The Use of Neuroimaging in the Assessment of

Brain Size and Social Structure in Odontocetes.

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Preface

This study is a representation of the author's original work and has not been submitted in any other form to any other university. The work of other authors has been fully acknowledged throughout the text.

The research documented in this study was carried out in the Department of Psychology, at the University of Natal, Durban, South Africa, under the supervision of Professor S.P. Henzi, the co-supervision of Doctor V. Peddemors, of the Sharks Board and the guidance of Doctor D. Royston, of Wentworth Hospital.

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Abstract

This study successfully utilised the non-invasive neuroimaging techniques of Computerised Tomography (CT) and Magnetic Resonance Imaging (MRI) to establish that dolphins have high relative brain size values, transcending the primate range for neocortex volume and neocortex ratio. Bottlenose dolphins superseded human values of the neocortex ratio and common dolphins marked the upper limit of the range for the dolphin species under investigation. In addition this study was the first to find a correlation between sociality and neocortex ratio in dolphins (R.I.M. Dunbar, pers.comm), which supports the hypothesis of neocortical development in relation to sociality/group size (Sawaguchi & Kudo 1990; Dunbar 1992) and social/Machiavellian intelligence (Byrne & Whiten 1988; Byrne 1995). The study devised new measures of relative brain size, including the grey-white matter and higher cortical ratios and these require further research before verification of their efficacy. Equations were calculated to allow estimation of: (1) MRI values of total brain volumes from CT values, (2) total brain volume from cranial volume using CT, (3) cerebral cortex volume from cranial or total brain volume (CT) and (4) cerebral cortex and cerebellar cortex volume from total brain volume (MRI). The effects of freezing and defrosting on volume and density of CT and MRI values were investigated. Additionally, the relationship between relative brain size (EQ) and sociality was investigated for other dolphin research, using previously published figures, but no significant correlations were found. Finally, dolphin values were compared to primate values for neocortex volume and neocortex ratio with the finding that the only primate within the dolphin range of neocortex was the human, positioned higher than the solitary humpback dolphin, but below all of the other, more socially complex , dolphin species.

Contents

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Glossary of Terms

ABS- Absolute Brain Size

AIS- Advanced Imaging Services

BM- Body Mass

BOT- Bottlenose Dolphin

BVBMR- Brain Volume- Body Mass Ratio

CT- Computerised Tomography

CBV- Cerebellar Volume

CCV- Cerebral Cortex Volume

COM- Common Dolphin

CRV- Cranial Volume

DWA- Dwarf Sperm Whale

GS- Group Size

GWR- Grey- White Matter Ratio

HCR- Higher Cortical Ratio

HUM- Humpback Dolphin

ITV- Infratentorial Volume

MRI- Magnetic Resonance Imaging

NCR/NR- Neocortex Ratio

NV- Neocortex Volume

PFV- Posterior Fossa Volume

RBS- Relative Brain Size

SPO- Spotted Dolphin

STR- Striped Dolphin

SV- Supratentorial Volume

TBV- Total Brain Volume

TBVC " " (CT)

TBVM " " (MRI)

1.1. Introduction

Numerous investigations have focused on potential selective mechanisms driving brain size, in an attempt to understand the evolution of more complex and larger brains. These studies include correlations of the brain with ecology (Clutton-Brock & Harvey 1980; Gibson 1986; Milton 1988), energetics (Martin 1981, 1990; Hofman 1983a,b; Armstrong 1983; Milton 1988); social organisation (Hemmer 1979; Sawaguchi 1990; Sawaguchi & Kudo 1990; Dunbar 1992, 1995); intelligence (Jerison 1973, Passingham 1982; Dunbar 1992) and cognition (Byrne 1995). (For a comprehensive review, refer to Appendix A).

Correlative brain studies have focused on different dimensions of brain size. Absolute Brain Size (ABS) is not considered to be an accurate measure for comparative analyses, as a larger animal with a greater body mass is likely to have a bigger brain than a smaller animal (Passingham 1982). When body size is taken into consideration in measures of brain size, smaller animals score favourably, as evolutionary changes in brain size are relatively smaller than changes in body mass (Stephan et al 1970).

