharks off the coast. Nets are currently installed at 40 selected beaches along the 326km coastline between Richards Bay and Mzamba (Figure 2.1).

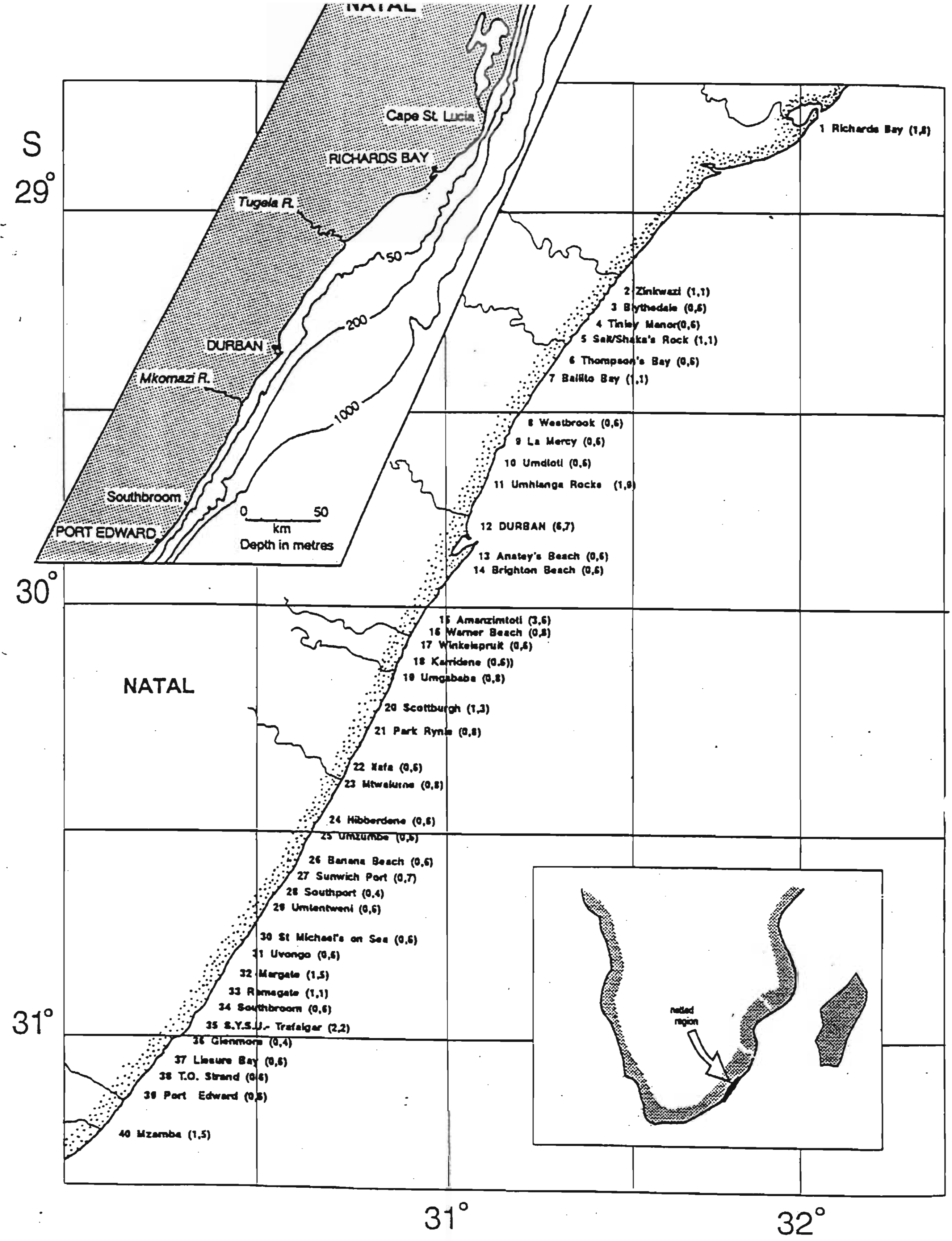


Figure 2.1: The KwaZulu-Natal coastline, indicating netted beaches and in parentheses, the length of nets in km. Beaches are numbered from north to south.

Dudley and Cliff (1993) note that the current number of large sharks captured annually ranges from 1200-1400 animals. However, in addition to the capture of sharks, other species of marine life are also caught in the gillnets, including batoids, sea turtles, teleosts and dolphins (Cockcroft, 1990a; Dudley and Cliff, 1993). Cockcroft (1990a) notes that the following species form the majority of dolphin catches in the shark nets, namely the common dolphin *Delphinus delphis*, at 46% of all annual cetacean captures, the bottlenose dolphin *Tursiops truncatus*, at 42% and finally, the humpback dolphin *Sousa chinensis*, at 10%. While the effect of the net captures on pelagic, migrant common dolphins is not considered to be significant (Cockcroft, 1990a) , this is not true concerning the bottlenose and humpback species. Populations of these two species inhabit the inshore waters of KwaZulu-Natal all year round and are relatively low (Cockcroft, Ross and Peddemors, 1990). This, in addition to their significant isolation may cause population depletion and subsequent unsustainable losses (Cockcroft, 1990b; Dudley and Cliff, 1993; Durham, 1990; Peddemors, 1993). The ecological ramifications of netting are a source of concern and controversy (Peddemors, 1995).

Additionally, several specimens were obtained from animals that stranded along the beaches of KwaZulu-Natal during the course of this study (Table 2.1). These inevitably represented offshore cetacean species not normally accessible for sampling.

2.2. Study animals

2.2.1. Odontocetes

Several species of the order Cetacea, more specifically from the suborder Odontoceti (toothed whales), were used in this study. The odontocete information is presented in Table 2.1. The three major species on which the study (especially the CT and MRI component) is based are the bottlenose dolphin *Tursiops truncatus*, the common dolphin *Delphinus delphis* and the Indo-pacific humpback dolphin *Sousa chinensis* (Table 2.1). While it has been mentioned that these three species comprise the greatest number of dolphin catches in the shark nets along the KwaZulu-Natal coast, they also have a significantly divergent range of social structure and dietary composition, which makes them suitable for testing the hypotheses in question (Tschudin, 1995; Tschudin, Daji, Henzi, Peddemors and Royston, 1996).

Other cetacean indicator species for which actual brain volume data were obtained include the dwarf sperm whale *Kogia simus*, Fraser's dolphin *Lagenodelphis hosei*, Risso's dolphin *Grampus griseus*, the spotted dolphin *Stenella attenuata* and the striped dolphin *Stenella coeruleoalba* (Table 2.1).

2.2.2. Humans

To enable a comparison of this study's findings to previously documented data for primates and humans (Stephan, Frahm and Baron, 1981) used in Dunbar's initial primate neocortex volume analysis (1992), live human subjects were scanned using MRI. The subjects were all volunteers with knowledge of the MRI procedure, who gave their informed consent to participate in the study. All of the subjects were sexually mature, with no known brain pathology and both sexes were scanned in equal numbers. There are no known documented or foreseeable harmful consequences of human subjects' participation, as MRI is a popular non-invasive, diagnostic technique commonly used throughout the world. The use of MRI with both dolphins and humans enables a standard method of comparison, as opposed to reliance on the secondary data from manual dissections as used previously (Stephan, Frahm and Baron, 1981). The human species data are thus also included in Table 2.1.

Table 2.1: Specimen information

Subject	tag #[1]	length (cm)	weight (kg)	sex[2]	age (yr.)[3]	sexual maturity[4]	method[5]	venue[6]
bot 1	ban 28	205	90	m	-	i	MRI	JRI
bot 2	bri 59	250	186	f	-	s	MRI	JRI
bot 3	bri 60	220	140	f	-	s	MRI	JRI
bot 4	gle 9	239	160	m	-	s	MRI	WH
bot 5	mg 60	206	105	f	-	i	C/M	WH
bot 6	mg 61	190	80	m	-	i	C/M	WH
bot 7	mg 69	235	152	m	-	s	FDM	J/W
bot 8	rb 69	235	160	f	-	s	FDM	J/W
bot 9	san 9	226	153	f	-	s	C/M	J/W
bot 10	to 15	234	208	m	-	s	FDB	WH
bot 11	to 16	243	190	m	-	s	FDB	WH
bot 12	umd 46	220	118	f	-	s	MRI	JRI
bot 13	ban 22	226	170	m	-	s	CT	WH
bot 14	uvo 29	200	94	m	-	i	CT	WH
bot 15	dur 244	214	114	f	-	s	MRI	JRI
bot 16	umh 140	240	186	m	-	s	MRI	JRI
com 1	ama 119	241	156	m	-	s	FDM	JRI
com 2	ans 67	240	164	m	-	s	FDM	JRI
com 3	ans 68	219	99	f	-	s	MRI	JRI
com 4	bal 25	180	74	f	-	i	MRI	JRI
com 5	bal 28	210	82	m	-	s	MRI	WH
com 6	bri 58	235	120	f	-	s	FDM	JRI
com 7	bri 62	213	90	f	-	s	MRI	JRI
com 8	dur 232	221	120	f	-	s	MRI	WH
com 9	dur 233	223	120	f	-	s	MRI	WH
com 10	dur 250	236	118	f	-	s	MRI	JRI
com 11	mbg 19	236	140	m	-	s	MRI	JRI
com 12	sun 19	190	58	f	-	i	MRI	JRI
com 13	umh 125	243	147	m	-	s	MRI	JRI
com 14	umh 128	245	142	m	-	s	MRI	JRI
com 15	umh 129	242	162	m	-	s	MRI	JRI
com 16	zin 18	239	140	m	-	s	FDM	JRI
com 17	win 11	239	140	m	-	s	CT	WH
hum 1	rb 56	206	100	m	-	i	MRI	JRI
hum 2	rb 70	208	110	m	-	s	MRI	JRI
hum 3	rb 71	227	140	m	-	s	MRI	JRI
hum 4	rb 72	225	132	m	-	s	MRI	JRI
hum 5	sco 37	202	118	f	-	i	MRI	JRI
hum 6	zin 15	220	120	m	-	s	FDM	JRI
hum 7	zin 16	254	210	m	-	s	FDM	JRI
hum 8	rb 47	220	140	f	-	s	C/M	J/W
spo 1	kzn9605	221	80	m	-	s	MRI	JRI
spo 2	swd	157	37	m	-	i	MRI	JRI
str 1	lsc s	146	32	f	-	i	MRI	JRI
fra 1	mg 72	219	110	f	-	i	MRI	JRI
ris 1	lsc s	330	-	m	-	s	MRI	JRI
dwa 1	dur s	198	106	m	-	i	MRI	JRI

Table 2.1/ ctd

subject	tag #[1]	length (cm)	weight (kg)	sex[2]	age (yr.)[3]	sexual maturity[4]	method[5]	venue[6]
hss 1	zb	-	85	m	46	s	MRI	JRI
hss 2	z5	-	66	m	24	s	MRI	JRI
hss 3	z4	-	50	f	23	s	MRI	JRI
hss 4	z	-	50	f	42	s	MRI	JRI
hss 5	zm	-	56	f	52	s	MRI	JRI
hss 6	zr	-	52	f	44	s	MRI	JRI
hss 7	z8	-	60	m	25	s	MRI	JRI
hss 8	z270	-	75	m	37	s	MRI	JRI
hss 9	zp	-	75	m	38	s	MRI	JRI
hss 10	zk	-	85	f	40	s	MRI	JRI

Note: [1]source of dolphin specimen; [2]f-female, m-male; [3]humans only; [4]s- sexually mature, i- immature; [5]CT- computed tomography, MRI- magnetic resonance imaging, FDM- frozen and defrosted scans using MRI, FDB- frozen and defrosted scans using both CT and MRI; [6]JRI- Jackpersad, Rooknoodeen Inc., WH- Wentworth Hospital, J/W- Jackpersad and Wentworth.

2.3. Apparatus and image processing

2.3.1. Computed tomography (CT)

In November 1885, Wilhelm Roentgen detected a new form of radiation and by 1896 x-rays were documented (Schenck and Leue, 1991). Just past its centenary, the discipline of radiology has progressed rapidly. Conventional radiography involves emitting a beam of x-rays that pass through the body. Differential attenuation occurs with different tissues. The ray then interacts with the screen and the image is captured, exposed and developed (Chynn and Finby, 1982). Where attenuation is high, for areas with a higher density and atomic number (bone), few photons pass through the object and the image is clear or white. Where attenuation is low (fluid), for areas with a lower density and atomic number, many photons pass through the object and the resultant image is dark or black (Chynn and Finby, 1982). A limitation of conventional radiography is that it is a two-dimensional projection of a three-dimensional object (Barnes and Lakshminarayanan, 1989). Another problem with conventional radiography is that one structural shadow can be imposed on another. Conventional tomography aims to resolve this problem, by mechanically manipulating images to allow visualisation of a slice or plane of interest. This is achieved by blurring out irrelevant areas. In contrast to conventional tomography, CT radiates only the slice or plane of interest, by special collimation, and not the entire body (Chynn and Finby, 1982). This allows for better demonstration of slice anatomy (Barnes and Lakshminarayanan, 1989).

CT scanning projects a narrow beam of x-rays onto the head, allowing the transmission of x-ray photons in the layers of interest. A series of slices is taken at successive intervals, whereafter the photon data is computed and the density information converted to a visual image of the internal structure of the brain. CT thus represents 'a marriage of conventional x-ray equipment with modern computers' (Chynn and Finby, 1982:3). CT scans in the current study were performed using the Picker PQ 2000 unit at Wentworth Hospital, Durban (Figure 2.2).

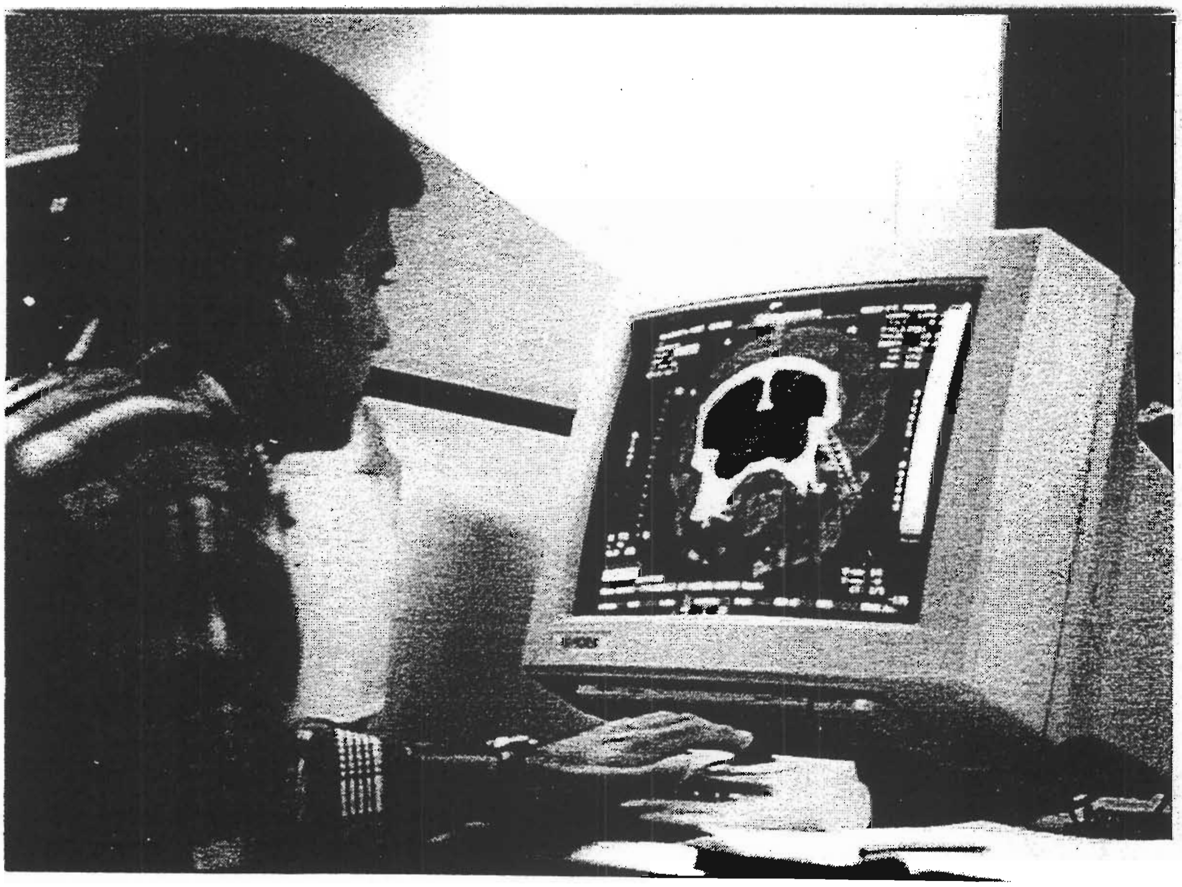


Figure 2.2: Picker PQ 2000 CT Unit.

2.3.2. Magnetic resonance imaging (MRI)

MRI is very different from CT scanning and other conventional radiographic procedures, as it does not use x-rays. Although the images produced by MRI resemble CT and ultrasound images, the process of MRI is completely different from CT. Whereas a radiographic image is based on the attenuation of x-rays by a body and requires ionising radiation, MRI is based on the interaction of atomic nuclei, located in a magnetic field, with electro-magnetic energy at a radiofrequency (Lee, Koehler and Heiken, 1989; Philips, 1984). Wehrli (1991) has proposed that the most substantial difference between MRI and CT is the extraordinarily large contrast inherent in MRI when compared to CT. Nuclear magnetisation depends on the ability of an object to produce a magnetic field at a distance. This magnetic moment of single nuclei has magnitude and direction (Dixon, 1989). Each stable element has a stable isotope with a magnetic nucleus (except for argon and cerium). Hydrogen has a proton as its nucleus and this proton has spin and is charged, which is essential for the process of MRI (Dixon, 1989).

The use of a high magnetic field permits the alignment of certain atomic nuclei, usually hydrogen protons, with the axis of spin in the direction of the field. A radiofrequency applied perpendicular to the fields alters the angle of spin (Heiken and Brown, 1991). This applied energy results in excitation of the protons, which produces a set of signals (Sigal, 1988). In other words, the return to equilibrium upon termination of the radiofrequency pulse is associated with the emission of a radiofrequency characteristic of the element and its physico-chemical environment.

The signal is dependent on three parameters, namely proton density (the number of protons in volume unit) and the T_1 (spin-lattice) and T_2 (spin-spin) relaxation times, or the time for protons to return to equilibrium after excitation (Sigal, 1988). In MRI, gradient magnetic fields in three directions allow for spatial detection of data and a two-dimensional image to be formed (Heiken and Brown, 1991). The high degree of correlation between magnetic resonance images and their corresponding anatomical sections has been recognised through comparative research (Flannigan, *et al.,* 1985)

MRI procedures were performed using two different units. These were the Siemens Magnetom Impact Scanner (1 Tesla Unit) at Advanced Imaging Services, St Aidan's Hospital, Durban (Figure 2.3) and the General Electric Sun Signa Scanner (1.5 Tesla Unit) at Wentworth Hospital, Durban (Figure 2.4). MRI on dolphins was conducted using both units, while human imaging was only conducted at Advanced Imaging Services.

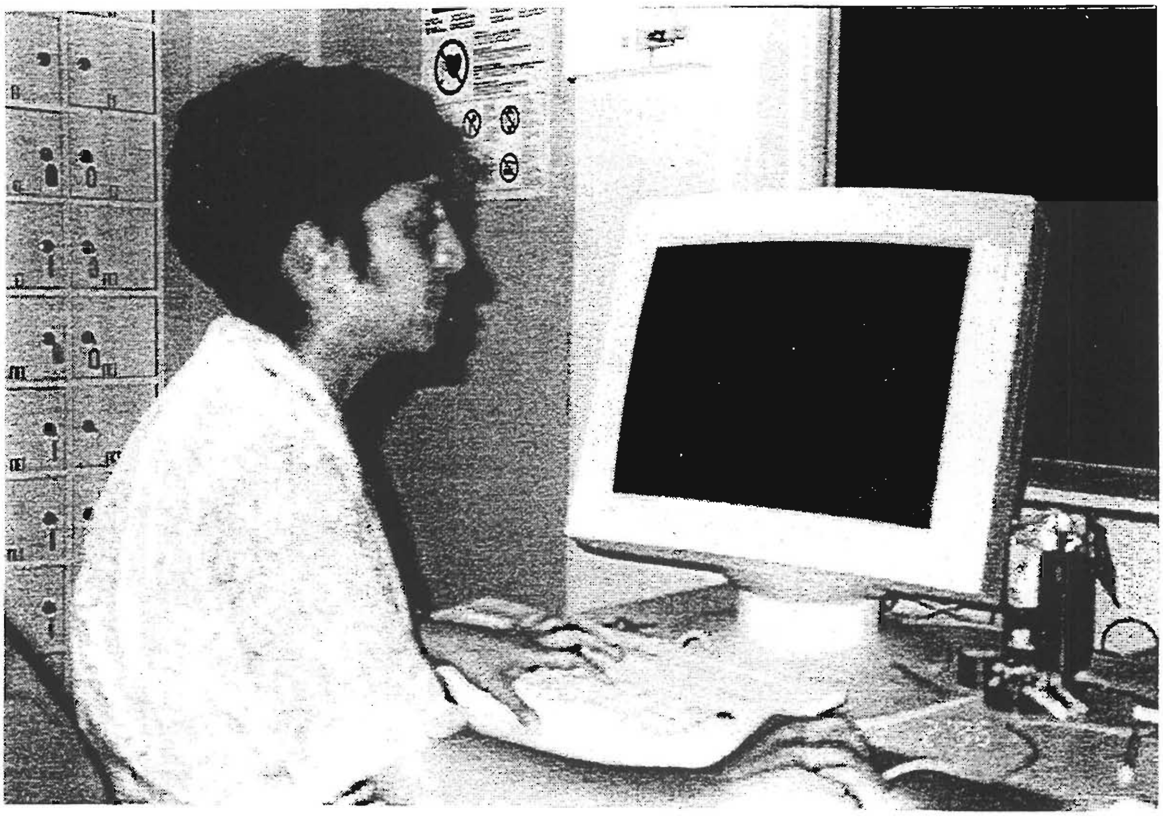


Figure 2.3: Siemens Magnetom Impact MRI Scanner.

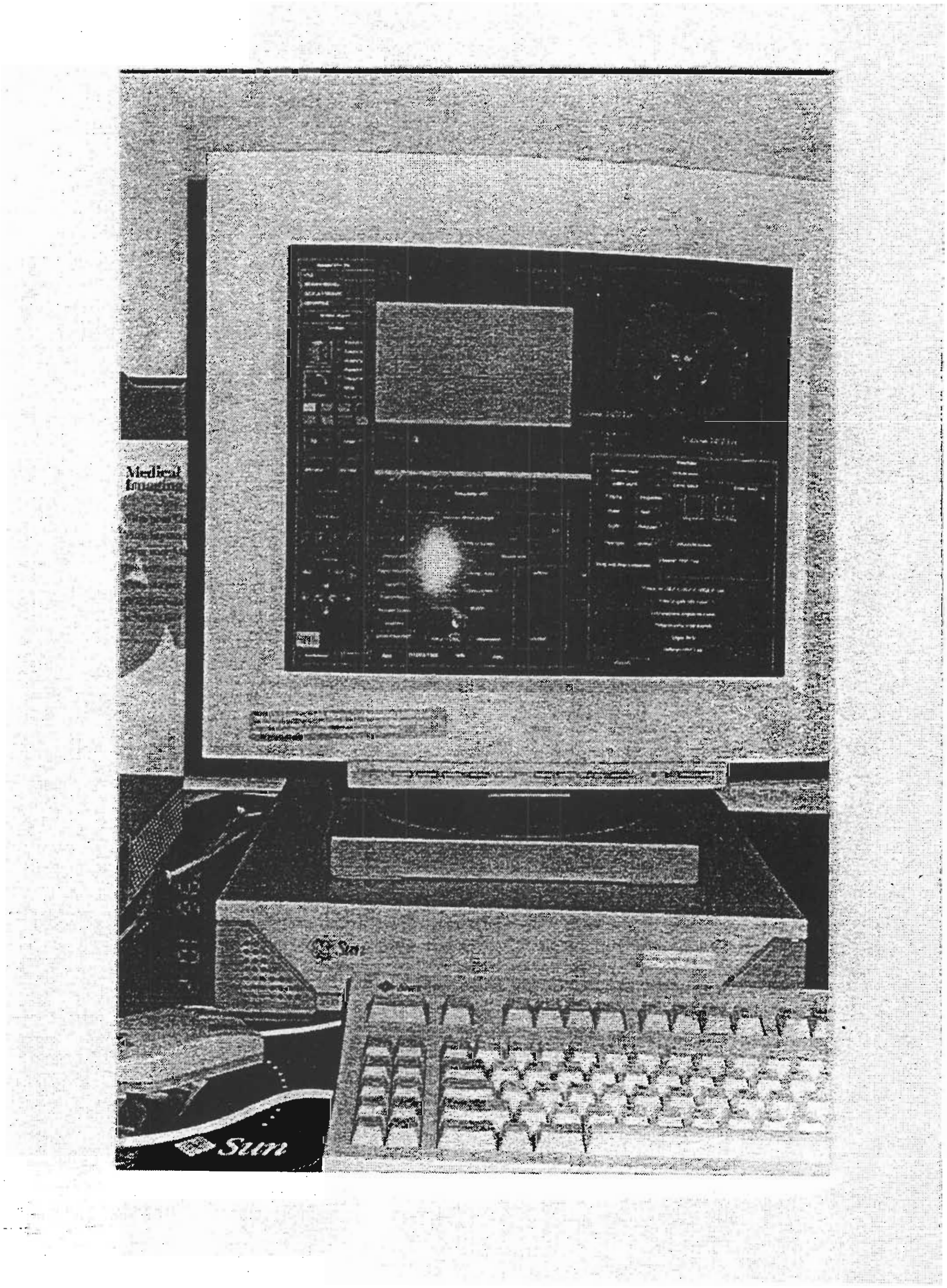


Figure 2.4: General Electric Sun Signa MRI Scanner.

2.4. Procedure

Comparative and correlative neuroanatomy provides an appropriate background for contextualised brain research. A limitation within this approach has been that the majority of tools of analysis have been provided by histology or cytoarchitectonics. The application of these techniques to comparative studies and the potential thereof have been discussed in section 1.2 of the current chapter and have been reviewed elsewhere (Tschudin, Hurribunce and Peddemors, 1998).

2.4.1. Dolphins

A standard procedure was used with respect to the investigation of all dolphin subjects in the neuroimaging component of the study. Dolphin specimens were collected from the shark nets, using the following procedure: The nets are checked for catches on an average of 17 days per month (Figure 2.5), with catches identified by trained field staff from the Natal Sharks Board (NSB) and subsequently delivered to NSB headquarters in Umhlanga Rocks, KZN, for research and dissection (Peddemors, 1995). Deceased stranded animals and subjects from Seaworld, Durban, were also delivered to NSB headquarters for dissection. Carcasses were weighed and measured prior to dissection. The head of each specimen was then removed from the top of the spinal cord (Figure 2.6). Several of the specimens available for research could not be scanned immediately. These had to be cold stored in a freezer at approximately minus 20 degrees Celsius, thawed out and subsequently scanned.

Figure 2.5: NSB crew inspecting the nets off Durban Bay.

Figure 2.6: Removal of specimen head following dissection.

As dolphin specimens are rarely acquired, it was considered necessary to establish whether such specimens could be reliably used in the analysis, or whether freezing and defrosting might have altered the volumes and ratios to a significant extent. To this end, four bottlenose, two common and two humpback dolphins were scanned fresh, then frozen, defrosted and re-scanned for examination. The effects of the use of specimens *post mortem*, in terms of tissue degeneration, freezing and defrosting are discussed below in section 2.3.3 and have also been documented by Tschudin, Hurribunce and Peddemors (1998).

From the inception of the study, all specimens were sealed in plastic bags, to prevent any possible contamination of the scanning units (Tschudin *et al.*, 1996). All specimens were identifiable by means of two plastic tag numbers, one attached through the mouth and the other to the outside seal of the bag. At the scanning units, the heads were either placed on a specially constructed foam mould or propped up with supports to stabilise them for scanning.

For CT scanning, the heads were positioned in a prone, `tail-first' position. Fresh and defrosted specimens were subjected to the scanning procedure and photographed in the coronal plane. On completion of the sequence, the areas above and below the tentorium, supra- tentorium (SV) and infra- tentorium (IV) respectively, were calculated by tracing each slice with a digitiser. These areas house the cerebral cortex and the posterior fossa respectively. A 3-D statistical measurement was applied using the Picker Voxel Q applications package to calculate the volumes of respective regions. The tentorial areas were combined to calculate overall total brain volume (TBV). Cranial volume (CV) was also calculated from these slices through the inclusion of fluid and ventricular volumes.

At AIS, the same procedure was used for MRI as for CT scanning, while at Wentworth, the specimens were positioned `head-first' when scanned. The images were viewed in all three planes, namely axial, coronal and sagittal. In addition to viewing total brain volume (TBV), it was possible to image the neocortex volume (NV), and the posterior fossa volume (PV), which comprised cerebellar volume (CBV) and brainstem volume (BV).

2.4.2. Humans

The human subjects used in the MRI component of the study were all aware of the nature of the investigation and gave their informed consent to participate. To assist in image analysis, their age, sex and weight details were recorded (Table 2.1). After the removal of any magnetisable metallic accessories which could potentially interfere with the scanner's magnetic field (such as watches and jewellery), subjects were placed in the scanning unit and prepared for the scanning procedure.

2.4.3. Image analysis

For comparative purposes, only the coronal images were analysed. The cerebral cortex, mid-brain and cerebellum were traced on both MRI machines, using a digitiser. Image reconstruction is based on the Fourier transform. According to this, the data from the received signal is the input, which leads to the output of a graph or digital representation of the frequency components of the signal (Joseph, 1991).

At Wentworth, the General Electric software package, "Advanced Windows", was used to calculate the volume of the different brain areas and the total brain volume. At AIS, the volumes were calculated according to the modified Cavalieri Principle (Solomon and Henneberg, 1992) whereby the separate slices were added before multiplying slice areas by slice thickness added to interslice gap:

$$T_V = (T-L)_A \times (St + Ig) + L_A \times St$$

where T_V = total volume, T_A = total area, L_A = area from last slice, St = slice thickness and Ig = interslice gap. In calculating the volume of the last slice, the interslice gap was excluded to improve the accuracy of the estimation.