To overcome the problematic nature of ABS, Jerison (1973) developed the Encephalisation Quotient (EQ) derived from Von Bonin's (1937) cephalisation coefficient. According to Jerison's EQ, the observed brain size of an animal is related to the expected brain size of a "hypothetically" related animal of similar body weight. While this measure is regarded as the first attempt at a measure of Relative Brain Size (RBS), Passingham (1982) argues that it is an abstract measure and thus not as accurate as the relation of brain size to a more direct measure of brain input and output, such as the size of the medulla.

RBS measures relating brain size to different brain proportions require further attention. Measures such as the neocortex ratio (Dunbar 1992), which compare cerebral cortex relative to the rest of the brain, as well as the measure of relative size of neocortex (RSN) (Sawaguchi & Kudo 1990), are important, as they study proportions of the brain in relation to each other. As such, one may classify these as true measures of RBS as opposed to pseudo-relative measures such as the absolutes of brain weight-body weight.

The correlation of RBS measures with ecological factors has been established (Milton 1988). However, in primates, RBS appears to offer a stronger correlation when compared with sociality (Sawaguchi 1990; Sawaguchi & Kudo 1990). Subsequent research by Dunbar (1992, 1995) has confirmed the view that social complexity drives increased brain size in primates. While data required for such correlative investigations for terrestrial mammals have been provided (Stephan et al 1981), there exists a paucity of more recent data to corroborate these values. While several investigations that have been conducted correlated RBS with ecological and social factors (Clutton-Brock & Harvey 1980; Milton 1988; Dunbar 1992, 1995; Sawaguchi & Kudo 1990) for terrestrial mammals, especially primates, comparative analyses for other orders of mammals with large brains, in both absolute and relative terms, are lacking. In particular, comparative data sets are not available for marine mammals, specifically the order of cetaceans, (dolphins, whales and porpoises). Sparse data are available on brain size, EQ, cortical surface area and RBS in dolphins (Kesarev 1971, Ridgway 1986a, Worthy & Hickie 1986), no correlational studies of RBS with sociality or ecology have been reported.

This study represents the first investigation of the hypothesis that increasing social complexity (crudely indicated by group size) drives an increase in neocortex size in the brains of dolphins, as has been proven for primates by

Sawaguchi and Kudo (1990) and Dunbar (1992). The hypothesis is investigated by studying the varying social structure of three different dolphin species in relation to their relative brain volumes, to establish whether or not a relationship exists between these two variables.

A strong case exists for the inclusion of marine mammals in comparative, evolutionary analyses and this verifies the value of the present study. Cetaceans present an important case for evolutionary analyses, as they represent the only mammalian order to display a complete secondary return to an aquatic environment (Kesarev 1971). This is noteworthy, as an aquatic environment varies significantly from the terrestrial environment in which the development and formation of the mammalian neocortex occurred (Kesarev 1971). In addition, cetaceans are genetically related to all terrestrial mammals (Deacon 1990) thus presenting an exceptional case in brain evolution. While Kesarev (1971) suggests that the vast neocortical development of dolphins is the result of visceral and somatic functioning, Ridgway (1986a) argues that this is not the case, as not all dolphins share a high EQ and recognises the need to find "other reasons for the large size of the dolphin brain" (1986:62).

Cetacean brains are large. In absolute terms, some cetacean species, along with certain megaherbivores, have the largest brains (Passingham 1982). Certain cetaceans possess the most convoluted brains and the greatest surface area of all species (Elias & Schwartz 1969) and the longest gyri as a function of brain size (Elias & Schwartz 1971, Jerison 1982a, Ridgway 1986b). Additionally, the family Delphinidae incorporates species such as the bottlenose dolphin (*Tursiops truncatus*) which exhibit the greatest brain-body size ratio amongst cetaceans (Ridgway 1990). Jerison (1982b) suggests that, other than humans, some cetacean species may possess the highest relative brain size to body weight ratio. Worthy & Hickie (1986) have noted that

odontocetes have similar RBS values to primates. Martin (1990, 1982, 1981) proposes that cetaceans and not simian primates share the closest cranial capacity to humans, the only primate with an exceptional brain size. For example, using a measure of the brain's processing capacity in relation to cortical surface area, a mouse with $4cm^2$ of cortex has 800 processing units (or modules), a chimpanzee with $800cm^2$ has 1.6 million modules and the human with $2000cm^2$ cortex has 4 million units (Jerison 1982a). If the dolphin were included, with a cortex of $3000cm^2$, it would possess 6 million processing units.

In addition to the high values obtained across a range of scores by cetaceans (above), there are further reasons to investigate them. Deacon (1990) argues that the dolphin brain has adapted and become derived to permit survival in an extremely altered environment compared to that of the standard terrestrial mammal. Finlay & Darlington (1995) recognise the need for studies of species occupying specialised niches or structures on the sensory periphery, as they argue that this provides the most important test of the developmental limits on brain evolution. Dolphins fit into this model, as their perceptual world is significantly different to standard mammals (Jerison 1986), with dolphins constantly engaging in three dimensional perception as opposed to standard, terrestrial, two- dimensional perception.

All the above reasons indicate that comparative analyses should include cetaceans. However, aside from the popularised notion of high dolphin intelligence and the above scientific results placing dolphin brain development close to (and sometimes higher than) that of humans, several problems exist with their inclusion in mammalian data sets. The cetaceans' aquatic residence as opposed to a terrestrial environment, as well as their morphological differences to land mammals may have lead to their lack of incorporation in data sets. Another problem relates to the infrequent scientific

capture of dolphins. The scarcity of access to cetacean species has led to the existence of minimal research on this mammalian group.

1.1. Aims of this Study

Given the infrequent collection of cetaceans, the skulls of deceased specimens require preservation for classification and other taxonomic purposes. Small samples thus present a problem to investigations of brain evolution in such rare specimens. As the techniques of manual dissection and histological analysis are not viable, the neuroimaging techniques of computerised tomography (CT) and magnetic resonance imaging (MRI) presented a possible solution. Relatively few cetacean neuroimaging studies have been conducted. Of those that have, CT studies have focused on acoustic features (Cranford 1988), subcutaneous airsacs (Brouwers *et al* 1990) and vaginal calculi (Woodhouse & Rennie 1991), while MRI techniques have considered the detection of growth recovery lines in fossil vertebrae (Sebes *et al* 1991). CT and MRI techniques have not previously been used for the type of research reported here (a summary of neuroimaging in behavioural and psychological research is presented in Appendix C).

The techniques of CT and MRI were used as a means of non-invasive investigation into the brains of the odontocetes collected off the KwaZulu-Natal coastline. Both techniques have positive and negative features. While CT is a more freely available and less expensive method than MRI, it is less accurate in determining volumes. CT can, however, detect cranial volume which is not possible using MRI. Thus CT and MRI results were compared and correction factors were generated to reduce the inadequacies of CT and permit estimations of brain volumes for MRI. Fresh, frozen and defrosted

material was studied, as species are often presented in these differing states. Relative brain size ratios were calculated for the different dolphin species, permitting interspecific comparison and an investigation of the relationship with sociality. After this relationship (between relative brain size and group size- as representative of sociality) was studied, dolphin brain volumes were compared to values for primate species, in terms of social complexity.

2. Materials and Methods

2.1. Study Animals

The specimens used in the study comprised several species with differing social organisation (Table 1) and these were obtained from several sources, including the Sharks Board (SB), Durban Sea World and the Kwazulu-Natal Stranding Network, after they had died either as a result of asphyxiation from entanglement in the anti-shark nets, death in the dolphinarium or stranding along the Kwazulu-Natal coastline (Table 2, Figure 1).