The neocortex ratio (C_R) was calculated from the following equation (Dunbar 1992):

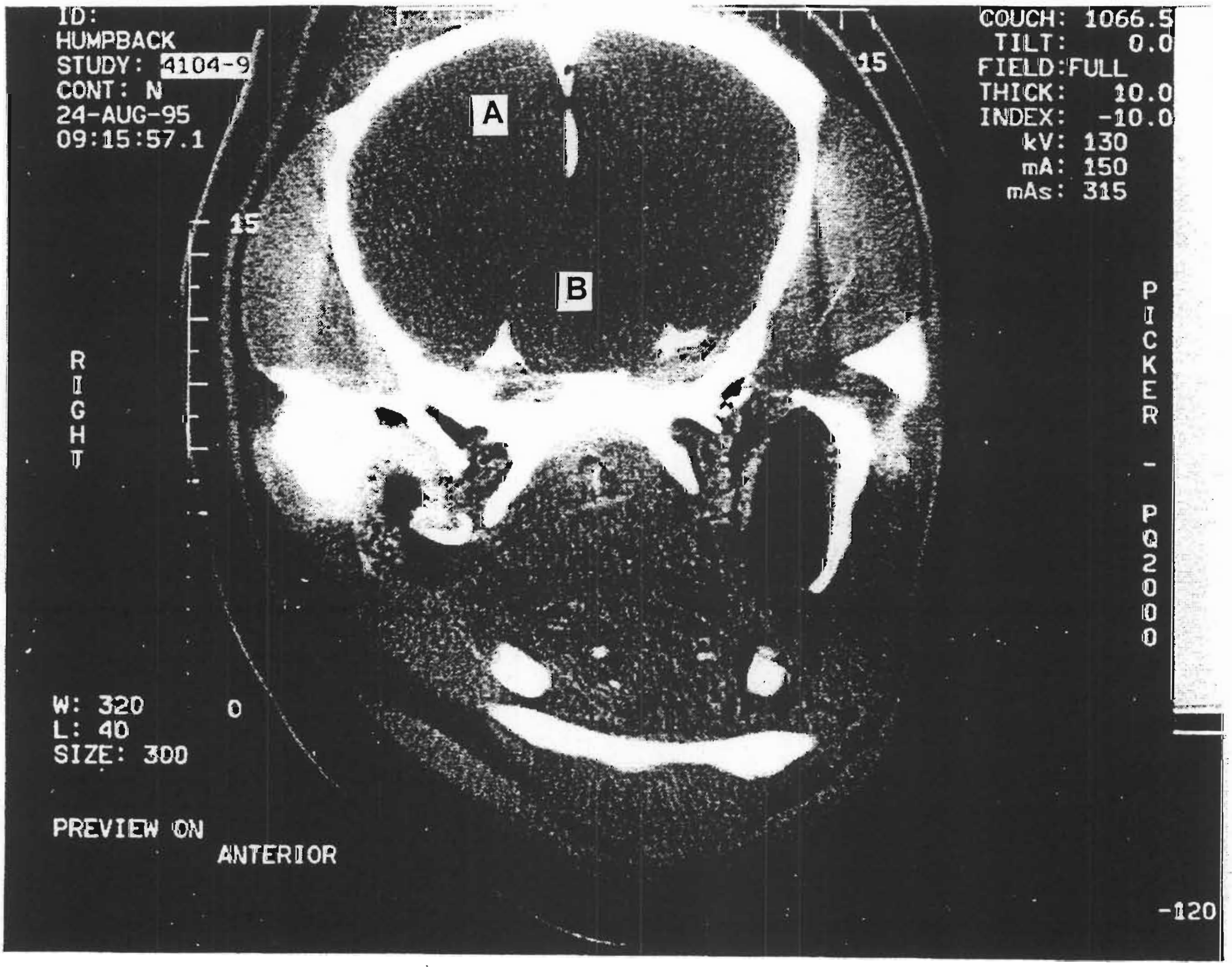
$$C_R = NV / (TBV - NV)$$

where NV = neocortex volume (cerebral cortex volume, cf Passingham, 1982); TBV = total brain volume;

2.4.4. Comparison of CT and MRI

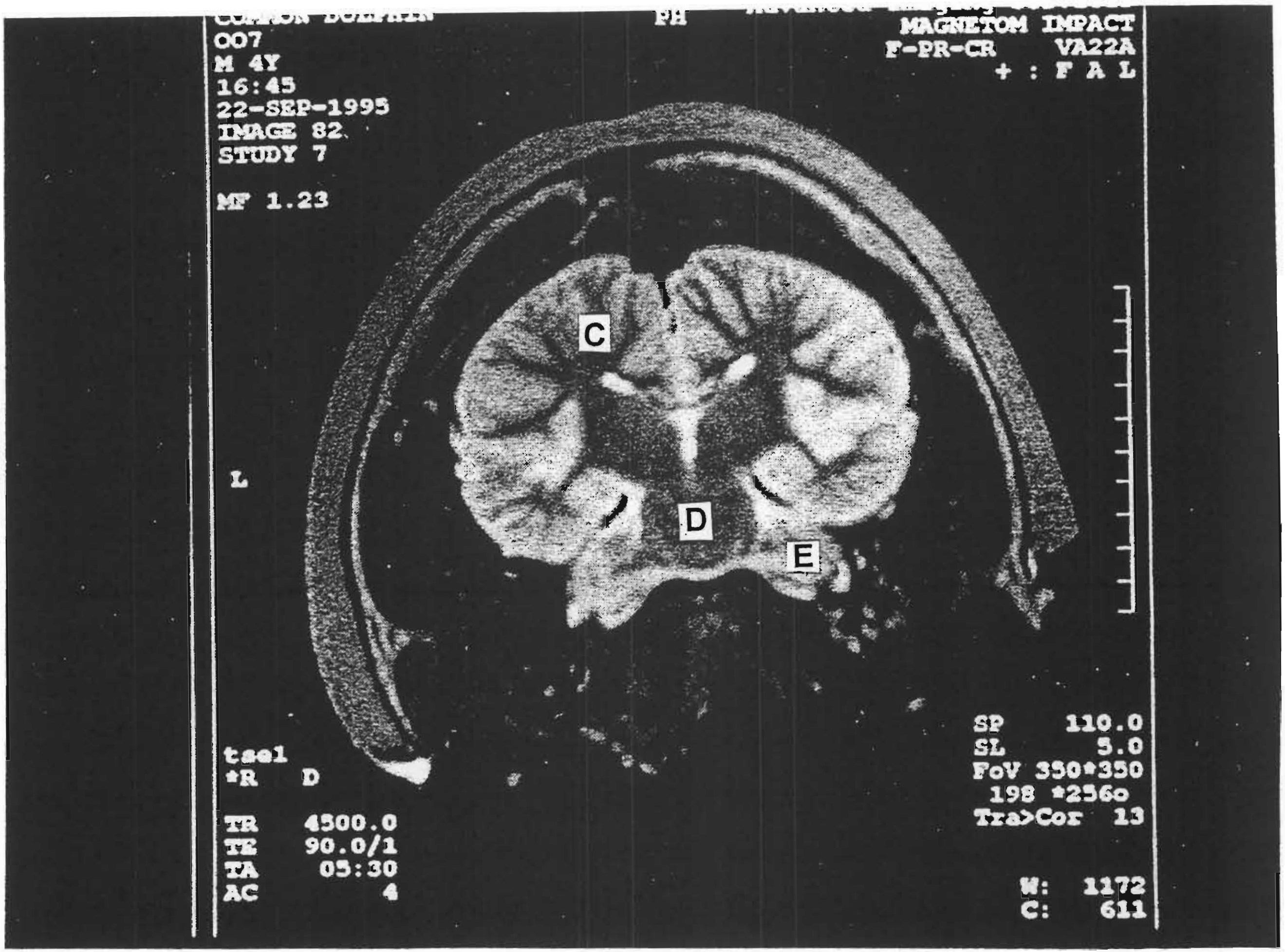
CT and MRI display different types of images of the brain. CT scans display air as black in colour, tissues as various shades of grey and bone as white. Although MRI images also depict air as black in colour and tissues as degrees of grey, this technique does not detect bone.

CT provides imaging of gross brain morphology and lacks the finer differentiation possible with MRI. Whereas the coronal plane of CT only allows discrimination between the supratentorial and infratentorial cortical volumes (Figure 2.7, marked as A and B respectively), the MRI coronal permits distinction between cerebral cortex (C) and the posterior fossa, comprised of the brainstem (D) and the cerebellum (E) (Figure 2.8). In addition to coronal imaging (the only plane possible using CT), MRI viewing in sagittal and axial planes allows for the detection of finer structures, for example the medulla (F) and corpus callosum (G) from the sagittal plane (Figure 2.9) and the differences between left and right hemispheres from the axial plane (Figure 2.10, marked as L and R respectively).



note: A- supra-tentorial volume, B- infra-tentorial volume.

Figure 2.7: Coronal image from CT.



note: C- cerebral cortex/neocortex, D- brainstem, E- cerebellum

Figure 2.8: Coronal image from MRI.

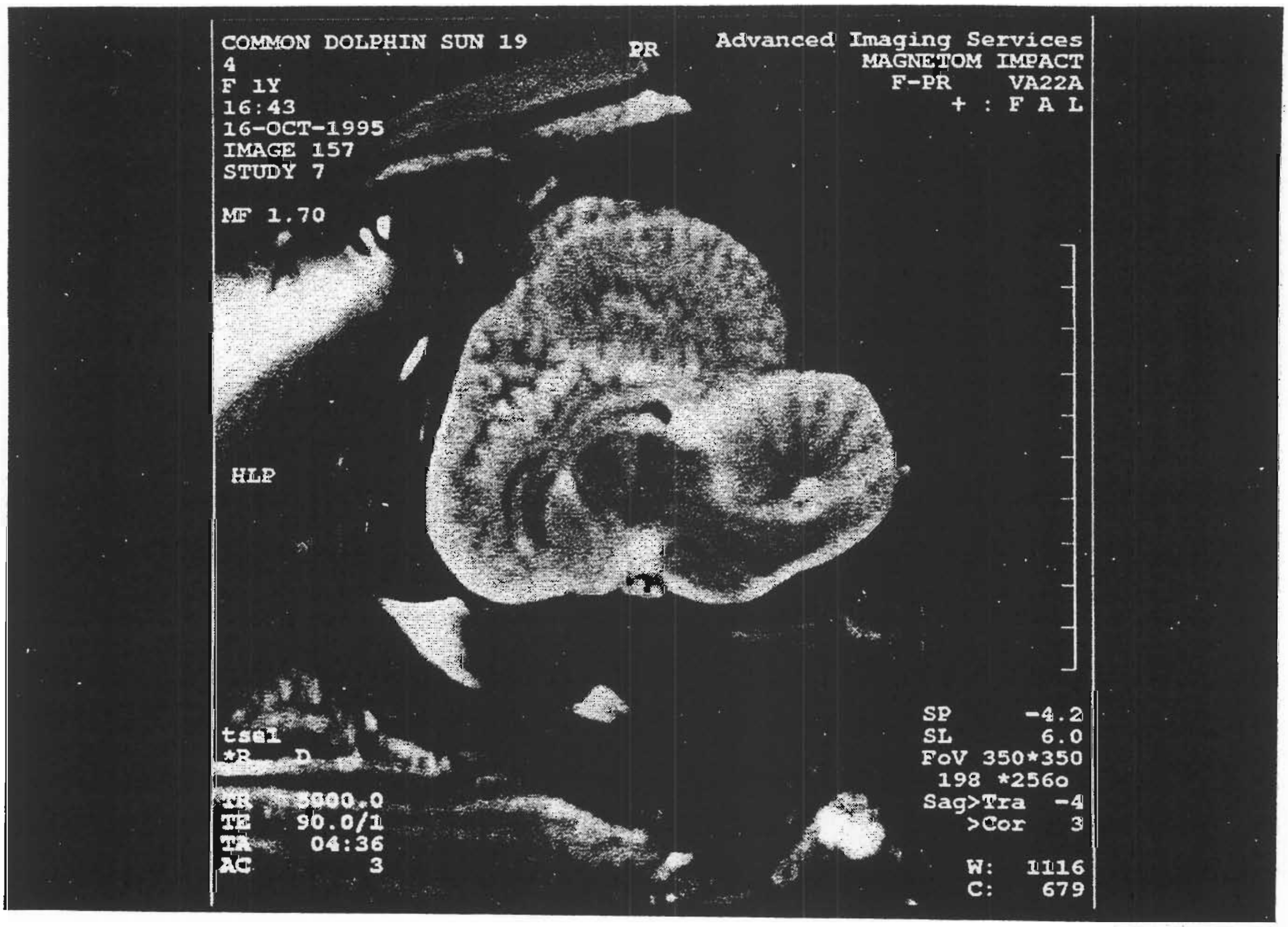


Figure 2.9: Sagittal image from MRI.

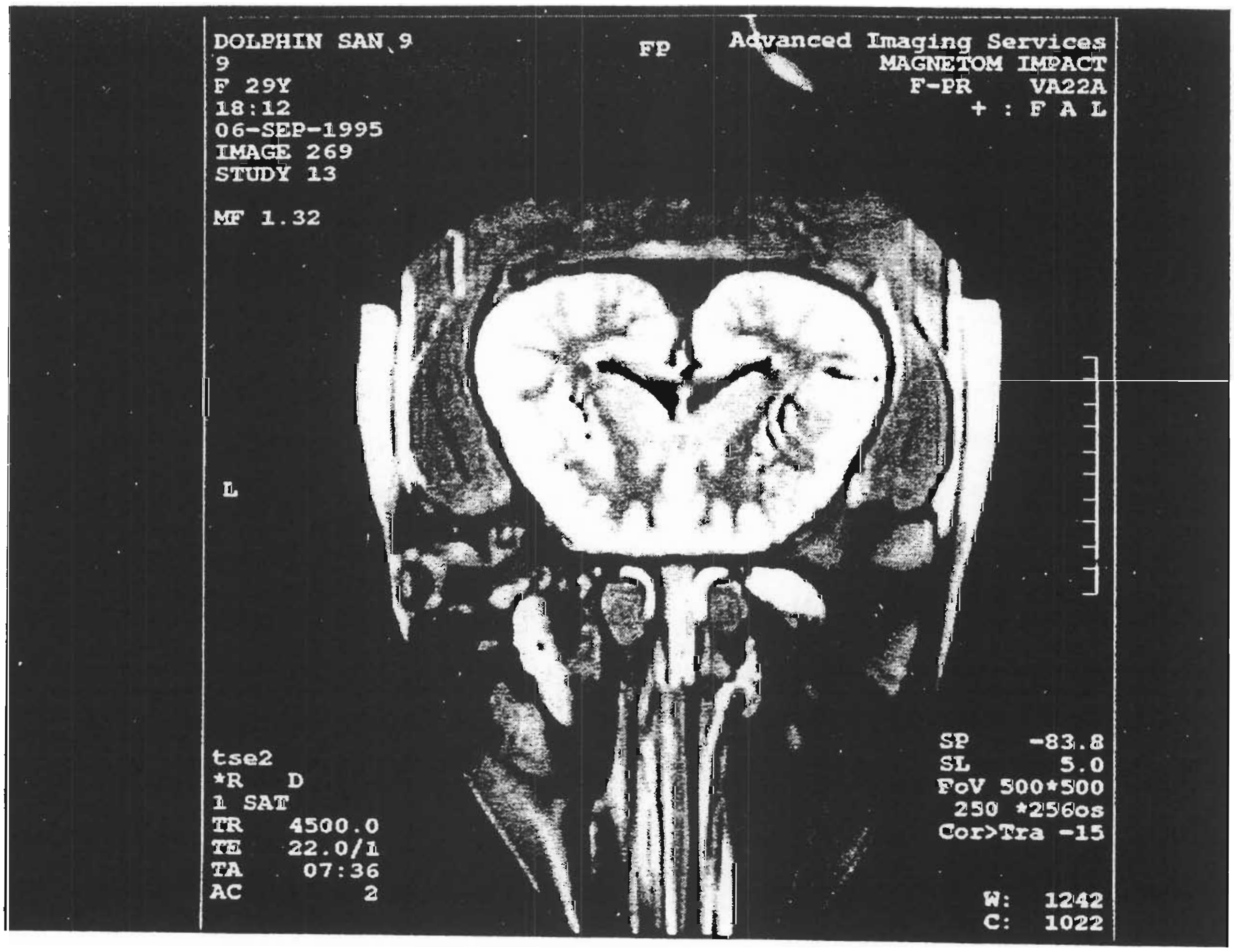


Figure 2.10: Axial image from MRI.

2.4.5. Reliability

An alpha reliability of 0.969 was obtained from the repeated trackballing of 15 MRI coronal images, which indicates that this method was sufficiently accurate for the purposes of this study.

2.4.6. Data presentation and analysis

All of the data were entered, sorted and analysed using SPSS for Windows (SPSS, Version 6.1, 1995). Results were accepted as significant at an alpha of .05.

3. Results

The results from CT, the initial method of investigation, are discussed prior to the findings from the more advanced technique of MRI. After discussing the general findings from each method for relative brain volumes and ratios, the distinctive results from each technique are presented. Following this, cross-technique relationships between CT and MRI are explored.

3.1. Neuroanatomical volumes and ratios using CT

CT was the first technique employed in the study. Neuroanatomical volumes and ratio values were obtained for individual dolphins using this method (Table 2.2). In addition to the calculation of brain and regional volumes for all CT specimens, cranial volume was also obtained for four specimens (Table 2.2). This was done to permit further analysis with inclusion of odontocete crania from the PE Museum (Chapters 3-6).

Table 2.2: Dolphin neuroanatomical volumes and ratios from CT

subject	cranial volume[1]	brain volume[1]	supratentorial volume[1]	infratentorial volume[1]	neocortex ratio
BOT 5	1166.55	1162.69	900.34	262.35	3.43
BOT 6	1298.41	1294.78	1052.51	242.27	4.34
BOT 9	-	2280.32	1838.02	442.31	4.16
BOT 10	1392.37	1374.31	1053.44	320.87	3.28
BOT 11	1514.24	1489.81	1190.23	299.58	3.97
BOT 13	-	2286.60	1766.94	319.32	3.40
BOT 14	-	2398.20	1941.10	457.10	4.25
COM 17	-	1748.00	1369.88	378.12	3.62
HUM 18	-	2122.67	1567.84	554.89	2.83

note: [1] cm^3

Although there was not a large range of difference between the maximum and minimum values for cranial volume, a different situation existed with respect to the total brain volume data, where large range, standard deviation and co-efficient of variation values were evident (Table 2.3). While the supratentorial volumes were slightly less diverse than the total brain volumes, the infratentorial volumes were much more uniform (Table 2.3). The neocortex ratio presented the smallest variance (Table 2.3).

Table 2.3: Summary statistics of dolphin neuroanatomical volumes and ratios from CT

variable	min.	max.	range	mean	Std Dev.	Std Error	variance (c.o.v.)[2]	N
cranial volume[1]	1166.55	1514.24	347.69	1342.89	147.06	73.53	21627.79 (16.105)	4
total brain volume[1]	1162.69	2398.20	1235.51	1781.65	469.74	156.58	220659.32 (123.851)	9
supra-tentorial volume	900.34	1941.10	1040.76	1408.92	384.41	128.14	147771.68 (104.883)	9
infra-tentorial volume	242.27	554.89	312.62	386.31	113.05	37.68	12780.41 (33.083)	9
neocortex ratio	2.83	4.34	1.52	3.70	.51	.17	.26 (0.070)	9

note: [1]cm^3; [2]co-efficient of variation;

As the CT analysis was almost exclusively based on bottlenose dolphins, species level data were calculated for bottlenose dolphins (Table 2.4). While there were fairly large standard deviations in brain size and regional brain volumes, the neocortex ratio appeared to be the most homogenous value (Table 2.4).

Table 2.4: Bottlenose neuroanatomical volumes and ratios from CT: means and standard deviations.

species	cranial volume[1]	total brain volume[1]	supratentorial volume[1]	infratentorial volume[1]	neocortex ratio
Bottlenose	1342.893 (147.064)	1737.741 (521.912)	1391.797 (438.433)	363.400 (108.076)	3.834 (.448)

note: [1] cm^3

The possibility of establishing the relationship between cranial volume and either total brain volume or regional volumes SV, IV or C_R for this species was investigated, in order to permit an estimation of brain volumes and neocortical data from the cranial subjects.

While CV is not significantly related to IV ($r = .649$, $N=4$, $p > .05$), it is interesting to note that it is significantly related to SV ($r=.966$, $N=4$, $p < .05$) and shares a highly significant relationship with total brain volume ($r=.999$, $N=4$, $p < .001$). This in turn implies that TBV and SV can be predicted with a fair degree of accuracy from cranial volume and that C_R can be estimated.

$$\text{TBV} = 75.207 + .935(\text{CV}) \quad (\text{adj. } r^2 = .999;\ p < .001,\ F_{1,2}=2275.370)$$

$$\text{SV} = 4.385 + .778(\text{CV}) \quad (\text{adj. } r^2 = .9;\ p < .05;\ F_{1,2}=27.984)$$

3.2. MRI findings

Although CT was the first technique to be utilised in the study, MRI was the major method of investigation. The detail and accuracy permitted by MRI were vastly superior to CT, although MRI could not detect bone and thus not cranial volume. The individual neuroanatomical and ratio data were calculated for each specimen (Table 2.5). Using boxplot analysis, animals BOT 8, COM 5 and COM 9 were subsequently identified as outliers and were therefore excluded from further analysis.

Table 2.5: Odontocete neuroanatomical volumes and ratios from MRI.

Subject	total brain volume[1]	neocortex volume[1]	posterior fossa volume[1]	brainstem volume[1]	cerebellum volume[1]	neocortex ratio
BOT 1	1419.42	1120.68	298.74	35.16	263.58	3.75
BOT 2	1553.76	1241.22	312.54	41.94	270.60	3.97
BOT 3	1492.62	1176.90	315.72	38.94	276.78	3.73
BOT 4	1340.20	1077.80	262.40	27.10	235.30	4.11
BOT 5	1075.30	868.40	206.90	33.50	173.40	4.20
BOT 6	1202.10	993.00	209.10	14.30	194.80	4.75
BOT 7	1356.66	1029.56	327.11	77.31	249.80	3.15
BOT 8	1428.97	1021.99	406.98	74.61	332.37	2.51
BOT 9	1387.60	1091.30	296.34	40.24	246.10	3.68
BOT 10	1269.40	1009.20	260.20	15.30	244.90	3.88
BOT 11	1457.10	1195.30	261.80	41.70	220.10	4.57
BOT 12	1210.66	948.96	261.65	32.85	228.80	3.60
BOT 15	1544.76	1240.80	303.96	38.28	265.68	4.08
BOT 16	1539.12	1225.50	313.62	36.30	277.32	3.91
COM 1	968.76	746.76	222.00	30.60	191.40	3.36
COM 2	1037.46	805.26	232.20	48.18	184.02	3.47
COM 3	830.22	651.90	178.32	25.02	153.30	3.67
COM 4	858.70	680.10	178.60	23.30	155.30	3.81
COM 5	916.70	784.00	132.70	16.10	116.60	5.91
COM 6	1035.30	799.80	235.50	32.40	203.10	3.40
COM 7	1005.72	805.86	199.86	29.88	169.98	4.03
COM 8	904.60	749.40	155.20	15.20	140.00	4.83
COM 9	906.70	758.10	148.60	17.40	131.20	5.10

subject	total brain volume[1]	neocortex volume[1]	posterior fossa volume[1]	brainstem volume[1]	cerebellum volume[1]	neocortex ratio
COM 10	988.86	772.44	216.42	32.28	184.14	3.57
COM 11	1004.64	794.46	210.18	32.34	177.84	3.78
COM 12	904.20	714.80	189.40	21.10	168.30	3.77
COM 13	885.36	678.60	206.76	26.16	180.60	3.28
COM 14	913.02	712.98	200.04	28.20	171.84	3.56
COM 15	1162.08	894.30	267.78	34.50	233.28	3.34
COM 16	1003.62	808.08	195.54	23.70	171.84	4.13
HUM 1	1296.40	987.80	308.60	40.30	268.30	3.20
HUM 2	1355.64	1078.56	277.08	-	-	3.89
HUM 3	1326.24	1037.40	288.84	34.26	254.58	3.59
HUM 4	1386.36	1111.62	274.74	35.70	239.04	4.05
HUM 5	1230.40	949.00	281.00	38.40	243.00	3.38
HUM 6	1326.60	1027.44	299.16	45.60	253.56	3.43
HUM 7	1468.32	1142.76	325.56	42.96	282.6	3.51
HUM 7	1318.03	1035.71	282.32	32.83	249.5	3.67
SPO 1	1005.20	784.20	221.00	42.10	178.90	3.55
SPO 2	562.40	439.30	123.10	25.60	97.50	3.57
STR 1	665.80	525.40	140.40	43.80	96.60	3.74
FRA 1	1112.28	877.02	235.26	40.68	194.58	3.73
RIS 1	1572.54	1245.66	326.88	36.78	290.10	3.81
DWA 1	463.80	381.30	82.50	24.10	58.40	4.62

note: [1] cm^3

As expected, the largest degree of variance was evident with respect to brain volume, followed by neocortical volume, cerebellar volume and finally brainstem volume (Table 2.6). Once again, the minimal degree of variance using the neocortex ratio is noteworthy, considering that the sample size is almost five times larger than the CT sample (refer to Table 2.2, section 3.1).

Table 2.6: Summary statistics of odontocete neuroanatomical volumes and ratios from MRI.

variable	min.	max.	range	mean	std dev.	S.E.	variance (c.o.v.[2])	N
brainstem volume[1]	14.30	77.31	63.01	34.12	12.85	1.96	165.06 (4.838)	43
cerebellum volume[1]	58.40	332.37	273.97	207.65	59.68	9.10	3561.93 (17.154)	43
posterior fossa volume[1]	82.50	406.98	324.48	242.56	66.93	10.09	4479.33 (18.467)	44
neocortex volume[1]	381.30	1245.66	864.36	909.56	215.50	32.49	46440.4 (51.058)	44
total brain volume[1]	463.8	1572.54	1108.74	1152.13	275.30	41.50	75787.49 (65.780)	44
neocortex ratio	2.51	5.91	3.40	3.83	.57	.09	.33 (.086)	44

note: [1]cm3; [2]co-efficient of variation

The three major species of interest in the study were also those for which the greatest number of specimens were sampled. The bottlenose dolphins appear to have the greatest variation in terms of brain volume, neocortex volume and posterior fossa volume, or the combination of brainstem and cerebellar volumes (Table 2.7). Regarding variation in total brain volume and posterior fossa volume, they are followed by common dolphins and finally humpback dolphins. Where neocortical variation is concerned, humpback dolphins display greater diversity than common dolphins. It is intriguing that common dolphins appear to have a substantially higher variance in the neocortex ratio than other species, although bottlenose dolphins display the most variance for neuroanatomical data. Furthermore, although bottlenose dolphins have the highest volume of neocortex, common dolphins have the highest neocortex ratios, followed by bottlenose and humpback dolphins respectively.

Table 2.7: Species neuroanatomical volumes and ratios from MRI: means and standard deviations.

species	total brain volume[1]	neocortex volume[1]	posterior fossa volume[1]	brainstem volume[1]	cerebellum volume[1]	neocortex ratio
Bottlenose	1376.976 (144.833)	1088.615 (116.648)	288.361 (50.962)	39.109 (17.881)	249.252 (38.861)	3.834 (.448)
Common	957.871 (83.710)	759.803 (61.775)	198.069 (34.615)	27.272 (8.271)	170.796 (28.142)	3.938 (.736)
Humpback	1338.499 (69.289)	1046.286 (63.300)	292.163 (17.720)	38.578 (4.682)	255.796 (15.086)	3.590 (.277)

note: [1]cm^3

Only the three species of interest were sampled in large enough numbers to permit generalisation to the species level (for further details, refer to section 3.4 below). A series of independent samples t-tests did not reveal any significant departures from normality or homogeneity of variance between different subgroups, whether analysing male versus female (Table 2.8) or sexually mature versus immature animals (Table 2.9). Consequentially, the total number of animals from each species has been included in further analysis.

Table 2.8: Summary of t-test statistics for MRI male and female samples.

variable	species	t- value (d.f.)	2-Tailed Sig.	variance
brainstem	bottlenose	.42 (9)	n.s	equal
volume	common	-.99 (12)	n.s	equal
	humpback	-1.11 (3)	n.s	-
cerebellum	bottlenose	1.49 (9)	n.s	equal
volume	common	-.91 (12)	n.s	equal
	humpback	-.39 (3)	n.s	-
posterior fossa	bottlenose	1.22 (9)	n.s	equal
volume	common	-.98 (12)	n.s	equal
	humpback	-.48 (4)	n.s	-
neocortex	bottlenose	-.14 (12)	n.s	equal
volume	common	-.65 (12)	n.s	equal
	humpback	-.82 (4)	n.s	-
total brain	bottlenose	.61 (9)	n.s	equal
volume	common	-.91 (12)	n.s	equal
	humpback	-.09 (4)	n.s	-
neocortex ratio	bottlenose	-1.14 (12)	n.s	equal
	common	.56 (12)	n.s	equal
	humpback	-.85 (4)	n.s	-

note: n.s- not significant

Table 2.9: Summary t-test statistics of MRI data for sexually mature/immature subjects.

variable	species	t- value (d.f.)	2-Tailed Sig.	variance
brainstem	bottlenose	-1.28 (12)	n.s	equal
	common	-.92 (14)	n.s	equal
	humpback	.40 (4.82)	n.s	unequal
cerebellum	bottlenose	-2.22 (12)	<.05	equal
	common	-.47 (14)	n.s	equal
	humpback	-.01 (5)	n.s	equal
posterior fossa	bottlenose	-2.18 (12)	n.s	equal
	common	-.60 (14)	n.s	equal
	humpback	.23 (6)	n.s	equal
neocortex volume	bottlenose	-1.69 (12)	n.s	equal
	common	-1.60 (14)	n.s	equal
	humpback	-2.86 (6)	<.05	equal
total brain volume	bottlenose	-0.91 (12)	n.s	equal
	common	-1.43 (14)	n.s	equal
	humpback	-2.20(6)	n.s	equal
neocortex ratio	bottlenose	1.41 (12)	n.s	equal
	common	-.29 (14)	n.s	equal
	humpback	-2.21 (6)	n.s	equal

As the other particular delphinid and more general odontocete specimens in the study do not exceed two animals per species, they are merely included in the analysis as indicator points, potentially representative of these other species.

Due to the importance of estimating neocortex ratios from brain volumes for different species, it is was essential to test for significant differences between species. Although no such differences were found to exist in terms of neocortex ratios, there are notable differences in brain volumes (Table 2.10).