Table 1. Odontocetes used in this Study

SUPERFAMILY	FAMILY	GENUS	SPECIES	COMMON NAME	ACRONYM	SAMPLE SIZE	SEX	SOCIALITY (MEAN GROUP SIZE)
DELPHINOIDEA	STENINAE	SOUSA	SOUSA CHINENSIS	INDO-PACIFIC HUMPBACK DOLPHIN	HUM	2	1 MALE, 1 FEMALE	SOLITARY-SMALL GROUPS (7)
	DELPHININAE	TURSIOPS	TURSIOPS TRUNCATUS	BOTTLENOSE DOLPHIN	BOT	6	5 MALE, 2 FEMALE	COHESIVE SOCIAL UNITS (67)
		STENELLA	STENELLA ATTENUATA	PANTROPICAL SPOTTED DOLPHIN	SPO	2	MALE	LARGE SOCIAL GROUPS (94)
		STENELLA	STENELLA COERULEOALBA	STRIPED DOLPHIN	STR	1	FEMALE	LARGE SOCIAL GROUPS (94)
		DELPHINUS	DELPHINUS DELPHIS	COMMON DOLPHIN	COM	5	1 MALE, 4 FEMALE	LARGE AGGREGATES (300)
PHSETEROIDEA	KOGIIDAE	KOGIA	KOGIA SIMUS	DWARF SPERM WHALE	DWA	1	MALE	SMALL GROUPS

Table 2. Specimen Information

SPECIMEN	SEX	MASS (KG)	LENGTH (CM)	LOCATION & TAG NO.	SOURCE	CT SCAN	MRI	MRI UNIT
BOT 1	F	153	226	San Lameer (9)	SB	-	fresh	AIS
BOT 2	M	160	239	Glenmore (9)	SB	-	fresh	Wentworth
BOT 3	F	105	206	Margate (60)	SB	fresh	fresh	Wentworth
BOT 4	M	80*	190	Margate (61)	SB	fresh	fresh	Wentworth
BOT 6	M	208	234	TO Strand (15)	SB	fresh, defrosted	fresh, defrosted	Wentworth
BOT 7	M	190	243	TO Strand (16)	SB	fresh, defrosted	fresh, frozen, defrosted	Wentworth
COM 1	F	74*	180	Ballito (25)	SB	-	fresh, frozen, defrosted	AIS
COM 2	F	58*	190	Sunwich (19)	SB	-	fresh	AIS
COM 3	M	82	210	Ballito (28)	SB	-	fresh	Wentworth
COM 4	F	120	221	Durban (232)	SB	-	fresh	Wentworth
COM 5	F	120	223	Durban (233)	SB	-	fresh	Wentworth
DWA 1	M	106	198	Durban (S)	stranding	-	fresh	AIS
HUM 1	M	100	206	Richard's Bay (56)	SB	-	fresh	AIS
HUM 2	F	118	202	Scottburgh (37)	SB	-	fresh	AIS
SPO 1	M	37*	157	Durban	Sea World	-	fresh	AIS
SPO 2	M	80	221	lower south coast	stranding	-	fresh	AIS
STR 1	F	32*	146	lower south coast	stranding	-	fresh	AIS