Table 2.10: Kruskal-Wallis test for significant differences between the neuroanatomical volumes of the major study species.

variable	chi-squared value	d.f.	significance
Neocortex volume	26.95	2	<.001
posterior fossa volume	22.501	2	<.001
total brain volume	27.159	2	<.001

Many researchers may have access to specimens, but not to scanning facilities, hence suitable formulae were derived to assist in calculating NV from TBV. Because of the interspecific neuroanatomical differences (Table 2.10), correlations and regression equations for the relationship between TBV and NV have been calculated for each species. As might be expected, TBV is strongly correlated with NV in bottlenose dolphins ($r=.947$, $N=14$, $p<.001$), common dolphins ($r=.931$, $n=16$, $p<.001$) and humpback dolphins ($r=.968$, $n=8$, $p<.001$).

Regression statistics for the estimation of MRI neocortex volume from total brain volume in the major study species are provided below:

a) bottlenose

$NV=38.757 +.762(TBV)$ (adj.$r^2= .888$, $F_{1,12}= 103.567$, $p < .001$)

b) common

$NV= 101.937 + .687(TBV)$ $(adj.r^2=.857, F_{1,14}=90.59, p < .001)$

c) humpback

$NV= -137.931 + .885(TBV)$ $(adj. r^2=.928, F_{1,6}=90.564, p < .001)$

3.3. Effect of dolphin specimen condition using MRI

Following the scanning of fresh, frozen and defrosted dolphin brains, pictures of varying image quality were obtained according to the condition under which the specimen was scanned (Figure 2.11).There were no significant differences between the paired fresh and defrosted variables (Table 2.11). This suggests that defrosted material can be accurately used in the analysis.

Table 2.11: Effects of freezing and defrosting on neuroanatomical data and correlation coefficients of fresh and defrosted neuroanatomical data.

Variable pair	Paired t-test		Pearson's co-efficient	
(fresh and defrosted)	t- value (d.f. =9)	p (2- Tailed)	r (N=10)	p (2- Tailed)
brainstem	-.39	n.s	-.005	n.s
cerebellum	-.87	n.s	.892	<.01
posterior fossa	.82	n.s	.812	<.01
neocortex volume	-.43	n.s	.925	<.001
total brain volume	-.01	n.s	.964	<.001
neocortex ratio	.59	n.s	.400	n.s

3.4. Human neuroanatomical data using MRI

The main focus of this chapter of the study has been on establishing brain volumes and neocortex ratio values in dolphins. However, for comparison, a human MRI convenience sample was obtained (Table 2.12).

Table 2.12: Human neuroanatomical volumes and neocortex ratio from MRI.

subject	total brain volume[1]	neocortex volume[1]	posterior fossa volume[1]	neocortex ratio
HOM 1	1596.18	1418.40	177.78	7.98
HOM 2	1491.90	1300.20	191.70	6.78
HOM 3	1327.32	1139.58	187.74	6.07
HOM 4	1261.62	1083.18	178.44	6.07
HOM 5	998.34	843.24	155.10	5.44
HOM 6	1234.02	1046.64	187.38	5.59
HOM 7	1536.42	1334.82	201.60	6.62
HOM 8	1262.28	1131.18	131.10	8.63
HOM 9	1413.66	1222.50	191.16	6.40
HOM 10	1160.30	1006.20	154.14	6.53

Following the calculation of summary statistics for human brain volume data, it was evident that there is not much difference in variation between total brain volume and neocortex volume (Table 2.13). The most significant finding is the mean neocortex ratio of 6.609. Additionally, the wide range of neocortex ratio values extends from 5.44 to 8.63. It is apparent that humans have a larger standard deviation than that calculated for dolphins.

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Table 2.13: Summary statistics of human neuroanatomical data and neocortex ratios from MRI.

variable	min.	max.	range	mean	Std Dev.	Std Error	variance (c.o.v)[2]	N
total brain volume[1]	998.34	1596.18	597.84	1328.204	183.762	58.111	33768.552	10
neocortex volume[1]	843.24	1418.40	575.16	1152.594	171.379	54.195	29370.789	10
posterior fossa volume[1]	131.10	201.60	70.50	175.614	21.953	6.942	481.924	10
neocortex ratio	5.44	8.63	3.191	6.609	1.002	.317	1.004	10

note: [1]cm^3; [2]co-efficient of variation;

A series of t-tests was conducted in order to determine whether or not there were significant differences between male and female human subjects, in terms of brain volumes or the neocortex ratio. Male displayed substantially larger total brain volumes, neocortex volumes and neocortex ratios than females (Table 2.14). The only variable for which the values were similar was the posterior fossa, while the only significant difference, taking type 1 error rate into account, was evident in the neocortex volume (Table 2.14).

Table 2.14: Summary of t-test statistics of male/female human neuroanatomical data and neocortex ratios from MRI.

variable	t- value (d.f.)	2-Tailed Sig.	variance
total brain volume	-3.27 (8)	<.05	equal
neocortex volume	-3.67 (8)	<.01	equal
posterior fossa volume	-.42 (8)	n.s	equal
neocortex ratio	-2.82 (5.55)	<.05	unequal

3.5. CT-MRI relationships

As CT and MRI are both neuroimaging techniques and as CT is more accessible than MRI, the study sought to establish the relationship between the two techniques. To enable a comparison of techniques and estimation of MRI values from CT, the correlation between cranial volume, the unit of analysis exclusively available from CT, and MRI values was studied. This was believed to be important, as cranial data from CT, fossil records or skull collections can be used to estimate MRI values with reasonable accuracy. Although not significantly related to posterior fossa volume and neocortex ratio ($p > .05$), CV is significantly related to the MRI values of TBV (adj. $r^2 = .963$, $F_{1,2} = 78.876$, $p < .05$) and NV (adj. $r^2 = .899$, $F_{1,2} = 27.765$, $p < .05$). This is important for the purposes of this study, as TBV and NV are required for C_R estimation (i.e. C_R = NV/TBV). From the regression data of the linear relationships between the above variables, MRI estimates from CT have been calculated:-

$$TBV = -185.061 + 1.069(CV)$$

$$NV = -172.309 + .885(CV)$$

As cranial volume is also available from other techniques (refer to Chapter 3), the capacity to estimate brain and neocortical volumes with accuracy is essential to increasing sample size and statistical power.

4. Discussion

A review of the use of CT and MRI neuroimaging techniques indicated that this is the first attempted application of neuroimaging to the present topic of study. The neuroimaging techniques of CT and MRI were both successfully used to examine dolphin and human neuroanatomical regions. This has resulted in the first established set of data on delphinid neocortex ratios and data on revised human neocortex ratios.

The current findings support the proposal that CT can be applied to large samples and to rare or precious anthropological specimens, as it is non-destructive, efficient and easily performed (Spoor and Zonneveld, 1995). As a consequence of this non-invasiveness and efficacy, CT has become the preferred initial imaging procedure (Anderson and Berland, 1989).

MRI has been the major technique used in this chapter. The many advantages of MRI include the provision of detailed information and the possibility of longitudinal studies without any harmful consequences (Wolf *et al.*, 1992). Although MRI is an expensive technique, it is the least invasive and most humane method for animal experimentation, in addition to being the most precise technique presently available for analysis. The CT and MRI analysis of a number of subjects representing several dolphin species resulted in several original discoveries. Although notable differences exist between dolphin species for the different neuroanatomical regions, as indicated by Kruskal-Wallis tests (section 3.2), bottlenose, humpback and Risso's dolphins possess large brain volumes that fall within the human range. MRI calculations also showed that these three species exhibited large neocortex volumes.

The above findings of relatively large brains and neocortices in dolphins might provide a new standard of comparison with simian primates. The brain appears to be the only organ better developed in simian primates than in other land mammals, as other simian organs are not significantly different in their relative size compared to other terrestrial mammals (Passingham, 1982; Stahl, 1965).

However, it is evident that absolute brain size (whether total brain size or total neocortex size) is biased towards certain animals. Therefore possession of large or small brains might not be of such great importance. Even measures that relate brain size to body size or that adopt allometric scaling for their analysis are fraught with difficulties. For example, the EQ cannot detect subtle or specific changes, such as the relative expansion of the neocortex. When this is taken into account, it is clear that the significance of general brain expansion has been exaggerated. For reasons such as these and following the fact that gross brain size reveals nothing about the finer differentiation of brain regions, this study elected to use an alternative measure of relative importance, the neocortex ratio.

Bearing in mind the prominence of the neocortex and its evolution, the neocortex ratio was chosen as the best relative index to use for comparison, as it has been documented for different mammals. Several original findings for dolphin neocortex from this study must be related to other mammalian data.

Comparison of the neuroanatomical findings and ratio values of the major study species, namely bottlenose, common and humpback dolphins highlighted several factors: Whereas the bottlenose possessed the largest brain volume, followed by the humpback and finally the common dolphin, the pattern differed for neocortex volume, where the bottlenose dolphin was followed by the common dolphin and finally the humpback dolphin. However, perhaps the most substantially different pattern was evident with respect to the neocortex ratio, where common dolphins superseded bottlenose dolphins and humpback dolphins respectively. This provides support for the suggestion that absolute volumes are not always indicative of relative importance and may distort findings.

A comprehensive series of t-tests (section 3.2) demonstrated that no significant differences in neuroanatomical regions or brain size were apparent based on sex or sexual maturity within each dolphin species. In addition, a striking result relates to the condition of the specimen being scanned. A series of paired t-tests revealed that defrosted brain material did not differ materially using MRI and as a consequence of this, such material could be included in the analysis (section 3.3). The findings addressed in this paragraph were crucial, as they permitted the use of a larger sample size through the inclusion and combination of fresh and defrosted material from male and female, mature and immature animals.

The greatest progression in the mammalian CNS is evident in the cortical formations of the telencephalon. Where sensory and functional systems have changed anatomically, they have transformed cortical formations with specialised functions (Kesarev, 1971).

Passingham (1982) has described the “extraordinary development” of the neocortex and cerebellum as best characterising their specialisation. Eccles (1973) recognises that the neocortex and cerebellum are closely related, with the neocortex receiving fibres from the cerebellum via the thalamus and returning fibres to the cerebellum via the pons. However, the neocortex, as the most phylogenetically recent cortex, is associated with complex cerebral activity, such as integrative and analytical functions. These higher mental functions are historically believed to be present only in humans (Kesarev, 1971).

The proportion of neocortex to total brain size in primates increases as brain size increases. The size of the human neocortex is as expected for a primate of our size, while the size of the association cortex in humans is as expected given the amount of neocortex. It follows that the design of the human brain is in keeping with the pattern of simian primates and, more specifically, the great apes.

From the mean values obtained at the species level, it is apparent that dolphins have large neocortex ratios when compared with other mammalian orders. The dolphin ranges were from 2.83 to 4.34 with CT and from 2.51 to 5.91 using MRI. Although there may be a fair degree of variance in brain size and neocortical size, the scores for the neocortex ratio are homogenous across species.

Out of the total MRI sample, only three specimens scored neocortex ratios lower than the average for the human's closest relative, the chimpanzee (mean = 3.22). Bearing in mind that one of these animals was an outlier and considered as an extreme value, the comparative significance of dolphin neocortex ratios should not be underestimated.

Previous research on the C_R (Dunbar, 1992, 1995) has supported the notion that human neocortical variance is predictable in terms of the pattern expected for higher primates, but not for mammals in general, who differ in brain size-neocortical relationships (Passingham, 1982). The predictability of human brain structure, given its size, is apparent in terms of the number and density of nerve cells present in the neocortex (Jerison, 1973). The findings of the current study support the assertion that the sizes of dolphin brain structures are more predictable than for those of humans, as dolphins display lower variance than humans.

It has been suggested that mammalian brains may share the same basic building blocks, as they display a comparable number of cells in similar cortical bands (Passingham, 1982). This makes the comparison of the neocortex ratio between dolphins and primates more relevant, as they share a common mammalian heritage (Chapter 1).

That the dolphin possesses the greatest area of neocortex for species tested to date (including humans), might lead one to argue that it is "the summit of creation, the highest achievement of nature in the sense of progressive development of the central nervous system" (Kesarev, 1971:53). However, this would be a misconception, as solely quantitative considerations do not suffice for assessments of the level of brain organisation or complexity.

The brain organisation of the dolphin has been defined as paradoxical (Deacon, 1990), on account of its superiority to humans in neocortex, yet inferior finer structural organisation to humans (Glezer, Jacobs and Morgane, 1988; Morgane, Jacobs and Galaburda, 1986a, 1986b). The low amount of paleocortex in dolphins may be due to more than mere telencephalic organisation, as in dolphins the olfactory analyser, located in the paleocortex, may be totally absent. As the cortical structures become more differentiated, the neocortical structures become more complex and specialised, while increasing in thickness. Although dolphins have the most convoluted brains and the largest relative brain size, they display the same cortical thickness as found in dogs, whereas humans have significantly larger thickness in both motor and limbic areas (Kesarev, 1971).

For evolutionary neuroanatomical analysis, a reciprocal relationship has to be demonstrated between the structural principles of cerebral organisation and the variation in the functional systems of the organism. Briefly, as described above (in Chapter 1, section 1.1), the development and formation of the standard mammalian neocortex occurred in a terrestrial environment, significantly different from water. The complete secondary return of cetaceans to water is a feature unique amongst mammals. This, coupled with their genetic relatedness to all terrestrial mammals, supports the suggestion that they are highly significant in evolutionary terms.

The comparative positioning of the dolphins between humans and other primates in this study may be notable. However, this pattern is not unique and was described earlier (section 1.1). Other examples follow: the odontocetes were placed between higher primates and humans in the study of Hofman (1982a), who considered them as unique in terms of encephalisation. Data on cetacean EQ (Jerison, 1973; Wood and Evans, 1980; Ridgway and Brownson, 1984) concur that the EQ of small odontocetes rank higher than other mammals, including all primates, with the exception of humans, who outrank all other species (Ridgway, 1986a). Although odontocetes have less body surface area than land mammals (Ridgway, 1972), they still rank higher when brain size is scaled to body surface area (Ridgway, 1986a). In addition, Worthy and Hickie (1986) found that odontocetes have similar relative brain sizes to primates, while the mysticetes and sperm whale had EQs significantly less than any other group. Most recently, from her comparative EQ study, Marino (1997) reported that four out of the five most encephalised species were dolphins. The results of this study, using the most accurate MRI technology, therefore highlight the position of dolphin C_Rs in comparison with those of primates.

In returning to the findings of large dolphin neocortex ratios relative to primates, it is necessary to mention the MRI findings for the human neocortex ratio. Dunbar (1992) documented the average human ratio as 4.1. This is substantially lower than the values obtained in this study, which ranged from 5.44 to 8.63, although several human values were regarded as outliers (section 3.4). Nevertheless, the mean neocortex ratio for humans, using MRI, appears to be 6.609. Although the values recorded for humans in this study have been recorded using highly precise imaging, which is almost perfectly correlated with the anatomical material (section 3.4), the reader should be aware of several cautionary notes. The sample for humans was a convenience sample and therefore not randomly selected. Within the human sample, all of the subjects were uniformly selected as sexually mature. However, there were significant differences between males and females in relation to total brain volume, neocortical volume and the neocortex ratio (section 3.4). This may be of potential interest, as it presents a contrast with dolphins, where no significant sex differences in the neocortex ratio.

It is possible that the data used by Dunbar (1992) from Stephan *et al.* (1981) for humans underestimated neuroanatomical volumes as a result of shrinkage endured during the preservation process. Perhaps findings such as these indicate the need for more accurate measurement or greater sample sizes. As the human sample in the current study only consisted of 10 subjects, further investigation will be required before either accepting the human neocortex ratio as averaging at 4.1 or 6.6, or somewhere in-betwixt or between. Until this can be achieved, the subsequent analysis in this study adheres to the documented literature (Dunbar, 1992, 1995), while remaining aware of the potential limitations of established values.

If the human neocortex ratio is accepted at 4.1, then the common dolphin, at 3.938, averages out as a tantalisingly close neighbour. Considering that this component of the study has only examined a handful of species, with substantial data for only three of these species, a legitimate call can be made for an extension of this work to other delphinid species, such as the killer whale. With verification of the findings for a larger number of species, it may be possible to speak of a special adaptation and fundamental reorganisation, or grade shift (Martin, 1980; Martin and Harvey, 1985) in the neocortex of dolphins. An extension of the work thus becomes vital and is possible following further analysis from CT, MRI and CT-MRI procedures used in this study.

Using CT (section 3.1), it was found that the total volume of the brain could be established with highly significant accuracy using the volume of the cranium ($p < .001$). The volume of the cerebral cortex could also be accurately estimated using cranial volume ($p < .05$). Of greater importance is the capacity to estimate the equivalent MRI total brain volume and neocortex volume using cranial volume, from CT, $p < .05$ (section 3.5). This is supported by the finding that neocortex volume for each species can be precisely derived from total brain volume ($p < .001$).

By definition, the calculation of the neocortex ratio requires the volume of the brain and of the neocortex (Dunbar, 1992). If one has access to the total brain volume and the neocortex volume, then it is possible to calculate or estimate the neocortex ratio. As mentioned previously, dolphins are rarely acquired for science. Consequentially, their physical brain material is hard to access, although it is relatively easy to gain access to their crania. Especially after regarding the high C_R in dolphins, the ability to estimate neuroanatomical data from skull collections thus becomes essential to any extension of the work to a wider range of dolphin species. This topic forms the basis for the following chapter.

Chapter 3. The use of cranial volume analysis and neuroimaging to estimate neuroanatomical data and relative neocortex size in odontocetes.

1. Introduction

Previous chapters have outlined the scarcity of toothed whales for research purposes. The need for the preservation of specimens acquired for scientific research assumes priority. Tschudin, Hurribunce and Peddemors (1998) note that dolphin skeletal material is sought after for taxonomic and morphometric research, which precludes damaging skulls to obtain access to the brain. In the past, this situation has minimised the possibility for actual brain research. Prior to the investigation documented in chapter 2, which accessed a relatively large dolphin sample through the use of non-invasive technology, it is understandable why other investigators experienced difficulties accessing study animals.

However, in the light of the scarcity of cetacean subjects, it would be convenient to be able to access regression data, allowing researchers to calculate neuroanatomical features and relative neocortical volume. Such abilities would be especially useful when dealing with rare species. Reflecting on the prominence of dolphins neocortex ratios established in Chapter 2, any study wishing to extend its scope would have to rely on cranial material. In applying the C_R equations calculated previously (Chapter 2) to cranial material, this chapter aims to estimate data on relative neocortical size in representatives of the family of delphinids and the wider suborder of odontocetes. Although measures of absolute brain size have been critiqued above, such indices may be useful when used to complement data provided for relative brain size. This especially applies to the measurement of cranial weight and volume.

The measure referred to as cranial capacity (CC) has been discussed by Martin (1990). CC is advantageous for investigations of skulls for which no information on weight is documented. CC can be measured using several different methods. These include filling the skull with sintered glass beads or alternatively establishing an artificial endocast volume via a latex mould of internal braincase contours (Martin, 1990). Alternatively, double graphic integration with the aid of x-rays may be used (Jerison, 1973). This final method relies on the superimposition of average height, width and length of cranial cavity on the braincasing's internal contours to obtain estimated cranial capacity (Martin, 1990).

Cockcroft (1989) successfully used the method of filling the cranium with sand to estimate brain volume in mature bottlenose dolphins, while Marino (1997) also successfully applied the bead filling method of cranial analysis to several odontocete species.

Cranial capacity is highly correlated with brain weight, according to Martin (1990). As the relationship between CC and brain weight is virtually isometric, CC has been used to provide an accurate indication of brain weight in primates.

It has been suggested that comparisons can be made between actual (C_A) and expected (C_E) cranial size across species, according to an index of cranial capacity (ICC), where ICC= C_A/C_E, (Martin, 1990). From an interspecific analysis of mammals, it should be noted that cetaceans, not simian primates, share the closest cranial capacity to humans- the only primates with an exceptional brain size (Martin, 1981, 1982, 1990).

This chapter aims to assess cranial capacity in odontocetes for several reasons. The first of these is to provide a means of assessing the representativeness of the neuroimaging subsample used in Chapter 2. This is necessary before engaging in any further analysis using the MRI data. Secondly, the regression relationships derived to predict the equivalent MRI total brain volume and neocortex volume from CT have been shown to be significantly accurate (Chapter 2). This suggests that estimates applied to cranial data, either from cranial analysis or neuroimaging, can be used to estimate the neocortex ratio. Skull volumes have been used to obtain primate neocortex data by Aiello and Dunbar (1993), who observed that as the neocortex ratio shares an allometric relationship with cranial capacity in primates, cranial capacity can be used to esimate the C_R.

The need for the establishment of such values for a wider range of species from the dolphin family and odontocete suborder has been described above. With estimated neocortex ratios for a broader range of species not scanned using MRI, the study can be extended to other delphinids and odontocetes. This may provide more insight into the general cortical evolution of toothed whales and allow for an appreciation of any distinctive variations particular to delphinid species.

2. Method

To verify that subjects from the sample used for neuroimaging were representative of the wider population, subjects from the wider population previously caught in the shark nets were randomly selected and their cranial volumes calculated. Equations estimating neocortex and brain volumes from the neuroimaging component of the study (Chapter 2) were also used to extend the scope of the study species. Individual values are presented in Table 3.2.

2.1. Study animals

The odontocete crania under examination were all obtained from the collection of the PE Museum. Skulls from the following species of toothed whales were subjected to cranial analysis. These include the bottlenose dolphin *Tursiops truncatus,* Burmeister's porpoise *Phocoena spinipinnis*, the common dolphin *Delphinus delphis,* the dwarf sperm whale *Kogia simus*, the dusky dolphin *Lagenorhynchus obscurus*, the false killer whale *Pseudorca crassidens*, Fraser's dolphin *Lagenodelphis hosei,* Gray's whale *Mesoplodon grayi*, the harbour porpoise *Phocoena phocoena*, the Indopacific humpback dolphin *Sousa chinensis,* the Indus river dolphin *Platanista minor*, the killer whale *Orcinus orca*, the pygmy killer whale *Feresa attenuata*, the pygmy sperm whale *Kogia breviceps*, Risso's dolphin *Grampus griseus* , the short-finned pilot whale *Globicephala macrorhynchus,* the spinner dolphin *Stenella longirostris,* the spotted dolphin *Stenella attenuata* and the striped dolphin *Stenella coeruleoalba* (Table 3.1).

Table 3.1: Study subjects

Subject	PEM#	length^1	weight^2	sex^3	sexual maturity^4
bot 17	332	233	167	m	s
bot 18	949	247	200	m	s
bot 19	1009	239	196	m	s
bot 20	1243	227	162	m	s
bot 21	1514	250	172	m	s
bot 22	1594	248	200	m	s
bot 23	1236	245	180	m	s
bot 24	168	217	150	m	s
bot 25	1573	237	177	m	s
bot 26	1007	245	186	m	s
bot 27	913	229	155	f	s
bot 28	1254	238	160	f	s
bot 29	1965	251	164	f	s
bot 30	1515	248	168	f	s
bot 31	1682	240	152	f	s
bot 32	1500	236	145	f	s
bot 33	1556	240	154	f	s
bot 34	1240	238	156	f	s
bot 35	2225	247	186	f	s
bot 36	1405	226	140	f	s
com 18	1060	228	124	m	s
com 19	1050	227	127	m	s
com 20	1391	232	127	m	s
com 21	1296	255	142	m	s
com 22	1541	241	145	m	s
com 23	1721	238	140	m	s
com 24	1917	242	148	m	s
com 25	2102	246	148	m	s
com 26	2301	241	154	m	s
com 27	1730	236	178	m	s
com 28	734	231	130	f	s
com 29	1406	226	120	f	s
com 30	1550	227	122	f	s
com 31	1617	230	133	f	s
com 32	1744	233	130	f	s
com 33	1434	239	141	f	s
com 34	1924	222	126	f	s
com 35	2093	236	122	f	s
com 36	2100	223	122	f	s
com 37	1912	231	120	f	s
hum 9	739	225	128	m	s
hum 10	742	254	221	m	s
hum 11	826	248	205	m	s
hum 12	1600	209	127	m	s
hum 13	1123	232	150	m	s
hum 14	1951	252	222	m	s
hum 15	1179	269	245	m	s
hum 16	1364	233	134	m	s
hum 17	1582	246	200	m	s
hum 18	181	279	289	m	s
hum 19	805	242	164	f	s
hum 20	1086	232	142	f	s
hum 21	1576	240	157	f	s
hum 22	1630	242	162	f	s
hum 23	1950	248	176	f	s
hum 24	1978	240	178	f	s
hum 25	2059	226	132	f	s

Table 3.1/ ctd

subject	PEM#[1]	length[2]	weight[3]	sex[4]	sexual maturity[5]
hum 26	544	233	180	f	s
hum 27	1266	233	159	f	s
hum 28	1314	240	148	f	s
spo 3	229	196	-	m	s
spo 4	264	228	-	f	s
spo 5	300	218	106	m	s
spo 6	935	235	130	m	s
spo 7	1119	244	157	m	s
spo 8	1585	222	113	f	s
spo 9	1650	220	110	m	s
spo 10	1378	224	129	f	s
spo 11	2136	228	127	f	s
spo 12	936	235	108	f	s
str 2	167	215	80	m	s
str 3	335	220	83	m	s
spi 1	1475	195	58	f	s
spi 2	1686	86	-	-	i
fra 2	959	240	140	m	s
fra 3	831	226	104	f	i
fra 4	827	226	113	f	i
fra 5	740	252	152	m	s
fra 6	1773	255	158	m	s
fra 7	395	259	161	m	s
fra 8	675	270	-	m	s
dus 1	405	-	-	-	-
dus 2	1215	-	-	-	-
ris 2	325	212	84	f	i
ris 3	697	283	204	m	s
ris 4	772	285	226	f	s
ris 5	782	294	-	m	s
ris 6	878	241	-	m	i
ris 7	1118	-	-	m	s
fal 1	485	192	80	m	i
fal 2	1283	-	-	-	pr
pyg 1	1828	-	-	f	pr
pyg 2	100	-	-	m	pr
kil 1	301	-	-	m	-
sho 1	191	450	-	f	s
sho 2	276	589	-	m	s
dwa 2	145	235	209	f	s
dwa 3	239	204	136	m	i
dwa 4	1564	239	240	m	s
dwa 5	2041	203	128	m	i
dwa 6	884	234	-	f	s
pys 1	1377	229	210	-	i
pla 1	-	-	-	m	-
har 1	-	-	-	-	-
bur 1	395377	-	-	-	-
gra 1	1024	472	-	f	-

note: [1]PE identification tag, [2]cm, [3]kg, [4]m-male, f-female; [5]s-sexually mature, i- immature, pr- presumed mature. Species abbreviations: BOT- bottlenose dolphin, COM- common dolphin, HUM- humpback dolphin, SPO- spotted dolphin, STR- striped dolphin, SPI- spinner dolphin, FRA- Fraser's dolphin, DUS- dusky dolphin, RIS- Risso's dolphin, FAL- false killer whale, PYG- pygmy killer whale, KIL- killer whale, SHO- short-finned pilot whale, DWA- dwarf sperm whale, PYS- pygmy sperm whale, PLA- Indus River dolphin, HAR- harbour porpoise, BUR- Burmeister's porpoise, GRA- Gray's beaked whale.

2.2. Procedure

The skulls were randomly selected from mature populations of the species described above. However, in certain instances where no weight or length data were available for specimens representing rare species, the fusion of the frontal-supraoccipital suture was taken as the most accurate indicator of sexual maturity (Vanwaerebeek, 1993).

Sand was collected from King's Beach and five density readings were taken prior to establishing an average density of the sand, where 100ml were equivalent to 158,7g (rounded off to 159g). For cranial analysis, each braincase was filled with the sand to obtain volumetric data, following the procedure documented by Cockcroft (1989). After all of the cranial apertures were moulded closed with plasticine, sealed with adhesive tape and the skull prepared for the analysis, a funnel was used to pour sand into the skull, through the base of the foramen magnum. The cranium was completely filled to capacity with sand. Following this, the sand was poured out into a measuring beaker, which was then weighed and the weight reading converted to a volume reading. Repeated measurements for obtained for 15 crania, with an alpha reliability of 98.6%, which indicates that this method is sufficient for dependable analysis.

Equations for estimating neocortex volume and brain volume, established using neuroimaging techniques of CT and MRI in relation to cranial volume (Chapter 2), were applied to the cranial data. This was considered useful in extending the scope of the study species. The data were entered into SPSS and an alpha of .05 was accepted as significant.

3. Results

The cranial analysis component of the study included 106 subjects (Table 3.2). Calculated data include cranial weights and volumes and estimated brain volumes, neocortex volumes and neocortex ratios (Table 3.2). The cranial volumes are diverse, as is evident with respect to the smallest value from the Indus River dolphin when compared to the largest value of the killer whale. It should be noted, however, that the regression equation failed in the case of the Indus River dolphin, as it was an outlier. Although there is a large variation in cranial weight and volume, the estimated neocortex ratios do not vary markedly from individual to individual. This is with the exception of the harbour porpoise and the river dolphin, who fall below a score of 3 for the C_R.

Table 3.2: Odontocete cranial data and estimated neuroanatomical data

subject	cranial weight[1]	cranial vol.[2]	est. brain vol.[2]	est. neocortex vol.[2]	est. C_R
bot 17	2184	1376.18	1286.08	1014.37	3.73
bot 18	2382	1500.95	1419.45	1121.07	3.76
bot 19	2017	1270.95	1173.58	924.38	3.71
bot 20	2137	1346.57	1254.42	989.04	3.73
bot 21	2016	1270.32	1172.91	923.84	3.71
bot 22	2408	1517.33	1436.96	1135.08	3.76
bot 23	2292	1444.23	1358.83	1072.57	3.75
bot 24	2326	1465.66	1381.73	1090.89	3.75
bot 25	2319	1461.25	1377.01	1087.12	3.75
bot 26	2190	1379.96	1290.12	1017.60	3.73
bot 27	2276	1434.15	1348.05	1063.95	3.74
bot 28	2338	1473.22	1389.81	1097.36	3.75
bot 29	2036	1282.92	1186.38	934.62	3.71
bot 30	1894	1193.45	1090.73	858.10	3.69
bot 31	2125	1339.00	1246.33	982.58	3.73
bot 32	2198	1385.00	1295.51	1021.92	3.74
bot 33	2049	1291.12	1195.14	941.62	3.71
bot 34	1932	1217.39	1116.33	878.57	3.70
bot 35	2334	1470.70	1387.12	1095.20	3.75
bot 36	1528	962.82	844.20	660.87	3.60
com 18	1712	1078.77	968.14	760.02	3.65
com 19	1533	965.97	847.57	663.56	3.61
com 20	1629	1026.46	912.23	715.29	3.63
com 21	1684	1061.12	949.28	744.93	3.65
com 22	1625	1023.95	909.54	713.14	3.63
com 23	1700	1071.20	960.06	753.55	3.65
com 24	1400	882.17	757.98	591.89	3.56
com 25	1490	938.88	818.60	640.39	3.59
com 26	1682	1059.86	947.93	743.85	3.64
com 27	1724	1086.33	976.22	766.49	3.65
com 28	1273	802.14	672.43	523.45	3.51
com 29	1297	817.27	688.60	536.39	3.52
com 30	1580	995.59	879.22	688.89	3.62
com 31	1391	876.50	751.91	587.04	3.56
com 32	1370	863.26	737.77	575.72	3.55
com 33	1659	1045.37	932.44	731.46	3.64
com 34	1441	908.00	785.59	613.99	3.58
com 35	1559	982.36	865.08	677.57	3.61
com 36	1286	810.33	681.19	530.46	3.52
com 37	1572	990.55	873.83	684.58	3.62
hum 9	2055	1294.90	1199.18	944.86	3.72
hum 10	2042	1286.70	1190.43	937.85	3.71
hum 11	2185	1376.81	1286.75	1014.91	3.73
hum 12	2091	1317.58	1223.43	964.26	3.72
hum 13	2237	1409.58	1321.78	1042.93	3.74
hum 14	2067	1302.46	1207.27	951.32	3.72
hum 15	1834	1155.64	1050.32	825.76	3.68
hum 16	1862	1173.28	1069.18	840.85	3.68
hum 17	2274	1432.89	1346.70	1062.87	3.74
hum 18	2297	1447.39	1362.19	1075.26	3.75
hum 19	1960	1235.04	1135.19	893.66	3.70
hum 20	1628	1025.84	911.56	714.76	3.63
hum 21	1927	1214.24	1112.96	875.88	3.69
hum 22	1933	1218.02	1117.00	879.11	3.70
hum 23	1882	1185.89	1082.65	851.63	3.69
hum 24	2107	1327.66	1234.21	972.88	3.72
hum 25	1799	1133.59	1026.74	806.90	3.67

Table 3.2/ ctd

Subject	cranial weight[1]	cranial vol.[2]	est. brain vol.[2]	est. neocortex vol.[2]	est. C_R
hum 26	1839	1158.79	1053.69	828.46	3.68
hum 27	1936	1219.91	1119.02	880.73	3.70
hum 28	1886	1188.41	1085.35	853.79	3.69
spo 3	1438	906.11	783.57	612.37	3.58
spo 4	1725	1086.96	976.90	767.03	3.65
spo 5	1483	934.47	813.89	636.62	3.59
spo 6	1524	960.30	841.50	658.71	3.60
spo 7	1567	987.40	870.47	681.88	3.62
spo 8	1430	901.07	778.18	608.06	3.57
spo 9	1436	904.85	782.23	611.29	3.58
spo 10	1423	896.66	773.47	604.28	3.57
spo 11	1631	1027.72	913.58	716.37	3.63
spo 12	1269	799.62	669.73	521.30	3.51
str 2	1246	785.13	654.24	508.90	3.50
str 3	1355	853.81	727.66	567.64	3.55
spi 1	738	465.03	312.05	235.15	3.06
spi 2	973	613.11	470.35	361.79	3.33
fra 2	1806	1138.00	1031.46	810.68	3.67
fra 3	1612	1015.75	900.78	706.13	3.63
fra 4	1474	928.80	807.82	631.77	3.59
fra 5	1889	1190.30	1087.37	855.40	3.69
fra 6	1795	1131.07	1024.05	804.75	3.67
fra 7	1909	1202.90	1100.84	866.18	3.69
fra 8	1647	1037.81	924.35	724.99	3.64
dus 1	1297	817.27	688.60	536.39	3.52
dus 2	1162	732.20	597.66	463.64	3.46
ris 2	2571	1620.04	1546.76	1222.92	3.78
ris 3	3698	2330.18	2295.21	1821.68	3.85
ris 4	3504	2207.94	2175.23	1725.69	3.84
ris 5	3850	2425.96	2408.29	1912.14	3.85
ris 6	3370	2123.50	2084.96	1653.48	3.83
ris 7	4490	2829.24	2839.39	2257.03	3.88
fal 1	3124	1968.49	1919.26	1520.92	3.82
fal 2	5406	3406.43	3456.41	2750.64	3.90
pyg 1	1390	875.87	751.24	586.50	3.56
pyg 2	1871	1178.95	1075.24	845.70	3.68
kil 1	10408	6558.29	6825.75	5446.11	3.95
sho 1	5981	3768.75	3843.73	3060.49	3.91
sho 2	4387	2764.34	2770.01	2201.52	3.87
dwa 2	1146	722.12	586.88	455.02	3.45
dwa 3	946	596.09	452.16	347.24	3.31
dwa 4	959	604.29	460.92	354.25	3.32
dwa 5	1174	739.76	605.74	470.10	3.47
dwa 6	940	592.31	448.12	344.01	3.30
pys 1	1658	1044.74	931.76	730.92	3.64
pla 1	298	187.78	15.67	-1.95	-.11
har 1	662	417.14	260.86	194.20	2.91
bur 1	867	546.31	398.95	304.67	3.23
gra 1	2666	1679.90	1610.75	1274.11	3.78

note: [1]grams, [2]cm^3. Species abbreviations follow from Table 3.1.

The summary statistics for the species of odontocetes are provided in Table 3.3. As some species are only represented by a solitary case or a pair of animals, the data should be treated with caution. The bottlenose cranial data exhibit the largest variance of the major study species, followed by the common dolphin and finally the humpback dolphin. In terms of the neocortex ratio across species, it is interesting that while the Indus River dolphin has a negligible C_R, the short-finned pilot whale and the killer whale display large values.

Table 3.3. Summary statistics of interspecific odontocete cranial volumes.

Species	Mean[1]	std dev[1]	Variance (c.o.v)[2]	N	Est. Brain Vol.[1]	Est. Neocortex Vol.[1]	Est. C_R
bottlenose d.	1354.159	133.260	17758.329 (13.114)	20	1286.08	1014.37	3.73
common d.	964.304	95.702	9158.812 (9.498)	20	968.14	760.02	3.65
humpback d.	1255.23	109.633	12019.412 (9.575)	20	1199.18	944.86	3.72
spotted d.	940.517	79.904	6384.699 (6.788)	10	783.57	612.37	3.58
striped d.	819.471	48.566	2358.677 (2.878)	2	654.24	508.90	3.50
spinner d.	539.067	104.707	10963.547 (20.338)	2	312.05	235.15	3.06
Fraser's d.	1092.087	100.82	10164.729 (9.308)	7	1031.46	810.68	3.67
dusky d.	774.732	60.151	3618.112 (4.67)	2	688.60	536.39	3.52
Risso's d.	2254.477	396.461	157181.395 (69.72)	6	1546.76	1222.92	3.78
false killer w.	2687.461	1016.772	1033825.66 (384.684)	2	1919.26	1520.92	3.82
pygmy killer w.	1027.410	214.316	45931.168 (44.706)	2	751.24	586.50	3.56
short-finned w.	3266.541	710.226	504420.728 (154.42)	2	3843.73	3060.49	3.91
killer whale	6558.286	-	-	1	6825.75	5446.11	3.95

Table 3.3/ctd.

Species	Mean[1]	std dev[1]	Variance (c.o.v)[2]	N	Est. Brain Vol.[1]	Est. Neocortex Vol.[1]	Est. C_R
dwarf sperm w.	650.914	73.446	5394.335 (8.287)	5	586.88	455.02	3.45
pygmy sperm w.	1044.739	-	-	1	931.76	730.92	3.64
Indus River d.	187.776	-	-	1	15.67	-1.95	.
Harbour p.	417.139	-	-	1	260.86	194.20	2.91
Burmeister's p.	546.314	-	-	1	398.95	304.67	3.23
Gray's beaked w.	1679.899	-	-	1	1610.75	1274.11	3.78

note: [1]cm^3, [2]co-efficient of variation, d-dolphin, p-porpoise, w-whale.

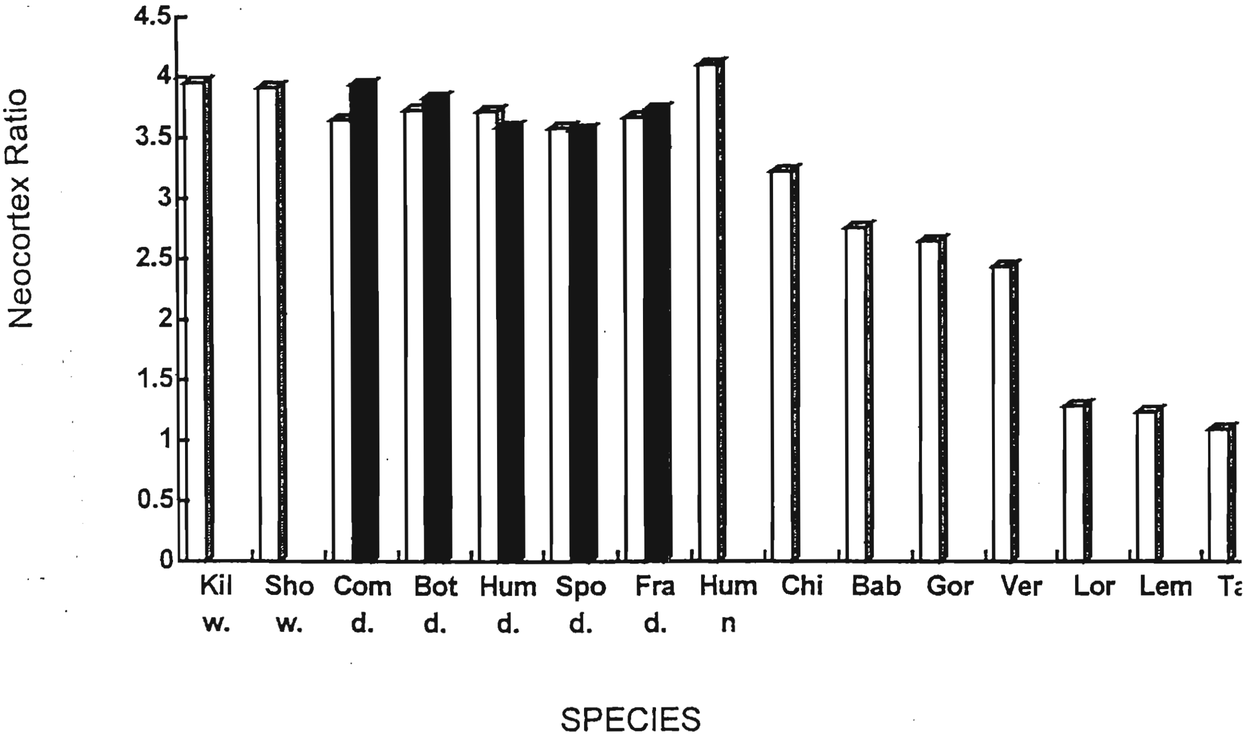
The summary statistics for the species of odontocetes that were also under neuroimaging investigation were established to permit comparison with the neuroimaging sample from Chapter 2 to assess their representativeness (Table 3.4). The dwarf sperm whale data and the striped dolphin data from MRI were excluded from further analysis, as they were not considered to be representative of the species due to the brains of these individuals not fitting the population parameters established for their respective species from cranial volume analysis.

Table 3.4: Cranial volume parameters for odontocete species also under neuroimaging investigation.

species	minimum[1]	maximum[1]	range	95% Confidence Interval- lower	95% Confidence Interval- higher	n
bottlenose	962.823	1517.328	554.505	1291.791	1416.526	20
common	802.142	1086.326	284.184	919.514	1009.094	20
humpback	1025.835	1447.385	421.55	1203.92	1306.54	20
spotted	799.622	1086.957	287.335	883.357	997.677	10
striped	785.129	853.812	68.683	383.12	1255.821	2
Fraser's	928.796	1202.899	274.103	998.844	1185.331	7
Risso's	1620.038	2829.238	1209.2	1838.417	2670.538	6
Dwarf Sperm	592.313	739.761	147.448	559.718	742.109	5

note: [1]cm^3.

Following the establishment of final MRI and estimated neocortex ratio values for different odontocete species that could be included with confidence in the analysis, these values were compared to documented primate neocortex data (Dunbar, 1992). The comparatively high delphinid neocortex ratios scores in relation to those of their primate counterparts are noteworthy (Figure 3.1).



Note: Kil w.- killer whale, sho w.- short-finned pilot whale, com d.- common dolphin, bot d.- bottlenose dolphin, hum d.- humpback dolphin, spo d.- spotted dolphin, fra d.- Fraser's dolphin, humn- human, chi- chimpanzee, bab- baboon, gor- gorilla, ver- vervet monkey, lor- loris, lem- lemur, tar- tarsier.

Figure 3.1: Barchart comparing MRI and estimated delphinid C_R values with documented primate data (Dunbar, 1992)

4. Discussion

The individual animals used in MRI as potential representatives of other species were compared to the population parameters established for these species' brains, using the randomly selected cranial analysis sample. The findings of this chapter were of substantial utility, insofar as the majority of MRI subjects were found to be representative of the broader population parameters using CVA, while a wider range of delphinid species and other species from the suborder *Odontoceti* became available for inclusion in the analysis (section 3). However, certain species scanned using MRI, namely the striped dolphin and the dwarf sperm whale subjects, were excluded from further analysis, as they did not fit the required parameters.

In spite of the large interspecific variation for obtained cranial weights and volumes, and estimated brain and neocortical volumes, it is interesting to observe that the neocortex ratios obtained were not of a diverse nature (section 3). In keeping with the trend discussed previously in chapter 2, it is consequential to recognise that the majority of species examined, although representing different species, obtained a neocortex ratio of 3.00 or above. The only exceptions to this were the Indus River dolphin and the harbour porpoise.

When studied in terms of families, it appears that the river dolphins are the least advanced in terms of the neocortex ratio, followed by the porpoises and then the sperm whales, the dwarf sperm whale and the pygmy sperm whale averaging 3.45 and 3.64 respectively. The family of beaked whales, represented by Gray's beaked whale at 3.78, may lie above the sperm whales. Finally, the family of delphinids appear to possess the largest neocortex ratios. Although there appears to be a large range from the spinner dolphin at 3.06 to the killer whale at 3.95, all of the other delphinids lie above a ratio of 3.5. Such findings are supported by the proposal that the river dolphins are thought to be more "primitive" than their fellow odontocetes, followed by the porpoises, white whales and narwhals, sperm whales, beaked whales and delphinids respectively (Dudok van Heel, 1981). The current ranking of C_R findings within the delphinids are explicable within such a classification where, amongst the delphinids, the bottlenose dolphin is regarded as being derived earlier than the common dolphin, the pilot whales or the killer whale (Dudok van Heel, 1981).

Martin (1990), in confirming the research of Bauchot and Stephan (1969), suggested that different grades of brain size exist for "basal" insectivores, "advanced" insectivores, strepsirhine and haplorhine primates. More specifically, Dunbar (1992) has found differences between strepsirhine primates and haplorhine primates in relation to the neocortex ratio, where the latter group display higher ratios than the former group. Applying the possibility that higher neocortex ratios are evident in more recently evolved species, the above findings within the odontocetes might be expected, as the delphinids are the most recently evolved cetaceans (Chapter 1). The evolution of the delphinids at some stage after the apes and before ancestral humans, might also contribute to an explanation of their neighbouring status to humans. However, it should be acknowledged that the human lineage is a much more recent evolutionary phenomenon than either the branch-offs of delphinids and apes.

If the delphinid and wider odontocete values are compared to the documented primate values, aside from the Indus river dolphin and the harbour porpoise, the only odontocete falling below the average chimpanzee value (3.22) is the spinner dolphin, at 3.06, while Burmeister's porpoise falls at 3.23. The proximity of the MRI scores for dolphin neocortex ratios to humans appeared convincing enough for further study (Figure 3.1). More compelling is the even closer proximity of the killer whale's estimated neocortex ratio (3.95) to the human value of 4.1 (Dunbar, 1992). The killer whale is regarded as the most adaptable of the delphinids and is the only odontocete to exist from the North to the South Pole. High killer whale C_Rs are interpretable in the light of their complex and varied foraging strategies and their diverse social organisation in different habitats (Leatherwood and Reeves, 1983).

This study empirically supports the hypothesis that dolphins have a high neocortex ratio. The corollary of the this hypothesis, namely that delphinid neocortex ratios would fall into the primate range, has also held up. The position of the delphinids between humans and other primates, where dolphins lie substantially closer to humans than to non-human primates, has been an unanticipated and positively encouraging finding. Perhaps this is one of the most substantial findings of the entire study.

However, it should be noted that these findings are open to several interpretations, as the human neocortex ratios in the current study are substantially larger than those previously documented by Dunbar (1992), who used the Stephan *et al.* (1981) database. Aside from the possibility that there is a large variation between the neocortex ratios of humans across different geographical locations, it is most plausible that the discrepancy arises out of methodological differences. Stephan et al. (1981) preserved his specimens in parafin, microtomed the sample and measured the area of each brain part, whereas the current study scanned freshly deceased dolphin brains and live human brains. It is possible that the preservation process used by Stephan et al. (1981) resulted in differential shrinkage of the neocortex and thus neocortex ratios that are not accurate. One would then have to scale the neocortex ratios of primates and dolphins, with the result that delphinid neocortex ratios fall into the range of the larger monkeys. However, until further investigation is undertaken into human neocortex ratios, this study presumes that the comparison holds, with the consequence that dolphins have neocortices that are slightly smaller than those of humans.

Although it is interesting that dolphins fall so near to humans in terms of relative neocortex size (Figure 3.1), this finding alone is not of much use, as it merely gives an idea of the extent of the neocortex in comparison with the rest of the brain. If the analysis were to stop here, the study would most certainly fall into the same trap as other studies, such as those based on the EQ or absolute brain size. However, it is as a result of the significance of the neocortex to cognitive functioning that the analysis does not end here. It is highly improbable that the neocortex would have evolved to its current relative size in dolphins without fulfilling some function. For if the brain is considered as a functional system, it follows that more cortex will be dedicated to vital functions (Luria, 1973, 1982).

In general, as brains are energetically expensive, the importance of different structures might be studied by considering the dimensions they occupy in the brain and the functions they serve. For example, Martin (1981) suggested that rather than relating brain size to body surface area, it is more appropriate to relate the former to metabolic turnover. This relationship between structure and function or anatomy and physiology is important. Kesarev (1971:52) regarded the schism between anatomical and physiological brain research as inappropriate, since the relationship between structure and function should be conceived of as “a complete if not ideal unity”.

The meaning of structural adaptations in brain and neocortical evolution only becomes more appreciable once the functional significance of such adaptations is identified. Bearing this in mind, one can consider different hypotheses of brain evolution. Finlay and Darlington (1995) propose two alternatives for brain evolution, developmental constraint or adaptation. The developmental constraint hypothesis holds that one can predict the size of any neural structure in any species by using a specific formula, while the adaptation hypothesis proposes that changes are not predictable. Using allometric information collected on volumes of different brain divisions, Finlay and Darlington (1995) found the developmental constraint hypothesis to be more acceptable, concluding that neocortex is highly predictable for almost all brain subdivisions.

The most powerful test of developmental limits on the evolution of the brain is evident with respect to species living in specialised niches, or through examining specific structures close to the sensory periphery (Finlay and Darlington, 1995). Such an analysis is readily applicable to sirenians and cetaceans, as the perceptual world of dolphins is significantly different from that of standard mammals (Jerison, 1986) and will form the basis for further investigations in this study (Chapter 5).

Cetaceans have been referred to as an exceptional case in brain evolution (Deacon, 1990). From an evolutionary perspective, it is interesting to realise that marginal brain size changes can result in a relatively large neocortical size change (Finlay and Darlington, 1995). This implies that only a slight initial divergence in brain size can result in markedly different neocortical evolution. The evolution of dolphins in such a radically altered environment displays the plasticity of the structural and functional organisation of the brain (for example the absence of an olfactory bulb and expanded auditory cortex), especially when considering the adaptability of the cerebral cortex (Kesarev, 1971). Therefore, rather than considering the dolphin brain as adaptive or conservative, it should be held as a highly “derived” brain, one geared towards adaptation in its specialised environmental niche (Deacon, 1990).

Several suggestions have been made to account for the large development of the dolphin neocortex. Some argue that it occurred as a result of the greater regulation required by their visceral and somatic functioning (Kesarev, 1971). However, although all cetaceans share common visceral and somatic functioning, they do not all share a high EQ, prompting the suggestion that the above explanation is not likely to be the case (Ridgway, 1986). Rather, Ridgway (1986:62) proposes that there must be "other reasons for the large size of the dolphin brain".

The aim of the following chapters 4-6 is therefore to assess what functional significance the large dolphin neocortex serves. This approach fits the mould of previous research documenting the neocortex ratio, where neocortical size has not been studied in isolation. Rather, it has been related to the behavioural ecology of different mammals. This has been achieved by relating the neocortex ratio to several variables representing foraging ecology and social structure in primates, insectivores and carnivores (Dunbar 1992, 1995; Dunbar and Bever, 1997). Different aspects of foraging or sociality are related to the neocortex of the various orders of mammals. For cetaceans, these are discussed in the relevant chapters relating to foraging ecology (Chapter 4), sound (Chapter 5) and sociality (Chapter 6).

Chapter 4. Foraging ecology and relative neocortical volume in dolphins.

1. Introduction

Since the 1960s, the term ecology has generally been taken to refer to the study of organisms in relation to the physical and biological environments in which they live (Ehrlich and Roughgarden, 1987; McNaughton and Wolfe, 1979; Smith, 1990). The study of animal behaviour in relation to ecology has thus come to be termed "behavioural ecology". In essence, the function of individual behaviour serves to maximise an individual's survival and reproductive success. However this behaviour is constrained by the ecological conditions within which the organism lives (Krebs and Davies, 1987). An understanding of these ecological constraints thus becomes essential to interpreting the evolutionary significance of certain adaptations.

Chapters 2 and 3 established that the relative size of the odontocete neocortex is extremely large when compared to that of all of the other mammalian groups. It was also acknowledged that such a structural adaptation would not occur without some notable functional correlate. Many researchers have sought to establish the nature of the relationship between aspects of brain size and the ecology of the animals. Authors such as Milton (1988) have suggested that the ecological complexity of foraging may result in larger brains. Using bats as a general example, it has been found that frugivorous species have significantly higher indices of relative brain size than insectivorous species (Armstrong, 1983; Eisenberg and Wilson, 1978; Pirlot and Stephan, 1978).

Following this tradition, the neocortex ratio has been correlated with measures of foraging ecology in several orders of terrestrial mammals, including insectivores and carnivores (Dunbar, 1992; Dunbar and Bever, 1997), although no correlation has been found for haplorhine primates (Dunbar, 1992). This study uses data from the previous chapters to relate the neocortex ratio to several aspects of dolphin foraging ecology.

Social ecology appears to be relevant to considerations of brain size in other mammals, such as carnivores (see Gittleman, 1986). It has been proposed that the formation of cetacean schools is either due to predation or to foraging demands (Norris and Dohl, 1980; Wuersig, 1986). Gaskin (1982) observes that most cetaceans either form schools when they cannot be concealed in the environment or when food sources are concentrated, as opposed to dispersed. The current chapter focuses on the selective mechanisms that influence schools and social systems, including predator protection, foraging, feeding and reproduction.

1.1. General delphinid foraging ecology

It is evident that dolphin group size varies in relation to habitat, from solitary riverine species, through coastal species in small to moderate sized groups to pelagic species in large aggregates (Wells, Irvine and Scott, 1980). Food sources also vary with habitat, resulting in riverine dolphins mainly eating crustaceans and demersal fish, while coastal feeders feed opportunistically (individually and with co-ordinated group foraging) on bottom fish, schooling fish and cephalopods, amongst others. Pelagic species feed on food clumps distributed in patches, such as schooling fish and squid, relying on co-ordinated foraging and feeding.

A diverse range of selective mechanisms influencing social systems is apparent from the wide range of adaptation across delphinid species. Pelagic species are adapted to life at sea, being relatively small and streamlined for enduring high speed search and pursuit of fish schools, these being captured with elongated jaws housing many small teeth. Coastal species mainly have shortened beaks with less teeth, allowing for the capture of more diverse food sources. These may be compared to riverine species who are highly manoeuvrable to avoid obstructions in the water and whose long, narrow jaws have a large number of teeth, specialised to catch a smaller variety of prey on the bottom (Wells, Irvine and Scott, 1980).

Cetacean schools feed primarily on schools of fish and squid species, many of which also exhibit aggregation tendencies. Norris and Dohl (1980) note that, as with findings related to schools of predatory fish and large terrestrial mammalian predators, foraging efficiency increases with increasing school size in dolphins.

Certain dolphin species such as the common dolphin and spotted dolphin, travelling in schools of hundreds or thousands, assemble in broader as opposed to longer formations relative to school movement (Norris and Dohl, 1980). These formations permit the scanning of larger areas with an incremental increase in efficiency, as opposed to single animal scouting (Wuersig, 1986). As most of the food of pelagic dolphin species is constituted from large schools of fish unevenly distributed in the open ocean, it is evident that a single location of prey can provide food for a large dolphin group. This is in contrast to the more even distribution of inshore prey, which may result in smaller groups of coastal and estuarine dolphins (Peddemors, pers. comm.).

Following successful foraging, feeding is enhanced by school formation, which may optimise energy supplies. Through random movements in the feeding area, and by altering the density of feeding animals relative to seasonal variation in food, the group can constantly feed on unexploited resources and allow the food supply time to reconstitute itself. Most dolphins (notably common, spotted and spinner schools) appear to use "pulse fishing", which involves an initial, heavy exploitation of a resource area, which is then left to reconstitute itself while another area is fished (Norris and Dohl, 1980).

Methods of food capture are notably different to search methods, with patterns of capture described as either spread school formations or co-operative capture methods (Norris and Dohl, 1980). Once clumps of food are located by ocean-going genera such as *Delphinus* and *Stenella*, the formation of the school changes. The school spreads out and loses its shape, with reduced school cohesion and greater numbers of smaller subgroups forming. According to Norris and Dohl (1980), some species alter their diving patterns when feeding instead of foraging, for example, schools of *Stenella* may continue to dive in synchrony, which may form part of a capture strategy. The same authors note that spread formation occurs at night in spinner schools, as opposed to daytime spreading in common dolphin schools, which may indicate a different sensory basis for school formation. "Mixed schools" comprising different species have also been observed feeding on similar types of food.

Species forming smaller moderate-sized schools appear to use more specialised kinds of food capture. Both bottlenose and humpback dolphins utilise a wide array of feeding tactics to herd and sometimes trap their prey (Dix, 1998; Leatherwood, 1975; Peddemors and Thompson, 1994; Silber and Fertl, 1995). Norris and Dohl (1980) propose that food capture appears more successful when the cetacean forces the prey against a barrier, either the shoreline, the surface, or underwater formations, as this results in the prey engaging in more predictable behaviour, thereby simplifying capture for the dolphins.

The final aspect of animal ecology relates to diet and energetics. Milton (1988) found that the composition of the diet was related to brain size in primates. Those primates who forage for high quality, less easily obtainable resources such as fruit, rather than leaves, appear to have larger brains than their non-specialist, catholic feeding counterparts. Although the equivalent detailed study is obviously not possible in free-ranging dolphins, an analogy is possible. Squid are easier to catch than fish, are of lower quality and hold less of an energy content than their piscine equivalent (Clarke, 1986; Sink, 1995). If fruit is comparable to fish and squid is comparable to leaves in dietary terms, then an analysis for dolphins becomes possible.

In terms of the importance of diet to odontocete ecology, it may be of interest to note that the abundance of pilot whales off the coast of Newfoundland was severely constrained by the depletion of the squid on which they prey (Mercer, 1975). Locally, Crawford and Shelton (1981) suggested that the declining availability of fish prey items resulted in the depletion the population of several species of southern African seabirds. By extrapolation, the same process could apply to local dolphin species. Partridge and Green (1985) support this notion, by observing that spatial and temporal variation in food supplies, the variation of individuals within a phenotype and frequency dependent pay-offs all have a profound influence on the feeding strategies of animals.

Dolphins, although being apex predators, are also preyed upon and the consequences of being prey may influence their foraging ecology and social systems considerably. For example, the water depth inhabited by the animal appears to be a consequential factor in influencing the social system. The further away from the protection offered by land and the coastline, the greater the threat of predation and the larger the school. Water depth therefore appears to be correlated with school size (Johnson and Norris, 1986). Peddemors (pers.comm.) observes that water depth controls the abundance and distribution of many fish species and hence indirectly influences dolphin abundance and distribution. According to Wells, Irvine and Scott (1980), one cannot reduce the determinance of group composition, stability or size to one environmental factor. They propose that the interaction of environmental forces of differing importance combine in determining group features.

Predation pressure also varies with habitat. Riverine species are almost free from predation and appear to group on a predominantly territorial basis, while coastal and pelagic species are preyed upon by humans, sharks and killer whales and form tight social bonds, evidenced by mass strandings and permanent family units (Wells, Irvine and Scott, 1980).

It appears that the ecological determinants of group size in larger delphinids are different than those of the smaller delphinids, thus the larger the animal, the smaller the group (Johnson and Norris, 1986). The threat of predation is less pressing for larger animals, where prey density and size, in addition to predator mobility may be more important (Wells, Irvine and Scott, 1980).

Parrish (1992) suggested that, with respect to fish schools, predators influence the physical and behavioural composition of the school, proposing that gregariousness may have evolved to reduce predation, to permit foraging efficiency or hydrodynamic advantage. Dolphins, who are preyed upon by sharks and killer whales, typically react to environmental stress by avoidance and tightening of the group, with the peripheral animals engaging in most of the aggressive activity, while young and vulnerable school members are protected by a "moving cup" of adults (Norris and Dohl, 1980). In dimorphic odontocete schools, adult males are often positioned at the wings of the school, while the mothers and calves are more centrally placed. As animals at the periphery of the school are more open to predation, larger males usually hold these positions, as they are better able to fend off predators (Norris and Dohl, 1980).

If the entire range of cetacean group size is considered, it is evident that variation in school size is as expected if predation were the propelling force behind schooling (Norris and Dohl, 1980; Norris and Schilt, 1988). Thus large whales are usually either solitary or form small reproductive units. Similarly, while river dolphins form small groups or remain solitary and coastal dolphins form small to moderate schools, pelagic dolphins form huge schools of up to several thousand members.

1.2. Foraging ecology of species in South African waters

Bottlenose dolphins have a diverse habitat, ranging from riverine and coastal to pelagic schools (Leatherwood and Reeves, 1983). There are distinct offshore and inshore populations, with inshore populations regularly displaying residency. Although generally considered to be opportunistic feeders, inshore bottlenose dolphins have been found to target specific prey species in South African waters (Cockcroft and Ross, 1990a). They mainly eat fish and feed co-operatively or individually. Bottlenose dolphins are occasionally preyed upon by sharks or killer whales (Cockcroft, Cliff and Ross, 1989; Wells, Irvine and Scott 1980). Individual feeding occurs on benthic and reef dwelling fish, while co-operative feeding occurs on schools of fish.

Off South African waters, the offshore bottlenose dolphin is unresearched, but probably ranges from the south-eastern Atlantic Ocean to the south-western Indian Ocean (Findlay, 1989). The inshore form occurs as far south as False Bay on the east coast and is restricted to Namibia and northwards on the west coast (Findlay, 1989). Two possible stocks are found on the east coast, migrants and residents (Peddemors, 1995). The inshore form is found in water less than 50 metres deep and avoids turbid water (Peddemors, 1995). Not only are co-operative and individual feeding techniques used, but a system of age and sex based resource partitioning has been shown off KwaZulu-Natal (Cockcroft and Ross, 1990b). Local species forage mainly on fish species, but also on cephalopods (Sekiguchi, Klages and Best, 1992). This can be contrasted with the results of stomach content analysis of bottlenose dolphins off Florida, which reveal that they prey exclusively on fish species and hunt in much shallower water than their local counterparts (Barros and Wells, 1998).

Common dolphins are resident throughout the year from Lambert's Bay on the west coast to East London on the east coast, only occurring seasonally in KwaZulu-Natal, during the sardine-run (Cockcroft and Peddemors, 1990). Approximately 20 000 common dolphins are estimated to occur on the south-east coast (Cockcroft and Peddemors, 1990). These dolphins are pelagic, generally inhabiting waters over the continental shelf, but also being found inshore on the east coast during winter, when feeding on sardines. Generally, these dolphins are opportunistic feeders (Young and Cockroft, 1994), eating shoaling fish and cephalopods. On the west coast, this species predominantly eats schooling fish in water less than 200m deep, but may feed on the deep scattering layer nocturnally (Sekiguchi, Klages and Best, 1992). On the east coast, the prey are usually small, easily captured, pelagic shoaling species (Young and Cockcroft, 1994). Although these dolphins are supposedly opportunistic feeders, five prey species constituted 86.9% of the dietary weight. There is also strong evidence for resource partitioning or the differential intake of prey between groups of males and females, as well as for juveniles and adults (Young and Cockcroft, 1994).

Humpback dolphins are found in coastal or estuarine waters, with year-round residents following habitual inshore routes (Durham, 1994). As opportunistic feeders, humpback dolphins prey on fish (mainly reef fish), hunting both co-operatively and individually (Saayman and Tayler, 1979). They are regularly preyed upon by sharks (Cockcroft, 1990). In KwaZulu-Natal, the humpback dolphin population is estimated at 200 individuals, mostly occurring on the Tugela Bank (Durham, 1994). However, they are found throughout the east coast, as far south as False Bay (Findlay, 1989). Although usually found in turbid nearshore waters, river deltas and estuaries, they have been observed in large harbours such as Durban and Richard's Bay (Peddemors and Thompson, 1994). They primarily feed on estuarine-associated and littoral fish species and cephalopods, although it has been acknowledged that not much is known about their feeding habits (Barros and Cockroft, 1991). In local waters, the humpback has been observed to prefer shallow waters, not greater than 25 metres deep (Barros, 1997). It has been suggested that although humpback and bottlenose dolphins share the same prey species, the closer inshore foraging of humpbacks allows them to co-exist with their bottlenose counterparts (Barros, 1997; Barros and Cockroft, 1991). Off the eastern Cape feeding increases during the rising tide (Saayman and Tayler, 1979). Elsewhere, the humpback dolphin moves onshore with the rising tide to feed in mangrove channels, sometimes incorporating purposeful beaching in pursuit of prey (Peddemors and Thompson, 1994).

Spotted dolphins have been sighted in the Mozambique channel and as far south as the Eastern Cape (Port St John's) (Peddemors, 1997). Two strandings on the west coast probably represent strays from the east coast (Findlay, 1989). Although usually sighted in water deeper than 200m, this species has been observed in water less than 30m deep, in association with spinner dolphins in Cape Vidal, Maputoland, and with common dolphins off the Wild Coast (Peddemors, 1997). Feeding is on squid and fish in the early morning near the surface, where advantage is taken of the vertical migration of their mesopelagic prey (Sekiguchi, Klages and Best, 1992).

The distribution of striped dolphins ranges from Mozambique to False Bay, but may round the Cape Peninsula in association with the Agulhas Current (Findlay, 1989). All sightings have been in water deeper than 500m, which suggests an oceanic lifestyle. The diet for east coast striped dolphins consists mainly of fish (80%) with squid (20%), while on the south coast squid appears to be the dominant food source (86%), which may reflect the greater abundance of squid on the Agulhas Bank (Sekiguchi, Klages and Best, 1992). Striped dolphins may target squid with luminous organs. The dietary presence of pelagic and oceanic squid species suggests offshore and inshore feeding, or regular feeding at the intersection represented by the continental shelf break (Sekiguchi, Klages and Best, 1992).

Not much is known about Fraser's dolphin, Risso's dolphin and the *kogiid* genera off the local coastline. However, in terms of local feeding knowledge, it has been suggested that Fraser's dolphins live in deep water, off the edge of the continental shelf (Sekiguchi, Klages and Best, 1992). Locally, Risso's dolphin feeds almost exclusively on cephalopods (Cockroft, Haschick and Klages, 1993) at a great depth in excess of 1000 metres (Ross, 1984). As regards dwarf sperm whales, juveniles live closer inshore than adults, over the outer part of the continental shelf and upper part of the slope, whereas adults inhabit deeper water (Ross, 1984).

Using data from the above species, dolphin neocortex ratios from Chapters 2 and 3 are related to foraging depth, dietary diversity, total number of prey species, fish species and cephalopod species and dietary complexity, evidenced by relative prey importance ratios for fish and cephalopods.

2. Method

An issue of methodological importance was raised by Deacon (1990) and elaborated upon by Dunbar (1992). This concerns the variation between ontogenetic and evolutionary terms. Whereas brain size may restrict group size ontogenetically, in evolutionary terms, selection pressures favouring an increased group size may drive the evolution of a larger neocortex. Although a behavioural requirement may cause a change in the brain, hypotheses are tested by regressing behaviour onto brain size. This is done as the behaviour of existing populations is restricted by current brain size (Dunbar, 1992). In the following analysis, the foraging variables are therefore considered as dependent variables and are regressed onto the neocortex ratio, the independent variable. Independent contrast analysis is not considered necessary, as the study species emerged during a similar period of time (Milinkovitch, Meyer and Powell, 1994). However, speculation exists with respect to the concept of star speciation in dolphin evolution. This study can, however, claim to overcome phylogenetic inertia, as the analysis proceeds as the genus level (each species represents one genus), where it has been suggested that genera are considered to be evolutionarily independent (cf. Dunbar, 1992).

2.1. Study animals

Only the MRI data for those species falling within the population parameters established using the CVA techniques, described in Chapter 3, were used. The qualifying species from MRI included the bottlenose dolphin *Tursiops truncatus,* the common dolphin *Delphinus delphis*, Fraser's dolphin *Lagenodelphis hosei*, the Indopacific humpback dolphin *Sousa chinensis,* Risso's dolphin *Grampus griseus* and the spotted dolphin *Stenella attenuata*. A summary of the relevant actual neocortex data is provided in Table 4.1.

Table 4.1: Neocortex ratios from MRI for selected delphinids

Species	C_R	$\text{Log}_{10}\, C_R$	n
Bottlenose	3.85	.59	14
Common	3.94	.60	16
Humpback	3.59	.56	8
Spotted	3.55	.55	1
Fraser's	3.73	.57	1
Risso's	3.81	.58	1

From the neuroimaging findings described in section 2.3.5, it was evident that cranial volume, measured using CT, could be accurately used to estimate the equivalent MRI brain and neocortex volumes. These equations were applied to the cranial volume data obtained in section 3.3 (Chapter 3) to provide estimates of brain volume, neocortex volume and the neocortex ratio in the species concerned. Data were estimated from crania representing the MRI species (above) and also for the following species: Burmeister's porpoise *Phocoena spinipinnis*, the dwarf sperm whale *Kogia simus*, the dusky dolphin *Lagenorhynchus obscurus*, the false killer whale *Pseudorca crassidens*, Gray's whale *Mesoplodon grayi*, the harbour porpoise *Phocoena phocoena*, the Indus river dolphin *Platanista minor*, the killer whale *Orcinus orca*, the pygmy killer whale *Feresa attenuata*, the pygmy sperm whale *Kogia breviceps*, the short-finned pilot whale *Globicephala macrorhynchus,* the spinner dolphin *Stenella longirostris* and the striped dolphin *Stenella coeruleoalba.* The relevant summary data are provided in Table 4.2.

Table 4.2: Estimated brain volumes and C_Rs for PE odontocetes species

Species	n	Family[1]	Est. brain vol.[2]	Est. neocortex vol.[2]	Est. C_R	LOG_{10} Est. C_R
bottlenose d.	20	1	1286.08	1014.37	3.73	.57
common d.	20	1	968.14	760.02	3.65	.56
humpback d.	20	1	1199.18	944.86	3.72	.57
spotted d.	10	1	783.57	612.37	3.58	.55
striped d.	2	1	654.24	508.90	3.50	.54
spinner d.	2	1	312.05	235.15	3.06	.49
Fraser's d.	7	1	1031.46	810.68	3.67	.56
dusky d.	2	1	688.60	536.39	3.52	.55
Risso's d.	6	1	1546.76	1222.92	3.78	.58
false killer w.	2	1	1919.26	1520.92	3.82	.58
pygmy killer w.	2	1	751.24	586.50	3.56	.55
killer w.	1	1	6825.75	5446.11	3.95	.60
short-finned pilot w.	2	1	3843.73	3060.49	3.91	.59
dwarf sperm w	5	2	586.88	455.02	3.45	.54
pygmy sperm w	1	2	931.76	730.92	3.64	.56
Indus River d.	1	3	15.67	-	-	-

Table 4.2/ctd.

Species	n	Family[1]	Est. brain vol.[2]	Est. neocortex vol.[2]	Est. C_R	LOG_{10} Est. C_R
harbour p.	1	4	260.86	194.20	2.91	.46
Burmeister's p	1	4	398.95	304.67	3.23	.51
Gray's beaked w.	1	5	1610.75	1274.11	3.78	.58

note: [1]Family= 1-delphinids, 2-sperm whales, 3-river dolphins, 4-porpoises, 5-beaked whales; [2]cm^3;

A series of documented variables on foraging depth, total number of prey species, numbers of fish and cephalopod species and the Shannon-Wiener Index of dietary diversity, or SWI (Sekiguchi, Klages and Best, 1992), were used in the analysis. From these measures ratios of total prey species to fish or cephalopod species and of fish to cephalopod species were also calculated. The values for different species are presented in Table 4.3.

Table 4.3: Foraging ecology variables in Odontocetes.

species	foraging depth[1]	fish species[2]	squid species[2]	total species[2]	SWI	total: fish ratio	total: squid ratio	fish: squid ratio
bottlenose	50	16	3	19	2	1.19	6.33	5.33
common	200	14	7	21	1.79	1.50	3	2
humpback	25	-	-	93	-	-	-	-
spotted	200	6	10	16	1.80	2.67	1.60	.60
striped	500	6	11	17	1.05	2.83	1.55	.55
spinner	250	-	-	-	-	-	-	-
Fraser's	500	6	3	9	.93	1.50	3	2
dusky	85	16	7	23	2.17	1.44	3.29	2.29
Risso's	1000	2	14	16	1.79	8	1.14	.14
False K.	1000	.00	8	8	.94	-	1	.00
Pygmy K.	-	2	.00	2	.67	1	-	-
Short-fin p.	1000	-	-	-	-	-	-	-
Dwarf Sp.	500	4	31	37	1.82	9.25	1.19	.13
Pygmy Sp.	500	12	31	49	2.30	4.08	1.58	.39
Indus River	15	-	-	-	-	-	-	-
Gray's b.w.	1800	1	.00	1	.00	1	-	-

Note: [1]m, [2]number. Data on prey species (total species, fish species, cephalopod species and SWI): Sekiguchi, Klages and Best, 1992. Humpback data from Barros, 1997. Data on foraging depth: Indus River dolphin: Waller, 1983; Dusky dolphins: Wuersig and Wuersig, 1980; bottlenose dolphins: Ross et al. 1987; common dolphins, dwarf sperm whale: Sekiguchi et al. 1992; false killer whale, spotted, striped dolphins, short-finned pilot whales: Findlay et al., 1992; Humpback dolphin: Durham, 1990; Risso's dolphin: Cockcroft et al., 1990; spinner dolphin, Fraser's dolphin: Sylvestre, 1995.

2.2. Materials

MRI data were obtained using MRI scanning units at St Aidan's and Wentworth Hospitals. These machines and their related imaging software are more comprehensively described in sections 2.2.3 and 2.2.4 (Chapter 2).

Cranial volume analysis utilised fine sand, with a known density and several measuring beakers to contain the sand. An electronic scale was used to weigh the sand. A more detailed description of these materials and methods has been provided in section 3.2.2 (Chapter 3).

2.3. Procedure

The MRI neocortex data for the major study species of dolphins, and MRI data for delphinids at large were analysed, in addition to using the estimated neocortex data for delphinids and, more generally, odontocetes. These values were related to a set of documented variables pertaining to foraging ecology, to assess the nature of the relationship between neocortex and foraging. The statistical analysis was conducted using SPSS version 6.1 and the results were accepted as significant at the .05 alpha level.

3. Results

3.1. Correlational analysis

The current study established the nature of the correlations of various foraging ecology variables with the neocortex ratio (Table 4.4). It is of interest to note that foraging depth and the neocortex ratio are not correlated in the major study species, nor in the other delphinid species data from MRI. When compared to the estimated values for CVA subjects, foraging depth is also not related to the C_R of the major species, although there is a possible trend towards a relationship for delphinids and for odontocetes at large.

The total number of prey species eaten appears to be negatively correlated with the C_R in the major study species from MRI. This does not appear to be the case for the more general MRI delphinid subjects, nor for the neocortex estimates of the major species, delphinids or odontocetes, where these variables are unrelated.

The number of bony fish or cephalopod species does not appear to be related to the C_R in any of the groups of analysis, neither from actual neocortex data, nor from estimated data.

The ratios of prey, for example, the proportion of fish or cephalopods to the total number of species, did not appear to be related to the C_R in the majority of the data, with the exception of the major subjects from MRI. Here, the proportion of cephalopods to total number of prey species was negatively related to the C_R.

Dietary diversity, as measured by the SWI, was unrelated to the actual and estimated data for the major species, delphinids and odontocetes.

Table 4.4: List of correlations for foraging ecology variables with C_R

Dependent Variable	Major species[1]	Major species[2]	Delphinids[1]	Delphinids[2]	Odontocetes[2]
foraging depth	n.s	n.s.	n.s	.467 (11) .074[3]	.454 (14) .052[3]
total species	-.963 (3) .087[3]	n.s	n.s	n.s	n.s
fish species	n.s	n.s	n.s	n.s	n.s
cephalopod species	n.s	n.s	n.s	n.s	n.s
total:fish prey ratio	n.s	n.s	n.s	n.s	n.s
total: cephalopod prey ratio	-.999 (3) .007*	n.s	n.s	n.s	n.s
SWI	n.s	n.s	n.s	n.s	n.s

Note: [1] refers to MRI neocortex data for major delphinid species of interest and delphinid species in general; [2] refers to estimated neocortex data for major delphinid species, delphinid species in general and the wider suborder of odontocetes; n.s.- not significant at $p < .05$; [3]potential trend, *significant relationship. Results presented i.t.o. r value, n, p value.

3.2. Weighted linear regression

The technique of linear regression was used in the analysis and weighting by least squares was applied to the regression. Weighting was included to provide a more accurate analysis, as it takes account of the individual numbers of animals used within each species. Variables were logarithmically transformed (base 10) in order to linearise the data (Dunbar, pers.comm.). The C_R was the predictor or independent variable, while the study variables were the predicted or dependent variables.

For the actual neocortex data from the MRI study species, the C_R is not significantly related to any foraging ecology variables, including foraging depth, dietary diversity, the total number of prey species, the specific numbers of fish nor cephalopod prey species, nor to the ratios of specific prey species to the total number of species nor to each other. The regression statistics are provided in Table 4.5. The only variable to show a trend toward approaching significance in relation to the C_R is the number of cephalopod species preyed upon.

Table 4.5: Foraging ecology variables in relation to C_R for MRI delphinids

Dependent Variable	adjusted r^2 value	F value (d.f.)	p value
foraging depth	0.218	2.393 (4)	n.s
total species	0.250	2.663 (4)	n.s
fish species	0.245	0.017 (4)	n.s
cephalopod species	0.511	6.225 (4)	.067*
total:fish prey ratio	0.197	0.177 (4)	n.s
total:cephalopod prey ratio	0.371	3.949 (4)	n.s
SWI	0.303	0.069 (3)	n.s
fish:cephalopod prey ratio	0.371	3.949 (4)	n.s

note: *although n.s- not significant ($P < .05$), this finding indicates a potential trend.

A similar pattern that in the MRI neocortex data is evident with respect to the relationship of estimated neocortex ratios for delphinids and odontocetes and the foraging ecology variables. From the regression statistics (Table 4.6), it is evident that none of the variables are significantly related to the C_R. The only exception is once again the number of cephalopod species, which shows a trend towards being related to the C_R for the suborder of odontocetes. However, this trend is not evident with respect to the more particular family of delphinids.

Table 4.6: Foraging ecology variables in relation to estimated C_R for species representing the delphinids and the wider suborder of odontocetes.

	Delphinids			Odontocetes		
Dependent variable	adjusted r^2 value	F value (d.f.)	p value	adjusted r^2 value	F value (d.f.)	p value
foraging depth	.096	.120 (9)	n.s	.050	.385 (12)	n.s
total species	.037	.676 (8)	n.s	.084	.069 (11)	n.s
fish species	.158	.047 (6)	n.s	.076	.293 (9)	n.s
cephalopod species	.010	.928 (6)	n.s	.276	4.434 (8)	.068*
total:fish prey ratio	.163	.017 (6)	n.s	.035	1.368 (9)	n.s
total:cephalopod prey ratio	.084	.457 (6)	n.s	.079	1.774 (8)	n.s
SWI	.106	.231 (7)	n.s	.103	.063 (9)	n.s
fish:cephalopod prey ratio	.144	.243 (5)	n.s	.079	1.774 (8)	n.s

note: *although n.s- not significant ($P < 0.05$), this finding indicates a potential trend.

4. Discussion

To eat and not to be eaten? While this appears to be the issue related to the neocortical evolution of some mammals, it does not appear to be the case for dolphins. On the whole, the findings of this chapter are not supportive of a relationship between foraging ecology and the neocortex ratio in dolphins.

The interrelationship of social structure and ecology has been noted previously (Crook and Gartlan, 1966; Jarman, 1974; Struhsaker, 1969), where it has been observed that ecological variability may encourage or constrain behaviour and sociality (Clutton-Brock and Harvey, 1976; Foley and Lee, 1989). It is therefore important to consider the function and context of behaviour in relation to the life strategy of the animal or its ecology (Dunbar, 1988). Some even suggest an individual population of animals be considered as a “separate trophic or ecological species”, as a consequence of the geographical variation in niches occupied by a species and the potential significance of ontogenetic effects on trophic relations (Williams, 1992:120).

Several theories have been proposed to explain the grouping behaviour of animals, ranging from the reduction in predation risk, or the anti-predation hypothesis (Van Schaik, 1983), to the foraging ecology hypotheses, such as resource dispersion (Macdonald, 1983) and resource defence (Carr and Macdonald, 1989; Wrangham, 1980).

If one conceives of dolphins as both apex predators and prey, then the findings of neocortical volume being unrelated to foraging ecology variables become of increasing interest.

It has been argued that in other orders of mammals, such as the primates, a major factor in determining the group size of animals, and one which may regard intellectual action, relates to the acquisition of food (Clutton-Brock and

Harvey, 1980; Gibson, 1986) or the structuring of ecological resources (Dunbar, 1988; Wrangham, 1979, 1980).

The main issue is perceived to be the complexity of cognitive mapping (mentally representing spatial and temporal food distribution) required to obtain patchily distributed but predictable sources of food (Byrne, 1995). Although range area or day range length have been used to measure such mapping, Byrne (1995) suggests that these variables underestimate environmental complexity. In spite of the correlation between brain size and range size (Clutton-Brock and Harvey, 1980), Byrne (1994) suggests that this may be an artefact of gut specialisation, as a large gut permits a wider, less specialised diet and smaller range area. In addition, he notes that a larger gut requires a bigger body frame, which decreases the relative size of the brain. However, Milton (1988) contends that differences in gut size do not account for differences in brain size.

Although the size of the gut does not appear to relate to brain size, other dietary concerns have presented a different picture in the comparative literature. It was therefore surprising that this study found that dietary diversity and dietary complexity were not related to the neocortex ratio in representatives of the delphinid family or the suborder of odontocetes. Particularly as research conducted on brain size in marine mammals by Worthy and Hickie (1986) shows that species belonging to Sirenia, which forage on poor quality food, have relatively small brains, while odontocetes have large RBS, akin to primates. Findings such as these tend to support the proposal of Milton (1988) that across different mammalian species, brain size (as well as sociality and breeding systems) correlates with diet.

Milton (1988) suggested that based on the measure of comparative brain size (Clutton-Brock and Harvey, 1980), strongly frugivorous primates show greater cerebral expansion than folivorous groups. Further, when considering Jerison's (1973) data in relation to dietary focus, Milton (1988) recognised that primates requiring more complex foraging matrices also had greater cerebral complexity. Research into cranial volumes (Eisenberg and Wilson, 1978) supported the notion that frugivores and nectarivores have larger cranial volumes than carnivores, insectivores or sanguivores. This appears to indicate that an aspect of hyperdispersed, patchy and high-quality food resources stimulate increased brain size (Milton, 1988).

A concern is that brain and gut tissue compete metabolically, as both are energetically expensive (Milton, 1988). All organs, with the exception of the brain, have sizes that are linear functions of body weight, where the metabolic rates of such organs correlate with body size. However, Aiello (in Byrne, 1995) suggests that this correlation may be artefactual, for without converting from a herbivorous diet, the brain and gut tissue could not both be enlarged.

In physiological terms, the mammalian basal metabolic rate (BMR) holds the relative oxygen consumption or heat production proportional to the 3/4 power of body weight (Hofman 1983a,b). Related research suggests that brain size may also scale to body size to the 3/4 power (0.73) rather than 2/3 power (Hofman, 1983a,b; Martin, 1981). As diet can influence metabolic rate and metabolic weight is isometric with brain mass, Milton (1988) observes that an effect of diet on achievable brain mass may be predicted (see Worthy and Hickie, 1986). Mammalian brain size and metabolism present large interspecific variation and correspondingly complex energetics (Hofman 1983a,b). Hofman (1983a,b) also notes that cortex-brain metabolic rate is independent of body size, increasing with the evolutionary level of brain development.

To recognise the importance of the non-relationship between foraging and dietary complexity, and the neocortex in dolphins, it is necessary to consider the metabolism of cetaceans in relation to their brains.

The initial concern that brain studies did not incorporate physiological considerations (Martin, 1981) has been addressed in subsequent studies of the brain, its size and evolution. For example, Armstrong (1983) examined mammalian relative brain size in terms of metabolism. From this, it was noted that brain-body scaling may be determined in the following manner: the brain controls body functions but is dependent upon the body for energy. As the brain is continuously metabolically active, it requires vast amounts of oxygen and glucose, both during sleep and while engaged in mental activity. By the same token, the brain's development may also be determined by the metabolic system. Armstrong concludes that "An analysis of the brain's energetics is necessary for a better understanding of the relation of brain to body" (1983:1304). What is interesting in this study is that odontocetes are placed higher than primates in the relationship of metabolism to brain size.

In a variation of these conclusions, Hofman (1983a) found that the ratio of cerebral cortex-brain metabolism depends solely on the degree of encephalisation, being independent of body size. In addition, Hofman notes that brain size is not only a function of metabolism, but also a function of the level of evolutionary development of the brain. He proposes that species with high encephalisation will have high brain-body metabolic ratios, mentioning odontocetes and simians as examples.

On the contrary, Kesarev (1971) notes that simpler cetacean brain structure may result from the fact that an aquatic environment is considered less complex than a terrestrial environment, in terms of homeostasis. In addition, he observes that cetaceans have no competitors at a similar CNS developmental level in the water.

Yet, although cetaceans may appear to be less homeostatically complex, they face a barrage of pressures not encountered by terrestrial mammals, such as the physiological pressures of depth and diving. To illustrate, a coping strategy for the energy demands of the brain under conditions of oxygen depletion may lie in the capacity of some vertebrates to engage in anaerobic respiration (Hofman, 1983a). Here, one cannot discard the aquatic environment of marine mammals and the fact that anaerobic respiration has been observed in cetaceans. Turning to aerobic respiration, cortical respiration is almost exclusively neuronal and the number of cortical neurons is a linear function of cortical surface area (Hofman, 1982b). Cetaceans, with the greatest cortical surface area (Elias and Schwartz, 1969), possess the largest number of neurons and thus appear to engage in the greatest amount of cerebral oxygen intake.

Although some of the correlations that approached significance may prove a slight degree of support for a relationship of neocortex with ecology and energetics, these were not supported by regression analysis. For example, foraging depth showed a trend towards a positive relationship with the neocortex ratio, while the total number of species preyed upon approached a negative relationship with the ratio. The only significant result of this chapter was the correlation between the ratio of total to cephalopod prey species and the neocortex ratio, where these variables were negatively related. However, the small sample might represent a distorted finding, as no trend existed for this in other study populations. Nevertheless, such a finding can be explained in terms of the above findings for primates, where a non-specialised diet or a folivorous diet is associated with the possession of a smaller brain, (Milton, 1988).

Upon shifting the focus to dolphins as prey, it was unexpected to find a lack of association between water depth and the neocortex ratio, especially in the light of the foregoing review on the positive relationship between water depth and predation (Johnson and Norris, 1986). It may be pertinent to reconsider the notion that an increased group size supposedly results in the increased fitness of individuals tending to group under threat of predation (Byrne, 1995). However, as a result of the open space environment inhabited by most cetaceans, Norris and Schilt (1988) support the proposals of Alexander (1974), who suggests that predation may be the primary reason for group living.

It has been suggested that several factors are influential in determining social organisation. For example, various sociality in carnivores, ranges from the solitary panda (Morris and Morris, 1966; Schaller et al., 1985) to seasonally social wolves (Fox, 1971; Klinghammer, 1975) and the more gregarious hyaenas (Kruuk, 1966).

Different reasons are often furnished to explain the social system of the same species. To illustrate: although the resource dispersion hypothesis has been thought to explain the sociality of spotted hyaenas (Henschel and Skinner, 1991; Lamprecht, 1978; Mills, 1990), this has been questioned by Hofer and East (1993) who propose rather that the commuting system of these animals influences their social structure. Within a single species, different factors may apply to the social structure of various classes. For example, grouping in cheetah sibgroups is against predators, while for mature cheetahs it is for access to mates; in lionesses grouping occurs to enable territory defence, while it is for easier access to mates in lions (Caro, 1994).

The large neocortex ratios displayed in dolphins do not appear to be predictive of several variables representing foraging complexity, foraging depth or dietary diversity. This is of consequence, as dolphins are more closely related to ungulates and carnivores, for whom neocortex and ecology are related, than to primates. In the light of this, the investigation moves to study a related are in dolphins- sound. Sound is not only used for sonar and hunting purposes in dolphins, but also for communication. As it falls between ecological and social domains and is involved in each domain, sound is considered to form a bridge between these parameters and, as such, is discussed in the following chapter.

Chapter 5. Sound and relative neocortical volume in dolphins.

1. Introduction

Earlier, it was found that the neocortex ratio was not significantly correlated with variables representing foraging ecology in dolphins (Chapter 4). Sound serves two major functions for dolphins, echolocation and communication. While echolocation is used to forage, the wider spectrum of sound production is used for social and communicative purposes. Based on this perspective, sound might be viewed as the intermediary between foraging ecology and sociality. It is therefore reasonable to consider the acoustics of dolphins in relation to their brain evolution, before moving to consider the variables representing sociality.

Sonar or echolocation refers to the process used by animals emitting acoustic energy and receiving returning echoes to detect, locate, differentiate and recognise objects, as well as for orientation or navigation (Au, 1993; Purves and Pilleri, 1983). Sonar was first discovered in bats at the beginning of this century (Maxim, 1912) and it was less than 50 years ago that a similar discovery was made in dolphins (McBride, 1956).

The dolphin's capacity for the production of sounds and sonar pulses is evident when one considers that peak frequencies range from 30 to 135 kHz, although the source of production is not specifically known (Au, 1993). Dolphin signals are used adaptively and dynamically, depending on the characteristics of the environment and the target, as well as the specific use of the sonar (Nachtigall, 1980; Penner, 1988). For example, the amplitude of a signal will increase if a target is of smaller size, if discrimination is more difficult, or if there is an increase in target range or masking noise (Au, 1993). In addition to being used for foraging, sonar is used for food capture or as a weapon through "pulse bursts" to stun the target (Morris, 1986).

Sound, aside from hunting or navigation purposes, also serves as a vital tool of communication in cetaceans (Tyack, 1981). For example, while on their breeding grounds, humpback whales sing long and complicated songs that vary progressively from year to year (Payne, Tyack and Payne, 1983). Killer whales appear to generate at least three distinct sound types, namely whistles, clicks and pulsed calls. While whistles are used during periods of rest, clicks and pulsed calls are used during activity. The pulsed calls appear to be most unique to a specific pod. (Ford and Fisher, 1983).

Ridgway (1986a) proposed that the large size of the dolphin brain may be the consequence of hypertrophy of their auditory system. While the medial geniculate and the inferior colliculus are substantially larger than in humans, the nucleus of the lateral lemniscus is enormously increased. Bullock and Gurevich (1979) support this, proposing that other brainstem nuclei are also substantially enlarged in dolphins. The cerebral cortex of dolphins may have expanded as a consequence of the acoustic and auditory demands placed on it (Langworthy, 1932; Wood and Evans, 1980). To Moore (1991:380), “the special part of the dolphin sonar system is the brain behind the signal receiver, the signal processor itself. Determining how this processor works will eventually lead to greater understanding of dolphin sonar.”

This chapter aims to study the relatively large neocortex ratios found for dolphins in relation to acoustic production and perception. Variables representing sound diversity, energy, frequency and the duration of signals have been appropriated from the available literature. These are related to actual neocortex data for the MRI delphinid study species (chapter 2), as well as to the estimated data for other delphinids and odontocetes (chapter 3). Bearing in mind that the auditory cortex appears highly adapted in the delphinids, it is quite possible that the relative size of the neocortex will be related to certain sound parameters.

2. Method

The method section of the current chapter follows the same format as that of the previous chapter. Briefly, the acoustic variables were considered as the dependent variables and these were regressed onto the independent variable, the neocortex ratio. For more comprehensive information refer to Chapter 4, section 2.

2.1. Study animals

The study animals comprised subjects from Chapters 2 and 3, with actual and estimated neocortex ratios. The same species were examined as in Chapter 4, with several exclusions, as there was no acoustic information for them. They include Burmeister's porpoise, the dusky dolphin, the dwarf sperm whale, Fraser's dolphin, Gray's beaked whale, the pygmy killer whale, the pygmy sperm whale and the striped dolphin.

A set of documented sound variables was used in relation to the neocortex ratio. These included the number of sound types, minima, maxima and range values for energy, frequency, peak frequency and signal duration (Table 5.1).

Table 5.1: Sound variables in Odontocetes.

Species	no. sounds	min. freq.	max. freq.	freq. range	min. ener	max. ener[1]	ener range	min. peak freq.[2]	max. peak freq.	peak freq. range	min. signal dur.[3]	max. signal dur.	signal dur. range
Bot	5	.1	300	299.9	15	130	115	110	130	20	50	80	30
Com	3	.2	150	149.8	4	60	56	23	67	44	50	150	100
Hum	3	-	-	-	3	30	27	-	-	-	-	-	-
Spo	2	6.5	150	143.5	-	-	-	-	-	-	-	-	-
Spi	1	8.7	14.3	5.6	-	-	-	-	-	-	-	-	-
ris	-	-	-	-	-	-	-	65	65	-	40	100	60
fal	-	-	-	-	-	-	-	100	130	30	100	120	20
kil	6	.1	80	79.9	.25	40	39.75	14	20	6	210	210	-
sho	-	-	-	-	-	-	-	30	60	30	-	-	-
pla	2	25	200	175	-	-	100	-	-	-	-	-	-
har	2	41	160	119	2	150	148	120	140	20	130	260	130

Note: [1]ener- energy, Hz; [2]freq- frequency, Hz; [3]dur- duration, seconds. Data on peak frequency and signal duration from Au (1993, p.134). Data on number of sound types, energy and frequency from Evans (1987, pp.12-17).

2.2. Materials

Data on the neocortex ratio in dolphins were obtained from MRI (Chapter 2), as well as from estimates applied to cranial volume data (Chapter 3). For more comprehensive details, refer to Chapter 4, section 2.2.

2.3. Procedure

In accordance with chapter 4 (section 2.3), C_R values from MRI and estimations using skull volumes were related to the dependent variables, in this instance, the sound variables. The data analysis was conducted using SPSS version 6.1 and an alpha level of .05 was considered to be significant.

3. Results

3.1. Correlational analysis

The sound variables were explored in terms of their correlation with the neocortex ratio (Table 5.2). Although the number of sound types does not significantly correlate with the MRI data, it does reach significance with the estimated neocortex ratios for representatives of the family of delphinids and the suborder of odontocetes. Minimum and maximum energy values were not significant, while energy range only showed a trend towards a negative relationship with the neocortex ratio in odontocetes.

Although the minimum frequency did not correlate with either the MRI or estimated neocortex ratios for the major species, there was a trend towards a negative relationship for the two variables for MRI delphinid data. In addition, minimum frequency was negatively related to estimated neocortex ratios for delphinids and odontocetes.

Maximum frequency and frequency range did not correlate with the neocortex ratio across the spectrum of study species. Minimum and maximum peak frequency were also not related to any categories, although there were trends towards a negative relationship with the estimated neocortex ratio in odontocetes.

Minimum signal duration was not significantly related with the neocortex ratio of any category, except for estimated delphinid data where a positive correlation was evident. Although maximum signal duration approached a negative relationship with the neocortex ratio, it was not otherwise significant. The range of signal duration did not relate to the MRI or estimated C_R with the exception of the estimated delphinid data, where a negative trend was apparent. However, signal range did share a significant, negative relationship with the estimated C_R for odontocetes.

appears to be a good predictor of sound frequency range in delphinids ($p < .05$). It appears that animals with a larger neocortex ratio are capable of perceiving or processing a wider frequency range of sound.

Although dolphins display a similar response to tone signals as that of terrestrial mammals, they differ significantly in terms of their wide frequency range. For example, whereas the dolphin audiogram follows the same pattern as that of the human, it is capable of detecting frequencies 10 factors higher than humans (Au, 1993). Distinguishing marks of dolphin audition are therefore the upper frequency ceiling as well as high hearing sensitivity (Johnson, 1986). This contributes to explaining the positive trend towards a relationship between maximum frequency and the neocortex ratio in delphinids.

Au (1993) recognises that the functional similarities of the dolphin auditory system to humans and other terrestrial mammals bear testimony to its sensitivity and sophistication. It is interesting to observe that a negative correlation exists with respect to minimum frequency and the neocortex ratio in dolphin and odontocete estimates ($p < 0.05$). This draws support for the literature on neocortical complexity (Nauta and Feirtag, 1986), as it implies that animals with relatively larger neocortices have an increased capacity to perceive and process lower frequencies.

Neither minimum, maximum nor signal duration range values were related to the relative size of the neocortex using regression analysis. This was unanticipated, considering the nature of dolphin signals, which are of a duration that is short enough to permit the distinction and recognition of differences pertaining to the sonar target. It follows that the capacity of greater target discrimination is restricted by the time or range resolution capability of the sonar signal (Au, 1993). This applies to interpreting the findings that minimum signal duration is positively related to the neocortex ratio in delphinids ($p < .05$), while

Unlike the song dialects of birds which constantly relate to geographical location (Krebs and Kroodsma, 1980), killer whale dialects exist in pods capable of interbreeding and not geographically isolated from each other. This led Ford and Fisher (1983) to suggest that killer whales possess true dialects, which remain consistent in spite of regular associations between pods. As killer whales live in highly stable kin groups, the utility of a dialect may be to maintain kin relations over time. Family traditions are considered vital to the survival and success of the group.

In view of this, the adaptive benefit of pod dialects to preserving pod identity and cohesion becomes apparent (Ford and Fisher, 1983). The social value of sound to dolphin groups is apparent when one considers that new sound types are often recorded during periods of dolphin socialising (Schultz, Cato, Corkeron and Bryden, 1995). The relationship between sound and sociality therefore should not be underestimated.

It is worth recognising that delphinid neocortex ratios appear more substantially related to the variables of sound than to those of foraging ecology. The significance of sound needs to be considered as not only for hunting purposes, but perhaps more importantly for its enabling and maintenance of social cohesion in dolphins. The possession of a relatively large neocortex may permit enhanced auditory perception and production, which may be in the interests of the evolution of sociality. It is appropriate that social complexity forms the subject of the next chapter, which explores the relationship of the neocortex ratio and sociality in dolphins.

Chapter 6. Sociality and relative neocortical volume in dolphins.

1. Introduction

Earlier chapters examined the relatedness of the neocortex ratio to foraging ecology and sound. The findings did not provide conclusive evidence that these variables are closely related with, or predictable from, the neocortex ratio, although aspects of sound production were correlated with the ratio. The major remaining category of analysis in relation to delphinid neocortex is sociality. Several studies have been conducted with primates and other terrestrial mammals where the neocortex has been studied in relation to sociality (Dunbar, 1992, 1995; Dunbar and Bever, 1997; Sawaguchi and Kudo, 1990). Within *Cetacea*, a wide range of social structure is apparent, synonymous with social organisation (Whitehead, 1997). Being social or being a part of a school or pod does serve several important functions. These not only include the ecological functions of hunting and protection from predators, but also enable functions such as reproduction and the consequences thereof, including gestation, lactation, maternal investment and individual learning.

Research has promoted the notion that social considerations, more significantly than ecological concerns, have selected for increased brain size in primates (Byrne, 1995; Byrne and Whiten, 1988; Humphrey, 1976). Although these studies have proposed that the developing social structures in primates are linked to the evolution of the brain, a study by Sawaguchi and Kudo (1990) represents the first attempt to provide evidence that neocortical development relates to social structure. The divisions of primate social structure investigated included solitary, monogynous and polygynous species, these being classified in congeneric groups, where congeneric species shared social and ecological commonalties (Clutton-Brock and Harvey, 1980).

Sawaguchi and Kudo (1990) found several interesting relationships. The relative size of the neocortex was independent of brain size or body size.

individual or group movement (Norris and Dohl, 1980; Pryor and Schallenberg, 1991).

Cetacean schools function to allow social integration, with the school being viewed as an equilibrium system, composed of centrifugal forces which promote school cohesion and centripetal forces which spread the school apart (Norris and Dohl, 1980). Different conditions result in drastic alterations to dolphin school size and the spacing of animals and subgroups. Cohesive influences include protection, fright, sleep or rest and familial or habitual associations, whereas dispersive patterns include alertness, aggression, feeding and a lack of association.

Sensory integration is perceived as being a crucial function of the dolphin school, as the school facilitates the integration of individual sensory information for more efficient environmental surveillance, faster reaction time to predators and also enhances the confusion effect (Norris and Johnson, 1994; Norris and Schilt, 1988). Sensory integration is multi-faceted, relying on visual, auditory (active echolocation or passive listening) or taste, temperature variation or tactile sensation. This provides animals with more environmental information, freeing them to engage in various forms of activity (Bel'kovich *et al.,* 1991; Norris and Dohl, 1980).

As dolphins are highly socially advanced (Wood, 1986), their intraschool relationships are expected to be complex. An additional point to consider is that schools are not fixed, invariant groups, but that they constantly vary through individuals or small groups changing from small to large groups (Norris and Dohl, 1980). This is highlighted by Smolker, Richards, Connor and Peter (1992), who suggest that bottlenose dolphins live in fission-fusion societies. Wells, Irvine and Scott (1980) propose that cetacean groups, especially in odontocetes, display great interspecific variation in typical group size, age and sex composition, frequency and duration of interactions and associations. While freshwater dolphins are often solitary or live in small groups, pelagic species reach aggregates of up to several thousand. However, most cetaceans are social (Wuersig, 1986), which confers an advantage to individual members of the group.

The school serves several functions related to more efficient reproduction and the consequences of this for mothers (gestation, lactation and maternal investment), in addition to facilitating individual learning.

The proximity of individuals in a school allows reproductive synchrony to occur at reduced energetic expenditure than if the animals were separated by large distances (Wells, Irvine and Scott, 1980). However, the cost of living in a group is incurred through sexual rivalry (Norris and Dohl, 1980). Reproductive synchrony occurs primarily in migrant species, whereas tropical and sub-tropical cetaceans tend to have broad, unseasonal reproductive modes (Wells, Irvine and Scott, 1980).

Lycett (1995) observes, with specific reference to primates, that females sustain significant reproductive costs. These incorporate prolonged gestation, lactation and weaning, and maternal investment. Life in a social group appears to ease the burden of these costs for dolphin mothers, as allomothering has often been observed (Wells, Scott and Irvine, 1987). In dolphins, the stage of an individual's development appears to determine its location within a school and individual learning is afforded by this (Norris and Dohl, 1980). Mother-young pairs are very common within schools and this dyadic relationship remains important through development of the calf into full maturity. It is often the case that juveniles are located throughout a school and that they may lead the school. Where dominance is concerned, the placing and spacing of subgroups and sexual segregation within the school are important (Norris and Dohl, 1980).

Odontocetes display a highly developed capacity for learning (Herman, 1986). Norris and Dohl (1980) argue that, as with other higher mammals, this capacity appears to suggest the importance of learning in the social systems of odontocetes. They propose that the school is the social unit within which learning becomes meaningful and that the school thus becomes vital as the setting within which the young animal learns and develops. Schools learn to avoid vessels that harass them and approach vessels that provide food. Play appears to be linked to learning, as has been noted with respect to the "practising" of aerial patterns, surf riding and tossing food (Norris and Dohl, 1980). The complexity of dolphin schools is thought to relate to their capacity for complex learning (Herman, 1980) and their comprehension of the contingency patterns necessary for learning to occur (Norris and Dohl, 1980).

1.2. The social structure of delphinid species off KwaZulu-Natal

The difficulties associated with observing dolphins in their natural habitat have precluded our current knowledge of many species (Johnson and Norris, 1986). However, the social structure of the local delphinid species, for which MRI and cranial data were obtained, is summarised using available data. It is important to note that all of the data described for local populations are based on estimates from different sightings. Some estimates are obtained using aerial photography, which has been documented as providing an accurate index of school size (Gilpatrick, 1993). Other estimates are taken from the water and although this method has limitations, it represents the only consistent way of studying grouping in cetaceans (Findlay, pers.comm).

Gaskin (1982) notes that riverine/estuarine bottlenose dolphins have a group size of 5-10 animals, consisting of family units with few adult males in attendance. However, Indian Ocean bottlenose dolphins have a mean group size of 67 animals (Findlay, 1992) with groups displaying dominance hierarchies (Wells, Irvine and Scott, 1980). These bottlenose dolphin group characteristics include adult males, females and offspring; subadult males; subadult females; mixed groups of males and offspring and fluid associations within a school

(Wells, Irvine and Scott, 1980). Inshore forms of bottlenose have maternity groups of 30-40 individuals, sometimes including larger groups of non-lactating females, mature males and adolescent groups for up to several days (Peddemors, 1995). There are also extended mother-calf relations for up to 3 years (Cockroft and Ross, 1990b). Saayman and Tayler (1973:994) suggest that grouping primarily occurs in local bottlenose dolphins to enable co-operative hunting and remark that large schools suggest a “successful adaptation to the exploitation of both the inshore and more prolific pelagic food supply”.

In terms of sociality, common dolphins have been referred to as one of the most gregarious cetacean species, occurring in large schools of up to several hundred and aggregates into the thousands (Cockroft and Peddemors, 1990; Leatherwood and Reeves, 1983). Findlay (1992) observes that the mean group size for common dolphins off the South African coast is 267 animals, although Cockcroft and Peddemors (1990) suggest that larger school sizes occur during the winter months, in association with increased fish abundance.

The small humpback dolphin group size can be contrasted with the large group sizes of other inshore species, such as bottlenose dolphins (Saayman and Tayler, 1973). Humpback dolphin group size is taken to vary from 2 to 5 members, consisting of small family groups and single animals (Gaskin, 1982). Wells, Irvine and Scott (1980) note that humpback dolphins are often alone or in pairs, with groups usually numbering less than 10 individuals and being very labile in character, while groups larger than 10 are of mixed composition. Saayman and Tayler (1979) propose that humpback dolphins display a highly flexible social organisation, with larger groups (above 10) having various subgroups. Most of the pairs or solitary animals are adults, while immatures usually associate in groups with more than one adult. Females appear more resident in an area than males (Durham, 1994). Saayman and Tayler (1973) propose that the restriction of the primary food sources of humpbacks to reefs and rocky feeding grounds may explain their smaller group size and social system.

World-wide, spotted dolphin groups range from 100-500+ members in size, with family units moving within larger, more flexible feeding aggregates (Gaskin, 1982). Findlay (1992) notes that average group size for spotted dolphins in Southern Africa is 94 members, with a range from 200-300 individuals.

Striped dolphin school size in southern Africa varies from four to several hundred members, with the average school size at 75 dolphins (Findlay, 1989). This can be compared with schools captured off the Izu Peninsula, Japan, where no seasonal variation was observed and where the range was from 25 to 2327 animals, with the mean school size at 415 animals. These large schools are often composed of numerous small schools, ranging from 20-200 dolphins. Groups were either composed of immature or mature members while some had mixed membership (Miyazaki, undated manuscript).

Not much information is available for the remaining species off local waters. Fraser's dolphin appears to be gregarious (Peddemors, 1997) and in South African waters groups range from 7 to 1000 individuals, with a mean of 183.1 animals (Findlay et al., 1992). Risso's dolphin is comparatively less sociable than many other species locally encountered, with group sizes ranging from 1 to 80 individuals with a mean of 11.09 (Findlay, 1992). Dwarf sperm whales have a school size of not more than 10 animals and the schools may comprise females and calves, immature groups or sexually mature males and females in the same group.

With reference to these data on group size and resultant sociality of odontocetes off KwaZulu-Natal, this study aims to test the hypothesis that neocortical evolution is correlated with sociality and social complexity in toothed whales and dolphins.

2. Method

It should be noted that the same method has been used as that of section 2 of Chapters 4 and 5 respectively. For the purposes of this thesis, the method sections are not repeated. Instead, for each subsection, the reader is referred to the relevant preceding sections of the thesis for comprehensive details.

2.1. Study animals

The study animals were drawn from the MRI sample and the cranial volume sample in the same manner as previously described in section 4.2.1 (Chapter 4).

The specific sociality variables of mean group size, maximum aggregate size, gestation, lactation and calving interval were obtained from the literature. These variables are noted in Table 6.1. However, it should be noted that data for certain species of different odontocete families are still unavailable, namely for certain platanistids (Brownell, 1984) and some porpoises (Gaskin, 1984).

Table 6.1. Sociality Variables in Odontocetes

Species	Group size (n)	Max. aggregate size (n)	Gestation (months)	Lactation (months)	Interbirth interval (months)
Bottlenose d.	67	1000	12	19	36
Common d.	267	1000	10.5	19	24
Humpback d.	7	20	12	-	36
Spotted d.	94	1000	11.5	19.5	32
Striped d.	75	3000	12	14	40
Spinner d.	128	1000	10.6	18	37
Fraser's d.	183	800	-	-	-
Dusky d.	35	500	11	18	-
Risso's d.	11	300	12	-	-
False Killer w.	16	300	16	18	-
Pygmy Killer w.	11	300	-	-	-
Killer w.	10	100	17.2	12	68
Short-finned pilot w.	14	500	15.5	24	78
Dwarf Sperm w.	8	10	-	-	24
Pygmy Sperm w.	4	10	11	-	-
Indus River d.	5	10	10.5	-	24
Harbour p.	5	250	10	8	18
Burmeister's p.	5	8	-	-	-
Gray's Beaked w.	5	10	13.9	7	24

Note: Data sources. Group size: bottlenose: Peddemors *et al.* (sub); common, dusky, false killer whale, Fraser's, Risso's, spotted, striped: Findlay *et al.* 1992; humpback: Durham, 1994; Indus River dolphin, spinner and Gray's beaked whale: Evans, 1987; porpoises: Evans, 1987; Leatherwood and Reeves, 1983; pygmy killer whale: Best, 1970; pygmy sperm whale: Leatherwood & Reeves, 1983; short-finned pilot whale: Ross, 1984; Killer whale: Findlay *et al.*, 1992 and Sylvestre, 1995. Maximum aggregate size: all species: Evans, 1987. Gestation: bottlenose: Cockcroft and Ross, 1990a, common: Mendolia, 1990; Gray's beaked whale, Indus River dolphin, pygmy sperm whale, short-finned pilot whale: Evans, 1987; harbour porpoise: Perrin and Reilly, 1984; humpback: Cockcroft, 1989; false killer whale: Evans, 1987, Perrin and Reilly, 1984; spinner, killer whale: Evans, 1987 and Sylvestre, 1995; striped and spotted- Perrin and Reilly, 1984 and Evans, 1987; Risso's: Sylvestre, 1995. Lactation: dusky dolphin, harbour porpoise, Gray's beaked whale, killer whale, short-finned pilot whale: Evans, 1987; bottlenose, common, spinner, striped and spotted- Perrin and Reilly, 1984, and Evans, 1987. Interbirth interval- bottlenose, Cockcroft and Ross, 1990a; dwarf sperm whale, harbour porpoise, Gray's beaked whale, Indus River dolphin, spinner: Evans, 1987, humpback, Cockcroft, 1989; common- Mendolia, 1990; short-finned pilot whale, striped: Perrin and Reilly, 1984 & Evans, 1987; spotted- Perrin and Reilly, 1984;

2.2. Materials

The materials used, both from the neuroimaging component and the cranial analysis component are described previously. For a brief description, refer to section 2.2 (Chapter 4).

2.3. Procedure

The actual MRI neocortex data for the major study species and the delphinids and the estimated neocortex data for the delphinids and the odontocetes from cranial analysis were related to the set of sociality variables. The data were analysed using SPSS and results were accepted as significant at an alpha level of .05.

3. Results

3.1. Correlational analysis

The nature of the correlations between the sociality variables and the neocortex ratio were established (Table 6.2). Mean group size does not generally appear to be related to the C_R, although there is a trend towards a negative relationship for these variables from the MRI delphinid data. Maximum aggregate size approaches significance with respect to the C_R, where a positive trend is evident.

Lactation is not at all related to the C_R. While gestation and the intercalf interval are not related to the C_R for the MRI sample of major species or other delphinids, several relationships are present with respect to the estimated neocortex data. Gestation is positively related to estimated C_R in delphinids and other odontocetes and shows a trend towards this in estimated data for the major species. The same situation is apparent for the intercalf interval (Table 6.2).

Table 6.2: List of correlations for sociality variables with the neocortex ratio

	major species[1]	major species[2]	delphinids[1]	delphinids[2]	odontocetes[2]
mean group size	n.s	n.s	n.s	n.s	n.s
maximum aggregate size	.969 (3) .08[3]	n.s	n.s	-.407 (13) .084[3]	n.s
gestation	n.s	.977 (3) .068[3]	n.s	.709 (11) .007*	.708 (14) .002*
lactation	-.975 (3) .07[3]	n.s	-.975 (3) .071[3]	n.s	n.s
interbirth interval	n.s	.977 (3) .068[3]	n.s	.554 (8) .077[3]	.572 (11) .033*

Note: [1] refers to MRI neocortex data for major delphinid species of interest and delphinid species in general; [2] refers to estimated neocortex data for major delphinid species, delphinid species in general and the wider suborder of odontocetes; n.s.- not significant at $p < .05$; [3]potential trend, *significant relationship. Results presented i.t.o. r value, n, p value.

3.2. Weighted Linear Regression

The dependent (study) variables of sociality and the independent variable, C_R, were logarithmically transformed to linearise the data. From this, linear regression analysis was performed. The regressions were weighted by the frequency of individuals represented within each species and the results are evident in Table 6.3.

Mean group size for delphinid species shares a significant relationship with the C_R. The resultant equation to predict group size from neocortex is provided below and the relationship is illustrated in Figure 6.1:-

$$\log(\text{mean group size}) = -17.58 + 33.411 \log(C_R)$$

Maximum aggregate size in delphinids is also positively related with C_R, although not as significantly as mean group size. The predictive equation for aggregate size from C_R is presented below and displayed in Figure 6.2 :-

$$\log(\text{maximum aggregate size}) = -18.955 + 37.128 \log(C_R)$$

The reader is cautioned to observe the outlier (humpback dolphin) in Figure 6.2. As a result of the small sample size, it was decided not to remove species data points from the analysis. However, it is possible that if the humpback dolphin were removed, the relationship might not hold. Finally, none of the other sociality variables are related to the C_R of the MRI study species.

Table 6.3: sociality variables in relation to C_R data from MRI

Dependent Variable	adjusted r^2 value	F value (d.f.)	p value
mean group size	.72	13.828 (4)	.021*
maximum aggregate size	.674	11.332 (4)	.028*
gestation	.235	2.228 (3)	n.s
lactation	.355	2.101 (1)	n.s
interbirth interval	.187	1.92 (3)	n.s

note: *significant, n.s- not significant at $p < .05$.

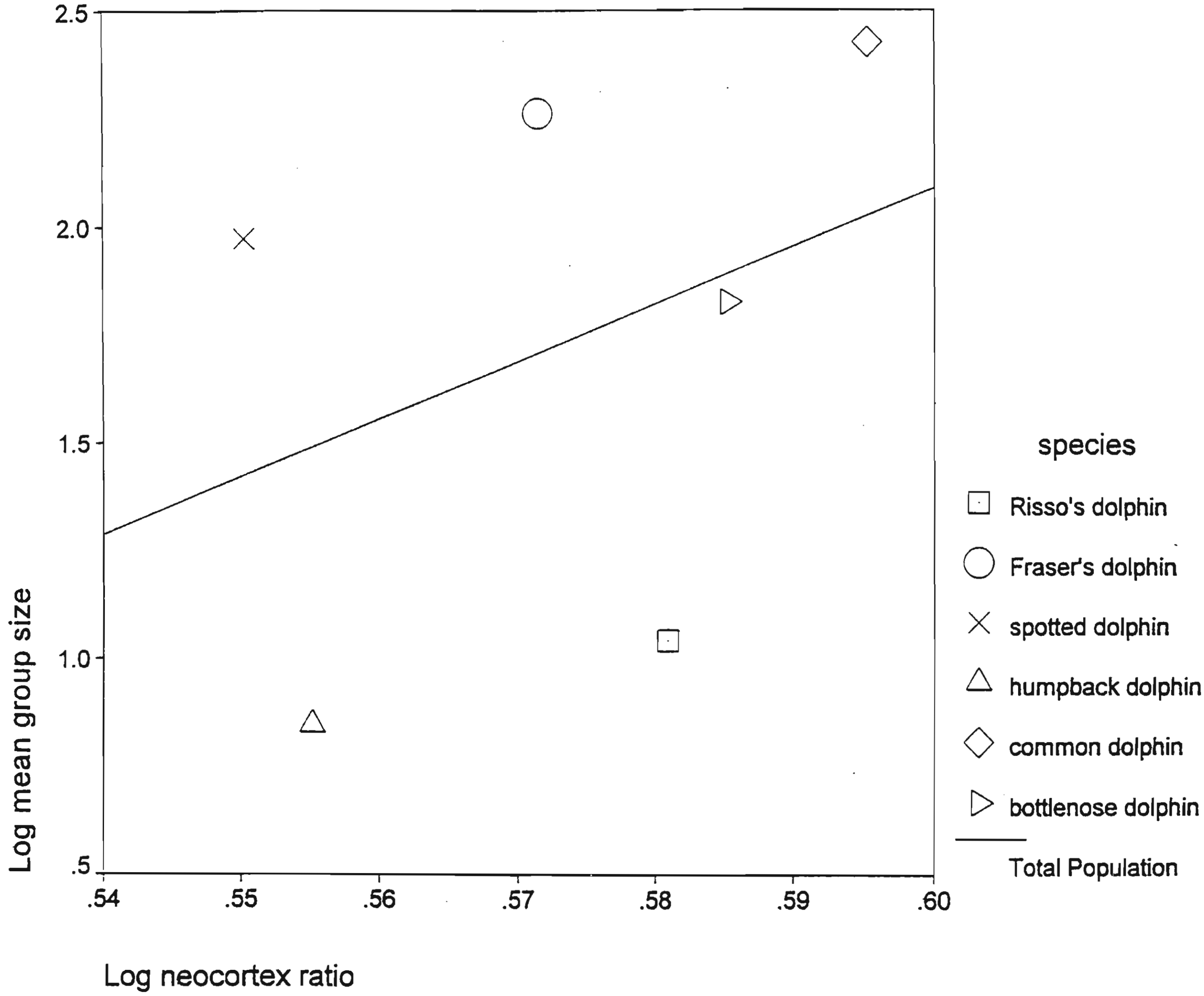


Figure 6.1. Mean group size and the neocortex ratio for MRI dolphin data.

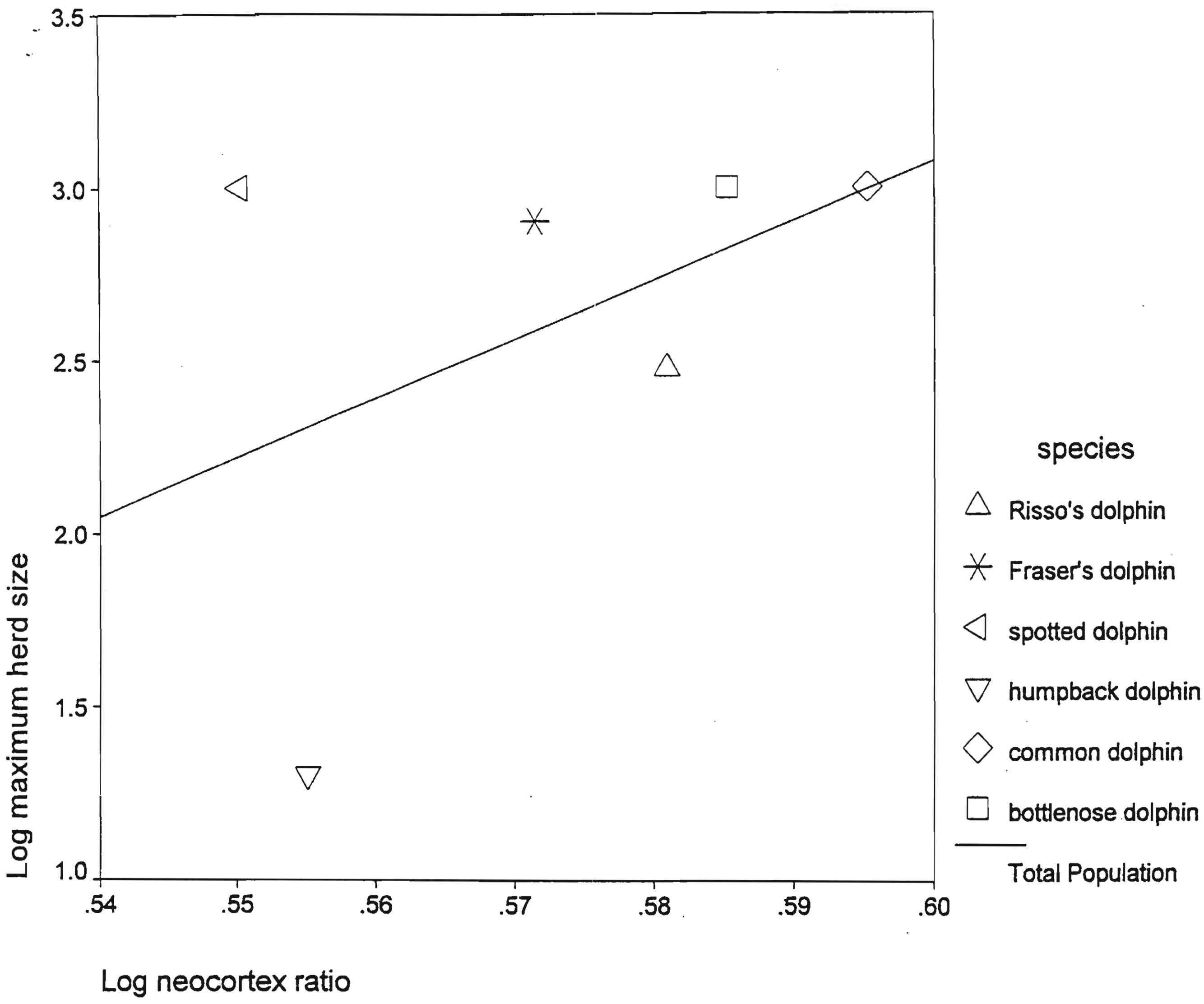


Figure 6.2. Maximum aggregate size and the neocortex ratio for MRI dolphin data.

The set of sociality variables were also tested for predictability in relation to estimated C_R values for delphinids and odontocetes. Once again, the variables were logarithmically transformed and the regressions were weighted by the frequency of individuals within each species (Table 6.4). The results of the correlations and regression tests are different as a consequence of the methods used in the regression tests (weighting by least squares).

For the delphinids, all of the sociality variables do not appear to be predictable from the C_R. The only variable that shows a slight trend towards relatedness with the C_R is the gestation period. A similar situation is evident with respect to the data for the order *Odontoceti*, where most of the variables are unrelated to C_R. The exception is gestation period, which is significantly related to the C_R for odontocetes. The predictive equation is as follows and is presented in Figure 6.3:-

$$\log(\text{gestation period}) = .377 + 1.226 \log(C_R)$$

Table 6.4: Sociality variables in relation to estimated C_R data.

	Delphinids			Odontocetes		
Dependent Variable	adjusted r^2 value	F value (d.f.)	p value	adjusted r^2 value	F value (d.f.)	p value
mean group size	.044	1.557 (11)	n.s	.059	.047 (16)	n.s
maximum aggregate size	.012	.875 (11)	n.s	.062	.001 (16)	n.s
gestation	.213	3.71 (9)	.086^1	.232	4.933 (12)	.046*
lactation	.117	.160 (7)	n.s	.005	1.054 (9)	n.s
intercalf interval	.071	.537 (6)	n.s	.087	1.958 (9)	n.s

note: ^{1}potential trend, *significant relationship, n.s- not significant at $p < .05$.

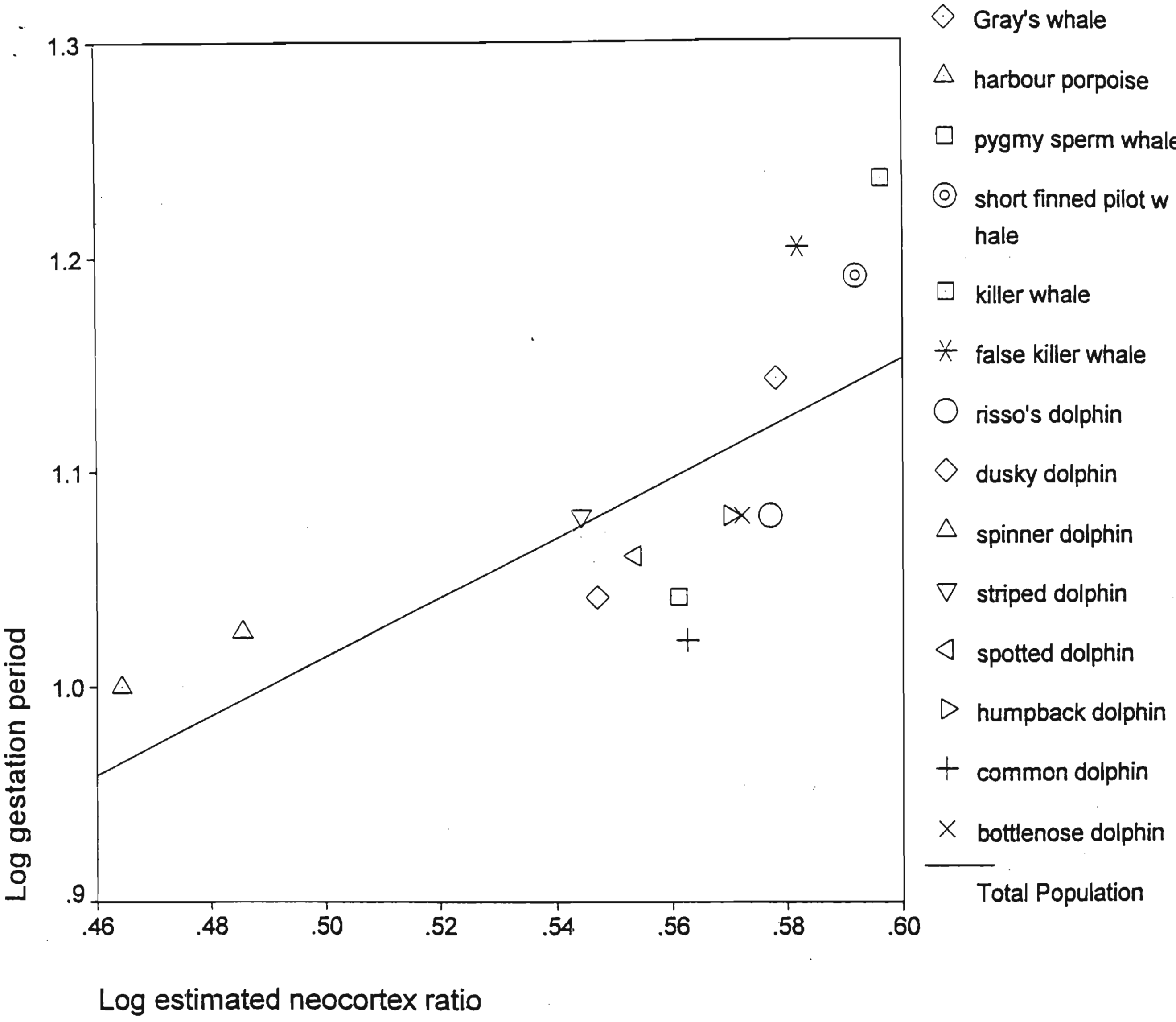


Figure 6.3. Gestation period and estimated C_R values for odontocete data.

3.3. Correlations of significant variables with other study variables

Mean group size and maximum aggregate size are related to C_R in the MRI study species, while gestation appears related with the estimated C_R in odontocetes. All of the study variables were subjected to a correlational analysis with group size, aggregate size and gestation period, to establish what other variables may be of potential significance.

This analysis operated at different taxonomic levels. In odontocetes, gestation appears to be significantly correlated with interbirth interval, foraging depth, number of sound types and dietary diversity. Gestation also shows a trend towards a relationship with mean group size and minimum signal duration in odontocetes (Table 6.5).

Table 6.5: Study variables significantly correlated with odontocete gestation

correlate	r	n	p
foraging depth	.698	13	.004*
interbirth interval	.828	11	.001*
mean group size	-.354	15	.098[1]
minimum signal duration	.624	6	.093[1]
sound types	.819	8	.006*
SWI dietary diversity	-.712	9	.016*

note: *significant relationship ($p < .05$), [1]potential trend ($p < .1$)

Maximum aggregate size in the MRI species appears to be perfectly correlated with minimum signal duration, although the small sample dictates caution. The next most significant relationship concerns the ratio of total prey species to fish prey species. It appears that this ratio is negatively correlated with herd size, implying that animals with less individual fish species in their diets live in larger aggregates. There is also a negative correlation with total number of prey species, implying that more diverse feeders are encountered in smaller aggregates. Mean group size approaches a positive association with herd size (Table 6.6).

Table 6.6: Study variables significantly correlated with aggregate size in species subjected to MRI

correlate	r	n	p
mean group size	.672	6	.072[1]
minimum signal duration	1	3	.000*
total prey species	-.739	6	.047*
total:fish prey species ratio	-.927	5	.012*

note: *significant relationship ($p < .05$), [1]potential trend ($p < .1$)

In the MRI study species, mean group size shares a significantly negative relationship with gestation period and the interbirth interval. A trend towards a positive association with maximum aggregate size is also evident (Table 6.7).

Table 6.7: Study variables significantly correlated with group size in MRI species

correlate	r	n	p
gestation period	-.973	5	.003*
interbirth interval	-.972	4	.014*
maximum aggregate size	.672	6	.072[1]

note: *significant relationship ($p < .05$), [1]potential trend ($p < .1$)

4. Discussion

Several features of sociality appear to be related to the neocortex ratio in delphinids and odontocetes. This is not surprising when one considers the social complexity of toothed whales from an aquatic perspective, in relation to other mammals.

The social structure or social organisation of an animal is perceived to be the consequence of a consistent network of social relationships, which are sustained through the social interactions of individuals (Hinde, 1976, 1983; Lott, 1991).

In the current study, an intricate regression analysis revealed that maximum aggregate size and mean group size were significantly predictable for the actual delphinid MRI neocortex data, although not predictable from the estimated data for delphinids (section 3.2).

When considering the sociality of marine animals, the most obvious causal difference between dolphin and fish schools stems from the complex sociality of delphinids and the phylogenetic difference to fish schools. In addition, the neural organisation of mammals is more advanced than that of piscenes (Norris and Dohl, 1980). Therefore, fish schools do not exhibit the social features of families or play groups, neither do they have well developed parental care and/or familial bonds. As opposed to the short duration of fish mating, dolphin reproductive patterns occur in different social contexts. In addition, Connor and Norris (1982) have indicated that dolphin schools possess a higher level of complexity than fish schools as a consequence of their cultural tradition, where culture is considered to be the transmission of behaviour between individuals through learning or teaching (Bonner, 1980). For such a society to confer an advantage on its members, there must be co-operation between individuals, predictable behaviour and certain compromises in the expression of individuality (Bonner, 1980; Norris and Schilt, 1988).

The complexity of dolphin societies is recognisable. Certain cetacean species have segregated age and sex subgroups, while most have mixed age-sex groupings (Wells, Irvine and Scott, 1980; Wells, Scott and Irvine, 1987). In bottlenose dolphins, the most common groupings include mother-calf pairs, mixed sex and single sex groups of subadults, bands of females and recent offspring and small units of adult males (Wells, 1991). The major subgroups observed in spotted dolphins include female-calf pairs, female-young subgroups, juvenile subgroups, adult male subgroups and young adults (Pryor and Schallenberger, 1991). The intensity of interaction and association may vary from swimming together in migration, for example common dolphins, to being part of a permanent family unit, for example, killer whales (Ford and Fisher, 1983). For bottlenose dolphins, the composition of the group may vary dynamically within a stable herd, although subgroup associations display a greater duration (Wells, Irvine and Scott, 1980).

Yet, it is interesting that the predictive relationship of group or aggregate size from the neocortex ratio does not extend to the suborder of odontocetes in general (section 3.2). As the delphinids are the youngest derived family within the odontocetes, this may indicate that social complexity is a recent evolutionary phenomenon. This assertion can be supported by considering the sociality of the relatives of the toothed whales, the baleen whales and terrestrial mammals.

It should be noted that baleen whale school structure does not generally resemble the tightly cohesive schools of toothed whales, as the schools of the former species are more widely dispersed or individuals live solitarily (Norris and Dohl, 1980). This may be as a result of their capacity for long distance communication. However, although being recognised as less socially complex, these cetaceans do form large aggregates at breeding, calving or feeding grounds (Norris and Dohl, 1980).

Comparisons between inshore odontocete and terrestrial mammal social behaviour and structure indicate that dolphins and ungulates both display allomothering, care-giving behaviour, dominance hierarchies and group defence. For example, African buffalos and bottlenose dolphins have herds and schools of fixed home ranges, with slight overlaps, while the groups display mixed and fluid constitutions, and group defence (Wells, Irvine and Scott, 1980). In addition, the convergence of the social structure of dolphins and carnivores, such as lions, has drawn comment and is believed to hold considerable evolutionary significance (Wells, Scott and Irvine, 1987). Even more relevant to this discussion are the similarities in sociality between certain cetaceans and primates.

The social organisation of bottlenose dolphins has been described as being very similar to that of certain primate species (Tayler and Saayman, 1972). For example, it has been found that bottlenose dolphins and baboons both form dominance hierarchies, mate via rotating consort relationships without permanent sexual pair bonds and both have group defence. Chimpanzees and bottlenose dolphins both have well defined, stable home ranges, with fluid composition of subgroups within the group, dominance hierarchies and co-operative hunting and defence also occurring (Wells, Irvine and Scott, 1980). Although Smolker, Richards, Connor and Pepper (1992) observe that the social structure of certain dolphins and primates is similar, they suggest that the biggest differences between the two are the less closed social units of dolphins and the greater rate of consistency in adult associations in dolphins.

Yet one may justifiably ask why there is such a fuss about sociality. Sociality serves the cause of adaptation in two main ways, through the prolonged dependence that allows infants to explore and through the possibility of allowing these younger animals to interact with and learn from older, experienced animals (Humphrey, 1976). It follows that there will be selection for a longer dependency and a larger number of learned animals and thus an enlargement of the group.

Joffe (1997) has partially confirmed this for primates, by verifying that social pressure has selected for a period of extended learning. However, the bigger and more complex the group becomes, the more difficult resources are to locate, obtain and share (Carr and Macdonald, 1984; Humphrey, 1976).

It takes considerable cognitive effort to maintain group cohesion under such conditions and Humphrey (1976) therefore suggested that such societies would become more complex. In the light of this, it was proposed that to promote social living, the animal would have to have evolved greater cognitive capacities (Sawaguchi and Kudo, 1990).

In primates, neocortex is closely related to social structure, where the association is not the result of the relationship between neocortex and diet or activity timing (Sawaguchi and Kudo, 1990). It was observed that polygynous monkey species had more fully developed neocortical areas than monogynous monkeys. This is relevant as neocortical areas are located in the prefrontal and temporal cortices, used in social behaviours such as facial recognition, allogrooming, vocalisations and maternal behaviour (Sawaguchi and Kudo, 1990).

According to Kling (1986), these cortices are vital for maintaining social cohesion and affiliative behaviour in polygynous anthropoids. Polygynous monkeys, prosimians and apes have larger prefrontal cortices than their monogynous counterparts (Sawaguchi and Kudo, 1990). As it is believed that social animals engage in more complex social interactions, they require greater social skills to survive. Social skills are necessary for what has been termed primate "Machiavellian" intelligence (Byrne, 1995; Whiten and Byrne, 1988) and it thus becomes apparent why more socially complex animals should possess larger relative neocortices. It is suggested that the prefrontal cortex, (deemed responsible for social interaction) is the greatest in humans over all other primates. As social bonds and communication are associated with polygyny, this is regarded as being linked to the development of neocortex and the prefrontal cortex in human evolution (Sawaguchi and Kudo, 1990).

Dunbar (1992) has argued that in primates, group size is a function of relative neocortex size, whereas ecological variables are not. He proposes that the number of neocortical neurons limits the capacity of information-processing in the individual, which in turn determines how many relationships the individual can sustain. Once the group limit is reached, it begins to splinter, providing evidence that there is a maximum limit to any species group size in which cohesive social bonds can be maintained (Dunbar, 1992).

The current findings for the relationship between neocortex and sociality for dolphins concur with those for primates (Dunbar, 1992), insofar as relative neocortical volume can constrain or extend group size (section 3.2). This is noteworthy as, to date, only carnivores have displayed such a relationship (Dunbar and Bever, 1997) and it appears that such a relationship in evolutionarily divergent dolphins has not been previously anticipated.

In the current study, the maximum aggregate size and mean group size of dolphins can in turn be shown to correlate with other study variables representing foraging ecology, sound and sociality (section 3.3).

Dolphins in smaller aggregates produce signals of shorter duration than animals in larger aggregates ($p < .001$). One might speculate that this may have something to do with the need of more solitary animals for more constant updates of information regarding prey or predators. Alternatively, it may have something to suggest about the communicative content of the signal, with animals in larger groups conveying more content to each other. It is apparent that further research is required to interpret such findings.

Animals that live in larger aggregates eat a smaller number of prey species and are less diverse foragers than those in smaller aggregates (p<

.05). In addition, members of larger aggregates eat a larger number of fish in proportion to their total diet than their counterparts, who prey more on squid ($p < .05$). Dolphins in groups can afford to be more selective in terms of their dietary intake, as co-operative hunting allows for the detection of optimal prey. Fish are more nutritious than squid (Clarke, 1986) and as such, are considered to be a more lucrative prey source for dolphins. It follows that animals in larger groups can hunt co-operatively and strategise to capture fish, whereas more solitary animals cannot (Johson and Norris, 1986).

Such relationships serve to illustrate that although it may be necessary to separate aspects of sociality from other aspects of ecology, such as foraging or sound, it is ultimately an artificial distinction. Although a larger neocortex may permit life in a bigger social group, the size of this group also has an impact on current and future communicative and foraging strategies.

This assertion can be justified in terms of the socioecological reasons proposed for dolphin group size. For example, the positive correlation of water depth and group size and the negative correlation of body size and group size are believed to be both a function of foraging strategies and predation pressure (Johnson and Norris, 1986). This basis of grouping may function in subtle ways. For example, it is apparent that dolphins with smaller mean group sizes exhibit longer gestation than their counterparts in larger groups ($p < .01$). A shorter gestation period could merely be a consequence of being a smaller animal. When one considers that smaller animals live in bigger groups (Johnson and Norris, 1986), the above finding becomes explicable. Variables of socioecology therefore only appear to be divisible to a degree, in the pursuit of theoretical clarity.

Early works on socioecology commented on the role of males in the categorisation of social structure (see Eisenberg, Muckenhirn and Rudran, 1972). However, in the light of the current theory on the importance of females, it seems more appropriate that later investigations considered the significance of females to social organisation (Andelman, 1986; Wrangham, 1980). It follows that maternal investment and infant relationships need to be conceptualised within the broader context of social structure.

Gestation period was positively associated with the estimated neocortex data for delphinids and odontocetes ($p < .01$), while the interbirth interval was positively correlated with the odontocete estimates ($p < .05$). Lactation was the only variable for the delphinid values from MRI that showed a trend towards a relationship with the neocortex ratio (section 3.1). However, when subjected to regression analysis (section 3.2), of all of the maternal variables, only gestation in odontocetes was predictable from the neocortex ratio ($p < .05$). This supports the suggestion of Ridgway (1986a), in relation to the postnatal environment, that the longer gestation period evident in cetaceans might allow the neonate to be involved in complex activities that require a more developed brain.

The reproductive success of the mother is essentially dependent on her capacity to provide sufficient resources for herself and her offspring through gestation and lactation (Pereira and Altmann, 1985). The determination of gestation limits appears to be crucial to mammalian brain development (Hofman, 1983b). It was found that two mammalian clusters exist in relation to neonatal indices, one for primates and certain cetaceans (with prolonged gestation) and the other for placental, non-primate mammals (Hofman, 1983). Hofman has suggested that this provides enhanced protection from environmental hazards, allowing optimal brain development to occur.

Lactation has been recognised as a highly beneficial way of transferring energy from the mother to her young (Pond, 1977), as well as being a means of delivering a constant supply of resources whereby the infant is not directly dependent on the surrounding environment (see Lycett, 1995). However, the cost of lactation is the energy that mothers have to expend to maintain their infants (Dunbar and Dunbar, 1988). Be this as it may, as young primates display prolonged dependency on their mother, her ultimate reproductive success lies in facilitating the development of her infant into an adult (Dunbar, 1988).

The best impression of maternal investment can be derived from the definition of parental investment. This encompasses any action taken by the parent in the survival interest of the infant, while forfeiting investment in other offspring (Trivers, 1974). Maternal investment therefore transcends the period of lactation and that of weaning, which in addition to a decline in milk transfer from mother to offspring also entails a vast period of behavioural transition to adult life (Lycett, 1995). Thus animals that display a longer interval between calves or offspring may be said to endure greater maternal investment. A consequence of this greater investment is the capacity for the offspring to learn and develop within a safe environment and social context.

Gestation relates to other odontocete study variables (section 3.3). The findings imply that deeper and less diverse foragers experience longer gestation ($p < .01$ and $p < .05$ respectively). These findings draw some support for Milton (1988), who proposed that sociality in itself is not sufficient in explaining human brain size and suggested that diet should not be excluded from consideration, as it is related to both RBS and sociality. In relation to other variables of sound and sociality, animals with longer gestation experience greater intervals between calves ($p < .01$) and are also more diverse sound producers ($p < .01$). From the current findings, it appears that mother-offspring variables, such as gestation and maternal investment, deserve greater attention in future studies of social complexity.

It appears as if the “symmetrical relations” between group members may serve a variety of functions aside from co-operation during hunting. Following the discussion on dolphin mothers, it may be pertinent to recognise that an important function relates to supervision of the young (Johnson and Norris, 1986).

Supervision of the young has been observed in the form of nursery groups of adults and young dolphins in dusky dolphins (Wuersig, 1986) and in "baby-sitting" by relatives, other mothers and adult males in spinner dolphins (Norris et al., 1992). It is interesting to note that animals in larger groups display longer intervals between births than those in smaller groups ($p< .05$), as the presence of helpers should imply shorter birth intervals. However, it may be that greater maternal investment is afforded within an extended social group, where relatives and care-givers can provide assistance and calves can enjoy prolonged learning and group membership (Wells, Irvine and Scott, 1980).

The suggestions of Hamilton (1964, 1972) on the evolution of social behaviour and the resultant increased fitness of interacting individuals draw support with respect to dolphins, for whom the co-ordination of roles and co-operation between school members allow for shared resources and responsibilities (Johnson and Norris, 1986).

Co-operative behaviour in cetaceans includes shared guardianship and care of the young, alloparental care, resource advertisement, co-ordinated foraging and hunting, defense of mature conspecifics, possible shared suckling, turn taking in forms of aerial behaviour, echolocation and social interaction and finally, stranding (see Bradbury, 1986; Norris and Schilt, 1988 for reviews). Dolphins are said to display "the co-operative disposition" (Norris and Schilt, 1988:169), in that they abide by the rules of the group. Such co-operation may transcend species and ordinal boundaries. For example, wild killer whales have been known to interact co-operatively with human whalers by detecting and assisting in the capture of prey (Jefferson, Stacey and Baird, 1991).

As membership of a group is thought entail much greater complexity than the more simple concept of aggregating (Norris and Schilt, 1988), it comes as little surprise that of the two variables maximum aggregate size and mean group size, the latter shared the strongest predictive relationship with the neocortex ratio. When compared to the findings of the other chapters, mean group size continues to be the strongest variable related to the neocortex ratio. For example, to extrapolate from the primate theory of neocortical evolution, one would expect the finding that humpback dolphins have lower neocortex ratios than bottlenose or common dolphins, as they evidence less diverse behaviour than these other species (Karczmarski, Thornton and Cockroft, 1997). Dolphin sociality is diverse, complex and comparable to that of other mammals and the current findings support the call for further investigation.

Consistent co-operative relationships have been referred to as alliances (de Waal & Harcourt, 1992) and these are considered to be rarely formed by non-primate species (Harcourt, 1988). Several documented cases of alliance formation have been reported in spotted dolphins (Pryor and Schallenberger, 1991) and in bottlenose dolphins (Wells, Scott and Irvine, 1987), with specific reference to the herding and theft of females (Connor, Smolker and Richards, 1992a). Multi-level alliances have been exclusively observed in dolphins and humans, with the suggestion that these may have contributed to the selection for and evolution of the large dolphin brain (Connor, Smolker and Richards, 1992a, 1992b).

It has been suggested that dolphins display reciprocal altruism (Connor and Norris, 1982). This concept can be considered as being the performance of an act at a cost to the actor, in the interests of a non-relative, the benefit of which accrues through the reciprocity of action by the recipient at a subsequent stage (Alcock, 1993; Axelrod and Hamilton, 1981; Trivers, 1971). Johnson and Norris (1986) propose that certain dolphin species satisfy the criteria for this model. These include: frequent and recurring contact between animals to either demonstrate reciprocity or to identify cheaters; fair life expectancy; learning of socially appropriate responses within a substantial period of development and finally, sufficient memory to monitor other individuals and the nature of their relationships. Norris and Schilt (1988) suggest that true reciprocal altruism may only exist in the fluid societies of pelagic species, where echolocatory capacities reduce the risk of predation and allow for the expression of mammalian social patterns (see Norris, Wuersig, Wells and Wuersig, 1990 with reference to spinner dolphins).

Smolker *et al.* (1992:66) consider that the social relationships of each individual dolphin are sustained within a dynamic social environment, "perhaps placing a premium on the evolution of cognitive abilities". Connor, Smolker and Richards (1992a) claim that the intricate nature of alliance formation supports the hypothesis that social complexity has been responsible for the selection of larger brains (Cheney, Seyfarth and Smuts, 1986; Whiten and Byrne, 1988; 1997). This appears to be the case (above) with respect to the neocortical evolution of dolphins, as the neocortex ratio is predictive of group size for several of delphinid species.

Before concluding the chapter, it may be of interest to consider the findings of Roehrs (1985), who suggested that domesticated animals displayed significantly reduced neocorticalisation when compared to their untamed relatives, the reduction being primarily correlated with their altered behaviour. Suffice it to say that the social complexity of behaviour is currently being afforded the greater attention that it deserves, in relation to neocortical and intellectual evolution.

If one takes a behavioural account of dolphins, their considerable maternal investment and the complex and fluid nature of their societies, the relationship between mean group size and neocortex becomes more appreciable. However, it does not suffice to stop the discussion at this point. Aside from certain primates sharing an association between relative neocortical volume and sociality, the only other order of mammals to show this relationship are the carnivores. Thus the significance of the current study is not only that dolphins have neocortex ratios higher than all other species, except for humans, but also that this appears to be more strongly related to sociality than is apparent in any other order of mammals. The sociality of dolphins is complex and this is reflected by evidence of reciprocal altruism in dolphins. The potential implications of these findings for a wide spectrum of research, ranging from comparative studies to cognitive evolution, are discussed in the following and final chapter.

Chapter 7. Comparisons of delphinid and primate neocortex and its correlates: Implications for mental evolution

1. Summary

This study has successfully established the relative neocortex size and neocortex ratios (C_R) of dolphins and related these to several variables of delphinid behavioural ecology. The findings are briefly highlighted and related to the wider literature.

The absence of data on relative neocortex size and its correlates in dolphins and other marine mammals was discussed and the importance of such data for comparative purposes was recognised in Chapter 1.

The novel application of the radiological techniques of CT and MRI for the establishment of data for the volumes of the cranium, the brain, the neocortex and other brain regions are described in Chapter 2. From these CT and MRI volumes, C_Rs were calculated for several species of dolphins resident off the KwaZulu-Natal coast. The discovery that dolphin cortical material could be frozen, defrosted and used with accuracy in MRI calculations was consequential, as it permitted the use of a larger sample. In addition, the lack of variance in the C_Rs between different delphinid sex and sexual maturity categories allowed for the combination of individual specimens in the analysis. Human C_Rs were also established and these appear to be substantially higher than those documented by Dunbar (1992). However, as these were obtained from a convenience sample and present a large degree of variance between sexes, it is apparent that more revision is required before drawing definitive conclusions. The most important finding, for the purposes of this study, was the high C_R displayed in all of the dolphin study species. These values lie above the range of those of non-human primates and are in close proximity to documented human scores at 4.1

(Dunbar, 1992, 1995), with the common dolphin at 3.938 displaying the highest value.

As a consequence of such high delphinid neocortex ratios, it became apparent that further investigation was required. Chapter 3 applied the equations developed from CT and MRI to cranial volume data obtained for 19 different species of toothed whales at the PE Museum. From the resultant estimated brain and neocortex volumes, neocortex ratios were estimated for animals randomly selected as representatives of species from the wider catch population. Data for MRI subjects not matching the species parameters were excluded from further analysis. In addition, access was gained to a much wider range of species than possible using MRI. The estimated neocortex ratios confirmed that the equivalent scores from MRI were accurate and verified that dolphins do have extremely large neocortices, in relative terms.

The MRI and estimated delphinid and odontocete neocortex ratios were related to variables representing foraging ecology in Chapter 4, as these variables appear to relate to the neocortical evolution of other, non-primate, mammals (Dunbar and Bever, 1997). It was therefore surprising to learn that dolphin neocortices do not appear to be related to foraging, nor predictive of aspects of foraging ecology.

However, before assessing whether or not delphinid neocortex ratios might be related to sociality, it was proposed that sound could be conceived of as a mediator between its use for foraging and social purposes in dolphins. Chapter 5 examined several aspects of sound production and perception in relation to the neocortex ratio. It was consequential that relationships were apparent between the neocortex ratio and sound frequency range, minimum frequency, minimum signal duration and the range of signal duration. More importantly, it appears as if the sound frequency range is predictable from the estimated delphinid neocortex ratios. This is of interest, as it is primarily their auditory capacity that sets dolphins apart in the mammalian world. Purves and Pilleri (1983:252) hint at the significance of sound in relation to the brains of dolphins:

> The really spectacular and mysterious feature of the dolphin is the immensely large size and complexity of the brain which is comparable with that of human beings. What proportion of the cerebral cortex is involved in the storage and processing of acoustic information is not known, but it must be quite considerable judging by the large size of the acoustic nerve.

The current findings are also supported by a wealth of literature describing delphinid auditory capacities. (Au, 1993; Herman, 1980, 1986, 1991; Herman, Pack and Wood, 1994; Richards, 1986; Richards, Wolz and Herman, 1984). In addition, sound shares an important relationship with other delphinid sensory capacities and this makes its relationship with neocortex even more interesting (Pack and Herman, 1995). Using experimentation with cross-modal transfer, it has been suggested that dolphins use echolocatory information as the basis of their object-based representational system (Harley, Roitblat and Nachtigall, 1996; Helweg, Roitblat, Nachtigall and Hautus, 1996).

It has been suggested that the auditory capacity of dolphins is best illustrated through their performance at sentence comprehension, where they display correct semantic and syntactic interpretation (see Herman, 1991 for review) and evidence of learning different syntactic rules, understanding novel sentences, labelling objects and reporting (Herman, 1986).

It is notable to recognise that the sound related findings of this study reinforce the notion that dolphins use sound for social purposes (Bauer and

Johnson, 1994; Herman, 1980; Janik, Dehnhardt and Todt, 1994; Reiss and Mccowan, 1993; Tyack, 1986; Wilson, 1975).

It has been proposed that killer whale dialects are passed to successive generations through cultural transmission (Ford and Fisher, 1983). Whereas initial efforts failed to establish a relationship between acoustics and social behaviour in mysticetes (Best, 1970), Clark (1983) found support for this relationship in Southern Right Whales, where sound complexity was directly related to the complexity of the social context . The large variation in annual humpback song is supposedly transmitted by learning and viewed as cultural evolution, as the songs are learned traits which evolved over time (Payne *et al.,* 1983). Such social tradition may also serve to transmit knowledge concerning prey, predators and the environment in social mammals and this may contribute to the phylogenetic difference in behavioural capacity and flexibility between mammals and fish (Wuersig, 1986).

The findings of predictive relationships of delphinid sound production, group size, aggregate size and gestation period from their neocortex ratios suggest that these features may have co-evolved in dolphins. This is interesting, considering that Dunbar (1993) has suggested the co-evolution of language, group size and neocortex size in humans. With the increasing social complexity of humans, language is considered to be a more effective means of social cohesion than the standard primate method of grooming (Dunbar, 1993). Aiello and Dunbar (1993) have noted that language is a recent evolutionary development in humans. However, Lilly (1978) proposed that unlike non-human primates, humans and dolphins share in possessing sophisticated capacities for elaborate communicative sound use. Perhaps future research will provide more insight into the combination of social and communicative evolution through comparisons between dolphins and humans. Nonetheless, this study suggests that delphinid sound and sociality are linked through their predictable relationship with the neocortex.

In the light of this, chapter 6 examined the delphinid neocortical data in relation to variables representing their sociality. This chapter yielded the most substantial findings of the correlational section of the study. Mean group size and maximum aggregate size were predictable from the delphinid MRI neocortex ratios, while gestation period was predictable from the estimated ratios for odontocetes. It was also interesting that these sociality variables were correlated with other variables representing sound and foraging ecology. However, the significance of the finding lies in that, to date, the relationship between neocortical evolution and sociality has apparently been exclusively displayed in primates (Dunbar, 1992, 1995; Dunbar and Bever, 1997). This distinction is not supported by the findings of this study, which reveal a strong association between delphinid neocortex and their intricate social organisation.

Once again these findings are supported by the documented literature regarding the complex nature of dolphin societies and social groups. Wells (1991:223) suggests that insight can be gained into the evolution of delphinid sociality by comparing their "social solutions" to various different environmental issues. Bel'kovich *et al.* (1991), although surprised by the diversity of dolphin hunting methods, were mainly impressed by the behavioural plasticity of these animals enabling them to adapt to changing environmental conditions. Additionally, reciprocal altruism has been reported in dolphins (Connor and Norris, 1982). Johnson and Norris (1986) note that animals who engage in reciprocal altruism have the ability to consider their actions and the consequences of these in relation to others and propose that substantial empathy fosters reciprocity in dolphins. The documentation of epimeletic behaviour in dolphins supports this proposal (see Caldwell and Caldwell, 1966 for review; Cockroft and Sauer, 1990; Pilleri, 1984).

It is necessary to elaborate on the significant relationships established between the neocortex ratio and several "maternal" variables such as gestation, lactation and maternal investment in delphinids and other odontocetes. In terms of delphinid matrilineage, Norris and Pryor (1991) propose that postreproductive females who are actively involved in the social group must serve some important social function. It has been suggested that these animals may nurse the offspring of others and provide allomothering. However, it has also been suggested that these old females serve the more important function of being the guardians of cultural information (Norris and Pryor, 1991), which fits the primate theory of social intellect (Humphrey, 1976). Furthermore, in certain primate species, the maintenance of social cohesion is dependent on the matriline and areas of relative expansion in the primate brain, such as the neocortex, are thought to be the developmental consequence of the maternal genome (Keverne, Martel and Nevison, 1996).

Returning to dolphins, Norris (1994) supposes that the best indicator of culture in a species is the presence of a juvenile period extending from the time of early maternal nurturance through to adulthood, during which learning and imitation occupy behavioural primacy. Dolphin societies, with extended maternal-offspring relations and intricate behaviours, are regarded as complex and are thought to possess culture (Norris, Wuersig, Wells and Wuersig, 1994; Pryor and Norris, 1991).

The significance of the relationships summarised in the findings of this study become apparent, if their implications are considered in relation to theories of social intelligence and the nature of mental evolution.

2. Implications

> The evolution of a social system capable of supporting advanced technology should only happen under conditions where improvements in technique can substantially increase the return on labour. This may not always be the case...the open sea is probably an environment where technical knowledge can bring little benefit and thus complex societies- and high intelligence- are contra-indicated (dolphins and whales provide, maybe, a remarkable and unexplained exception) (Humphrey, 1976:311).

Why would the evolution of sociality necessarily have to be related to technology as we, humans, conceive of it? What if the "advanced technology" of a very different species was represented by the use of something substantially different from, or perhaps even unanticipated by, humans. For example, the highly advanced sonar and auditory capacity of dolphins has only recently been acknowledged. We are only beginning to comprehend delphinid acoustic complexity, many aspects of which remain inexplicable and transcend the reproductive capacity of human technology (see Au, 1994).

Survival and successful life in the open sea, by its nature, would benefit from technical knowledge such as echolocation and communication. From this perspective, complex societies and high intelligence in dolphins should be expected and explained and not passed off as "contra-indicated, remarkable or exceptional". This suggestion is supported by the findings of the current study, which have upheld the hypotheses that dolphins have high neocortex ratios and that these are related to social complexity and auditory communication.

Within this context, the commonalties between dolphin and human relative neocortex volume are striking. The neocortex ratios in these cetaceans and primates are extraordinarily high in comparison with other species. Further comparative studies are required, as the relative neocortical volume appears to be exclusively related to social and communicative complexity in dolphins and humans.

However, in many ways, the position of uniquely human mental evolution, supported by evidence of the beginnings of mentality in our undisputed physical primate relatives, still reflects the mainstream of thought about comparative and social intelligence (Povinelli, 1993; Tomasello and Call, 1997).

Primate social intelligence is believed to have unfolded in the following manner. As social life is complex and often problematic, an individual needs to co-operate with others to maintain solidarity and enjoy the benefits of grouping, while being able to exploit and manipulate others (Humphrey, 1976). Animals with greater “intellectual prowess” were said to enjoy more substantial “social success”, which increases biological fitness and resulted in greater pressure for the evolution of strategic intelligence (Humphrey, 1976:311). An individual in a social group would benefit by occasionally obtaining resources at the expense of its group members, but would sustain great cost in leaving the group. This potential cost may be responsible for the evolution of social intellect (Whiten and Byrne, 1988). Within Machiavellian intelligence, this has been referred to as “tactical deception”, whereby an individual outwits its conspecifics for resources (Cheney and Seyfarth, 1985; Whiten and Byrne, 1988).

If strategic intelligence is related to neocortical evolution, then a larger neocortex ratio could be indicative of this capacity (Dunbar, 1992). Not surprisingly, when an index of tactical deception is plotted against the neocortex ratio for primates, the ratio predicts the frequency of deception (Byrne, 1993, 1995). It would be interesting to investigate whether or not such a relationship also holds true for delphinids.

Nonetheless, one may suggest that the approach to the evolution of the brain and intelligence has been predominantly primatocentric, if not homocentric in nature. Recently, Jacobs and Raleigh (1993) accused Dunbar (1993) of being primatocentric in his study of the neocortex, suggesting that other complex orders, such as cetaceans, should be considered in subsequent analysis. In his reply, Dunbar noted,

> the primatocentrism is deliberate (and unavoidable). The *Machiavellian Intelligence hypothesis* that underpins my argument is specifically concerned to explain why primates have significantly larger brains than other animals; it *hinges on the unique nature of primate groups* (tightly bonded groups made possible by deep social knowledge)... (1993:722) (emphasis added)

From the current study, it is apparent that primates are not the only animals with large neocortices. In addition, if Machiavellian Intelligence hinges on the uniqueness of primate groups, what does one make of the finding that dolphin neocortex is also related to group size and social complexity? Perhaps primate social intelligence and human brain evolution are not that unique after all, as has been suggested previously (Tschudin, 1998).

A major implication of this work is that hypotheses seeking to explain brain and intellectual evolution, such as Machiavellian Intelligence, may require substantial modification. However, the primatocentric approach does not seem to be an intentional movement to preserve the theory of discontinuous human cognitive evolution. Rather, it appears to be related to the lack of available data for species representing other orders (Dunbar, 1993). This may be remedied, in part, by adopting advanced technology, in accordance with the method of the current study, for the procurement of rare or intricate data. This is possibly what Jerison (1993) was hinting at to obtain data for other species of animals. Nevertheless, after taking cognisance of the dolphin neocortex findings presented through the course of this thesis, it appears that a primatocentric view of cognitive evolution will be inadequate for future investigations.

In terms of evolutionary theory, homoplasy or morphological similarity is frequently observed with respect to the physical characteristics of different species. It is conceivable that similar relative neocortical evolution in primates and dolphins may possibly present a case of convergence, with respect to mental evolution. Such an association yields support for further research into comparative cognition, with special reference to dolphins. This implies that future studies be conducted into intentionality, theory of mind and consciousness in other animals. Research of this nature may support or refute the hypothesis that the evolution of the human mind and social intelligence may be less discontinuous than, or qualitatively different from, that of other mammals.

3. Constraints in theory and practice and Recommendations

3.1. Brain size, neocortex size and the neocortex ratio

The assumption still exists that the larger the brain, or its components, the greater the intellectual potential, although empirical proof of this relationship is not easily achieved (Byrne, 1993). If the brain is viewed as a super computer, then larger neural brains make better computers (Byrne, 1995). However, this ignores an intelligent system of brain functioning, which includes both sensorimotor activity and computational intelligence (Byrne, 1995, Jerison, 1973; Passingham, 1982).

Although Byrne (1995) argues that increased intelligence is the major advantage which compensates for the costs associated with larger brains, research by Barton, Purvis and Harvey (1995) has questioned the notion that larger brains are indicative of greater intelligence. Rather, from their comparative studies of visual and olfactory systems, they suggest that the evolutionary growth of the brain is initiated towards the sensory systems required for the animal's survival.

In spite of the criticism levelled at the size of the brain or its components, there must be some significance attached to the enlargement of brain size or relative neocortical volume. This is apparent, as humans endure the costs of enlarged brains. Being born with relatively large brains through an undersized birth canal has risks for the mother and/or infant. Additionally, lengthened postnatal brain growth means an extended period of vulnerability for the infant (Byrne, 1995). More specifically, Dunbar (1993) notes that the neocortex is energetically expensive and thus the possession of a large volume of relative neocortex must confer some benefit.

Although the neocortex ratio appears to provide a good indicator of processing capacity and intellectual potential, it is based on the assumption that intelligence is localised in the cortex and possibly underestimates the role of the hindbrain and subcortical structures in intellectual performance (Byrne, 1995).

Furthermore, the C_R has been criticised as a crude measure of the neocortex, due to the lack of separation of the functional layers of cortex (Glezer and Kinzey, 1993) and it is indeed a fairly gross measure of brain organisation. However, in spite of the criticism levelled at the neocortex ratio, it is still believed to be a better indicator of relative cortical evolution than other measures such as the EQ, which are more simplistic and less meaningful.

Nothwithstanding the fact that the neocortex ratio may be a gross measure of undifferentiated cortex, it is an improvement on more primitive indices and will have to suffice until more intricate data on the neocortex become available for analysis (Dunbar, 1993; Holloway, 1993; Jerison, 1993). Recent research indicates that brain evolution enquiries are becoming more specialised. For an example concerning primate neocortex, group size appears to be specifically correlated with non-visual neocortex, which has been argued to be a processor for social information (Joffe and Dunbar, 1997).

It is hoped that future research will be able to provide more detailed information about the brain and its complex organisation. A review of the literature indicates that there has long been a desire for more specific knowledge of the brain and its functional organisation (Kesarev, 1971; Passingham, 1982). However, researchers have been hamstrung by the lack of technology. For example, Kesarev (1971) suggested that there may be more accurate measures of neocortical evolution, but was unable to study these, as he could not determine the volumes of certain cortical areas.

With the current technology available for research, these limitations are being gradually addressed and overcome. Sergent (1994) notes that methods such as CT and MRI, in addition to other brain imaging methods, have increased the capacity to visualise the brain at work. In essence, neuroimaging techniques might hold the key to a more detailed and precise understanding of relationship between brain function and structure, as has been suggested by Stuermer (1985) for interdisciplinary analysis and Velmans (1999a) with respect to studies of consciousness.

3.2. Study variables

It has been argued that a variable such as mean group size is a crude indicator of sociality and is therefore inadequate as a yardstick of social complexity (Deacon, 1993; Jacobs and Raleigh, 1993; Whiten, 1993). Although animals who appear to lead solitary lives, such as pandas, often demonstrate complex social organisation (Schaller *et al.,* 1985), it is believed that social intelligence is generally a consequence of life in a social group (Dunbar, 1992; Humphrey, 1976; Sawaguchi and Kudo, 1990). It has been conceded that limitations do exist with respect to variables representing the complexity of behavioural ecology (Dunbar, 1993). However, in a similar fashion to the constraints encountered with brain variables, it is only through the passage of time that more appropriate and intricate study parameters will develop.

With respect to the study variables selected for analysis in the current study, the limited scientific knowledge of species such as dolphins is humbling. The current study represents the first investigation of delphinid neocortical evolution and its correlates, and is exploratory in nature. As a consequence of "flying blind", so to speak, an attempt was made to obtain a comprehensive range of different variables representing delphinid foraging ecology, audition and sociality.

However, as dolphins live in a radically different environment to primates, certain variables in one order are not evident in the other and one has to improvise. For example, frugivorous versus folivorous diets have been considered in primates for an indication of dietary complexity. Cetaceans have totally different dietary resources to primates and thus fish and squid had to be substituted for their terrestrial equivalents, in terms of their differing nutritional value and scarcity of availability. Although limited by the scarcity of dolphin information, where possible, variables held in common with terrestrial mammals were used for analysis (e.g. gestation, mean group size, total number of prey species). These are open to direct comparison. However, some variables remain difficult to compare, such dolphin foraging depth.

Finally, the separation of foraging ecology, sound and sociality into discrete categories is widely regarded as artificial. The differentiation of these aspects of behavioural ecology in relation to neocortical evolution has been undertaken in the current study for conceptual and theoretical clarity. However, one should remain aware that research has supported the notion of extensive interrelatedness between the social and ecological correlates of primate neocortex (Barton, 1996; Sawaguchi, 1992). With specific reference to dolphins, Bearzi *et al.* (1997) have recognised that the highly flexible social organisation of bottlenose dolphins in the Adriatic is an adaptive coping mechanism to deal with environmental conditions and limited resources.

3.3. Study animals and study methods

As dolphin specimens are rarely acquired, a concern was the relatively small sample size in comparison with terrestrial mammal data. However, if one considers the number of animals from which actual and estimated neocortex data was obtained, this compares favourably with other studies (Dunbar, 1992; Stephan *et al.,* 1981). In addition, any fears relating to the representativeness of the dolphin data were addressed by obtaining population parameters for the study species. The human data, although obtained from a small convenience sample, did reveal some interesting neocortical features and present several avenues for future research.

Another limitation relating to the scarcity of dolphins for research was that the dolphin material was obtained from deceased specimens. However, to prevent the distortions associated with the degeneration of material *post mortem*, the specimens were scanned as soon as possible after death had occurred. Where scans could not be conducted immediately, the material was frozen, defrosted and subsequently used, with acceptable reliability.

The costs associated with the radiological scanning technology of CT and MRI used in this study are exorbitant. For this reason, although the imaging costs were sponsored by a private practice of radiologists, Jackpersad, Rooknoodeen Inc. and our Medical School's Department of Radiology, a conservative approach was taken in subjecting only the essential specimens to imaging analysis.

3.4. ***Weltanschauung*- Worldview**

The current study has actively avoided the assumption of a specialist position or a reductionist approach to what can be perceived as complex phenomena, namely the brain, evolution and intelligence. This may be viewed as a limitation by specialists or reductionists. However, although this approach may differ from a conventional perspective, it has proved to be beneficial in many respects, as has been noted in the implications.

4. Future Directions

Following the findings of high neocortex ratios in dolphins, and after establishing that these values are related to delphinid sociality and communication, this thesis suggests that dolphins and humans may share similar neocortical evolution. In the light of this, the implication is that dolphins and humans may display convergent mental evolution, that is of a social nature. "In many ways the groups are cognitive cousins, though at opposite poles in sensory specialisations and ecology" (Herman 1980:420).

It is reasonable to ask why substantial importance has been attached to the theory of social intelligence. Briefly, the Piagetian approach to the evolution of human intelligence (Parker, 1985) has drawn mixed commentary (see Gibson, 1985). Alternatively, the theory that social complexity is interrelated with intellectual evolution gains more support if one adopts the theoretical position of the mind as developing first interpersonally, to serve a social function, whereafter it is internalised (Vygotsky, 1978).

The acquisition of information via social or cultural transmission that stems from social interactions is believed to be optimal (Galef, 1988; Mainardi, 1980, Nishida, 1987), as its minimises the risks involved for the learner (Galef, 1976; Nishida, 1987; Rozin, 1977). As most of the social interaction of an infant occurs with its mother, it allows for the observation of her activities, relationships and community traditions (Attili, 1985; McGrew, 1977). This supports the theory of social cognition, where the developing individual only reaches the "proximal development" through the mediated efforts of a cultural guide, as primary caregiver and learning referent (Vygotsky, 1978). The social context which surrounds an individual exercises considerable influence on ontogenesis (Moshman, Glover and Bruning, 1987) and thus cognition should be studied in relation to the evolution of sociality or culture (Cole, 1985; Hinde, Perrot-Clermont and Stevenson-Hinde, 1985).

In practical terms, the question of how to test hypotheses relating sociality to intelligence has been asked previously (Humphrey, 1976; Jolly, 1966). During the 1970s and 1980s, although study parameters of sociality and intelligence were being developed, conflicts were still apparent in relation to theories of brain evolution and social complexity (see Gittleman, 1986 and Hemmer, 1979). More recently, the relationship of neocortical processing capacity to elements of social complexity (Dunbar, 1992, 1995; Sawaguchi, 1990; Sawaguchi and Kudo, 1990) and tactical deception (Byrne, 1995) provide empirical support for a relationship between sociality and intelligence in primates. As neocortical size does not appear to be clearly related to sociality in other terrestrial mammals, with the possible exception of certain carnivores and bats (Barton, 1993; Dunbar and Bever, 1997), social intelligence has appeared to remain the sole domain of primates.

According to the *scala naturae,* humans represent the zenith of primate intellectual and cortical evolution. Previous research has suggested that human brains are geared towards social relationships and social cognition (Hinde and Stevenson-Hinde, 1973; Humphrey, 1976). Barkow, Cosmides and Tooby (1990) suggest that our substantial cognitive adaptations have arisen to enable us to cope with social relationships. That humans are far better applied to solving social problems, than to logico-mathematical complexities, has subsequently been verified (Cosmides and Tooby, 1993). Yet there appears to be a considerable overlap between the performance of human and non-human primates on tasks of social intelligence (Essock-Vitale and Seyfarth, 1987). In view of this, tests of social intelligence need to be considered and developed in other non-primate species, especially in highly adapted species such as dolphins.

In the absence of both cross-species research into the links between brain morphology and behaviour (Henneberg, 1987) and an interspecific definition of intelligence (Byrne, 1995), there is still hope for comparative cognitive research. This lies in the discipline of comparative cognition, which pursues the significance of similar and different mental capacities between species by incorporating knowledge from comparative psychology, ethology and behavioural ecology, neuroscience, and cognition (Roitblat, 1987).

Tschudin, Basson and Peddemors (1999) have proposed that comparative analysis has much to offer studies of the evolution of what Searle (1992) synonymously terms “mind or consciousness”, although specific distinctions and connections between consciousness, thought and other mental processes are discussed elsewhere (see Davies, 1999a; Ryle, 1990; Velmans 1991, 1999b). It is believed that a mind, and ultimately consciousness, is revealed, in part, through the displays of its content (Tschudin, Basson and Peddemors, 1999). This is only partially applicable as only a certain part of consciousness, access consciousness, is available for study (Block, 1995; Davies, 1999b, Davies and Humphreys, 1993). Elements of subjective experience, or phenomenological consciousness, “What is it like to be a dolphin?” (adapted from Nagel, 1974), appear to remain beyond the parameters of analysis or human comprehension (Davies, 1999b; McGinn, 1989, 1991; Nagel, 1986).

The current study has emphasised that social relationships and social complexity are crucial in promoting mental evolution and therefore deserve more attention in studies of mind. In the words of Searle (1992:248) vis-à-vis the rediscovery of the mind, “a final guideline is that we need to rediscover the social character of the mind”.

The concept of socially strategic intelligence necessitates that an individual displays intentionality and the beginnings of a theory of mind (Tomasello and Call, 1997; Whiten and Byrne, 1988). Moreover, within the philosophy of mind, intentionality is considered to be an integral part of the content of mind or consciousness (Davies and Humphreys, 1993; Dennett, 1996; Tomasello and Call, 1997). While certain intentional behaviours have been noted in non-human primates (Byrne and Whiten, 1992), most authors remain dismissive about the presence of higher order intentionality in non-human primates (Cheney and Seyfarth, 1990; Tomasello and Call, 1997).

Davies and Humphreys (1993:9) suggest that "conscious intentional thought...may constitute a crucial component in our problem-solving ability, marking a qualitative advance on non-human animals". More conservative sceptics insist that so-called "intentional behaviours" in other animals may simply be behavioural repertoires (Smith, 1996). However, anecdotal evidence has been provided in support of potential intentionality in dolphins:

> Gambit was taught by his trainer at the aquarium to retrieve packets that might fall into his pool. On retrieval and presentation of the packet to his trainer, he would receive a fish. When finding a packet, Gambit proceeded to chew it up into a few smaller pieces, deposit these in cracks in the pool and "selectively" hand these in to his trainers to receive multiple fish rewards (Tschudin, Basson and Peddemors, 1999:4).

If one supposes that Gambit's behaviour is not the result of a repertoire, but the consequence of higher cognitive functioning, as evidenced by intentionality, then the concept of a theory of mind might not be solely applicable to humans and certain primates. Another major implication of this study is therefore that the possibility of a theory of mind needs to be investigated in dolphins.

Premack and Woodruff (1978) suggest that a theory of mind implies that an individual attributes mental states to oneself and to others, making inferences about the knowledge of others. Davies and Stone (1995:2) suggest that, armed with a theory of mind, or the folk psychology constituted by "a rich conceptual repertoire", the individual is capable of reasoning about the knowledge, intentions or actions of others.

A notable amount of research has been successfully conducted into false beliefs and the underlying theory of mind with non-human primates and children (Baron-Cohen, Leslie and Frith, 1985; Call and Tomasello, 1998a, 1998b; Gopnik and Wellman, 1995; Povinelli, 1993; Tomasello and Call, 1997; Tomasello, Call and Gluckman, 1997; Wimmer and Perner, 1983). Such experiments have indicated that non-human primates and even human children of certain ages do not display any evidence of a theory of mind (Tomasello and Call, 1997). Studies have also demonstrated that autistic children, who experience difficulty with social interaction and relationships, do not display a theory of mind (Baron-Cohen, Leslie and Frith, 1985). This appears to provide corroborating evidence for the assertion that mental evolution and intellectual development are essentially social in nature.

In theory, equivalent research into false beliefs and theory of mind should be possible to execute with dolphins, whose intellectual capacities and accomplishments are briefly discussed below. These examples indicate that dolphins may possess representational thought, which is not believed to be dependent on speech or language (McComb and Semple, 1998).

Complex experiments have already been conducted with dolphins in several cognitive domains. For example, dolphins have displayed the capacity to use "eaves-dropping", through passive echolocation, for object recognition (Xitco and Roitblat, 1996). Recently, self-view television was used to confirm that dolphins engage in the primate equivalent of self-examination and self-recognition (Gallup, 1970, 1975) and not social behaviour toward a conspecific (Marten and Psarakos, 1995). Finally, Smith *et al.* (1995) demonstrated interesting cognitive parallels between humans and bottlenose dolphins in terms of uncertainty responses, suggesting that the capacity for continual cognitive monitoring and the beneficial use of uncertainty represents mental adaptation in both species.

Theory of mind research with dolphins will require substantial modifications to the experimental framework and method used for recent false belief tests conducted by Call, Tomasello and co-workers with primates (reviewed above). However, it is believed that such modifications are possible and that, through the use of captured dolphins, this is the logical progression of the study. This may be of substantial importance to comparative cognition.

In a recent summary of primate cognition, Tomasello and Call (1997) propose that it is distinguished by the capacity to understand and categorise third party social relationships and tertiary relational categories among physical objects. Within primates, apes and monkeys do not differ notably in how they "cognize" their physical and social worlds (Tomasello and Call, 1997). Although foraging may have selected for the evolution of cognition early in simian evolution, the subsequent complex social organisation of some species encouraged the comprehension of conspecifics' social relationships via strategic intelligence (Byrne and Whiten, 1997; Tomasello and Call, 1997). Ultimately, the difference between human and non-human primates is postulated as the inability of non-human primates to understand the behaviour of conspecifics intentionally or to interpret the behaviour of objects causally in human-like ways (Tomasello and Call, 1997).

Theory of mind studies with dolphins may or may not result in a refutation of the perceived "difference" between human mentality and the mentality of other species. Research into the minds of an extended range of species is critical in assessing whether human mental capacities, such as deception, are "evolutionarily ancient" in nature, or rather a recent hominid phenomenon (Hauser, 1997:139).

In addition to this, the notion of primate Machiavellian intelligence has recently been questioned (Strum, Forster and Hutchins, 1997), while Goody (1997) recognises that the study of co-operation requires more attention. Humphrey suggested that the "chief role of creative intellect is to hold society together" (1976:307) and in line with this, de Waal (1991) has indicated that a greater focus should be dedicated to aspects of reconciliation. It appears as if more comprehensive data on social complexity is needed before definitive conclusions can be drawn (Cords, 1997). These aspects of intelligence diverge from popular Machiavellian logic. Yet, if one considers the primary role of co-operation in maintaining the complex societies of animals such as dolphins, it is apparent that such topics hold vast potential for future studies.

In the final analysis, this study has suggested that comparable features of relative neocortex size and its correlates with sociality and communication exist almost exclusively between dolphins and humans. This may have substantial implications for the theory of social intelligence and the discipline of comparative cognition. Forthcoming research into the possibility of a theory of mind in dolphins is therefore imperative. If widely divergent species such as dolphins do turn out to have similar mental capacities to humans, by way of a theory of mind or its beginnings, there seems little choice but to reconceptualise and revise our current theories of mental evolution.

5. Concluding remarks

This study has combined science, technology and philosophy in aspiring to tackle the topic of comparative cognitive evolution. Of original importance is perhaps that the hypotheses of high neocortex in dolphins relative to primates and the relatedness of delphinid neocortex with sociality and sound have drawn empirical support. This calls for further studies of comparative mental capacities in non-human species.

Current researchers are "not yet convinced" that other species possess "minds as replete with social intelligence as our own" (Povinelli, 1993:507) and this is problematic. Darwin was a proponent of *continuous* physical evolution and in all likelihood, held a similar view of mental evolution:

> In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history. (Darwin, 1859:458).

It is encouraging to note that this is certainly not the first, and hopefully not the last, proposal that humans may share continuous mental evolution with other animals. However, substantial enquiry still awaits us before any conclusions can be reached regarding mental evolution. Improvements and additions to the study, such as theory of mind research and the use of fMRI, may assist in broadening our understanding. One certainty remains: If the evolution of the mind does appear to be continuous across species, then humans differ only in degree and not in substance. This may have potential implications for medicine, philosophy, science and theology. Perhaps, of equal importance, might be the impact on the ways in which humans conceive of the world and of our own human nature.

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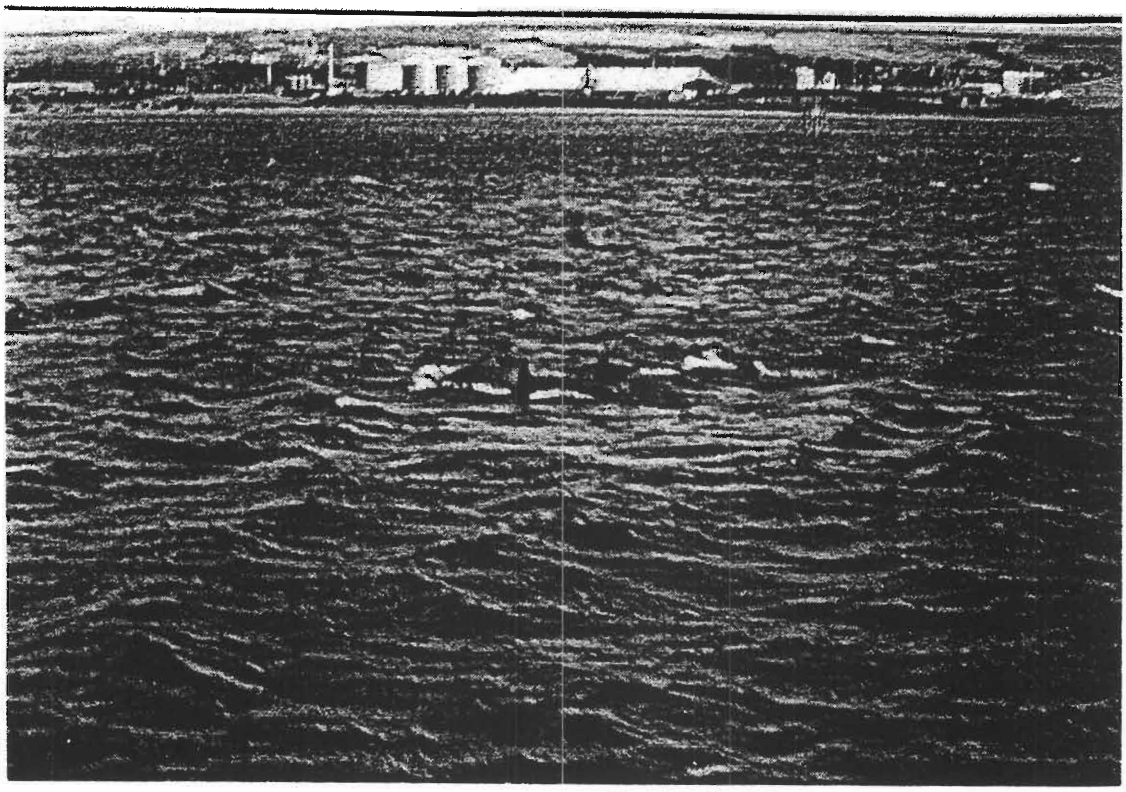
APPENDIX

Table of selected abbreviations

Abbreviation	Meaning
ABS	absolute brain size
BV	brainstem volume
CBV	cerebellar volume
c.o.v.	co-efficient of variation
C_R	neocortex ratio
CT	computed tomography
CV	cranial volume
CVA	cranial volume analysis
C/M	CT and MRI
d.f.	degrees of freedom
EQ	encephalisation quotient
f	female
FDB	frozen, defrosted, scanned using CT and MRI
FDM	frozen, defrosted, scanned using MRI
i	sexually immature
IV	infra-tentorial volume
JRI	Jackpersad, Rooknooden, Inc.
KZN	KwaZulu- Natal
m	male
Ma	million years ago
MRI	magnetic resonance imaging
n.s.	not significant (at $p < .05$)
NSB	Natal Sharks Board
NV	neocortex volume
p	significance
PE	Port Elizabeth
pr	presumed sexually mature
PV	posterior fossa volume
RBS	relative brain size
s	sexually mature
SV	supra-tentorial volume
SWI	Shannon-Wiener Index
TBV	total brain volume
WH	Wentworth Hospital
Ya	years ago



Bottlenose dolphins socialising off the Moray Firth, Scotland.