* denotes a sexually immature animal
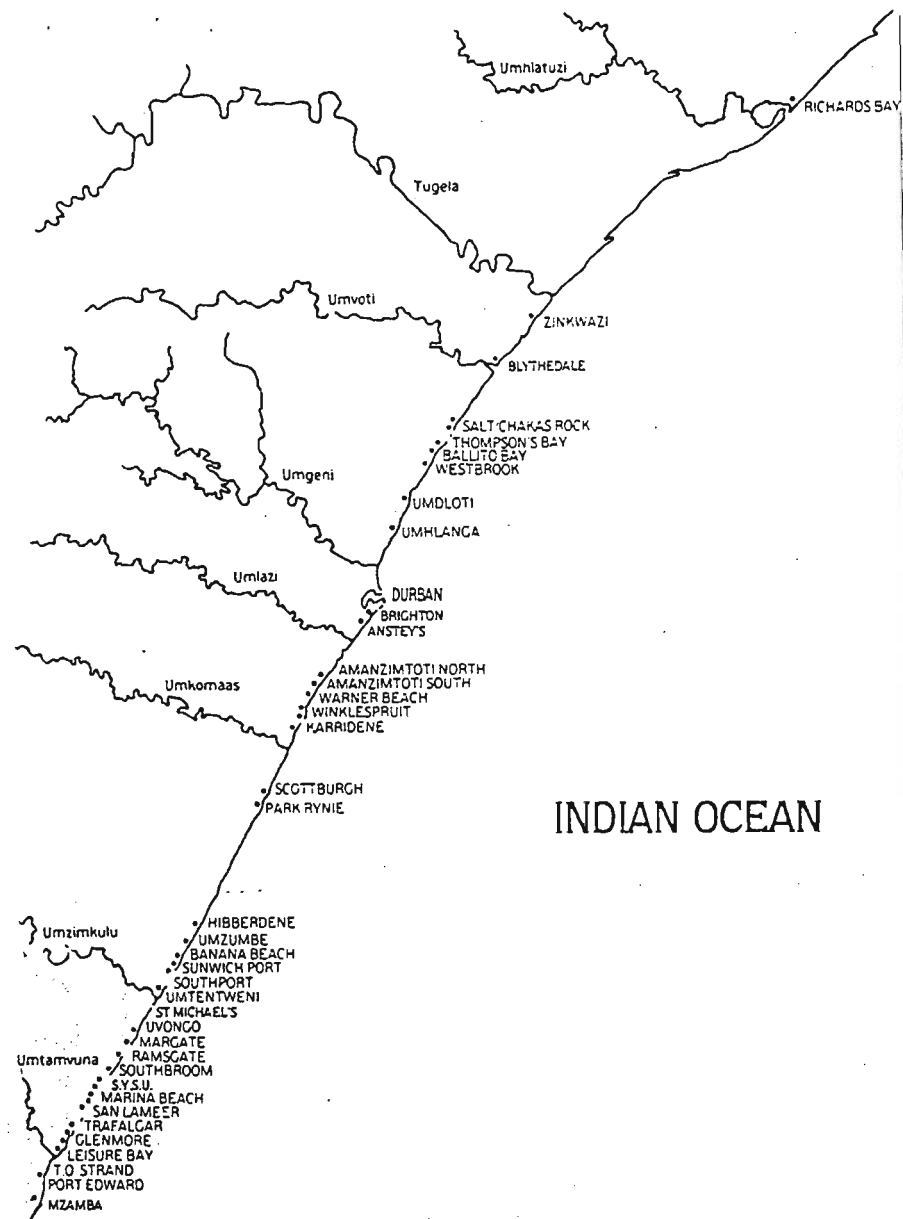
Figure 1. Kwazulu-Natal Coastline, indicating dolphin capture sites.

The specimens used were sexually mature, with the exception of one bottlenose dolphin (BOT 4), two female common dolphins (COM 1 & 2), the dwarf sperm whale (DWA 1), a spotted dolphin (SPO 1) and the striped dolphin (STR 1) (Table 2). The study animals were scanned under different conditions, either fresh, frozen or defrosted. Results from juvenile specimens were not included in the analysis. The specimens were not diseased or scavenged, but in a condition of normal health prior to their death. The small

sample size precluded an investigation of sex related differences in brain size.

The wide range of social structure in the sample size of this study allows for an investigation into the relationship between relative brain size and social complexity. For a more comprehensive review of cetacean sociality and ecology, including the functions of cetaceans schools, refer to Appendix B.

2.2. Apparatus

The CT scanning was performed using a Picker PQ 2000 unit at Wentworth Hospital, Durban (Figure 2). The images were viewed in the coronal plane (see Figure 4), with 10mm thick slices taken at an inter-slice gap of 10mm. The image size was consistent at 300mm.
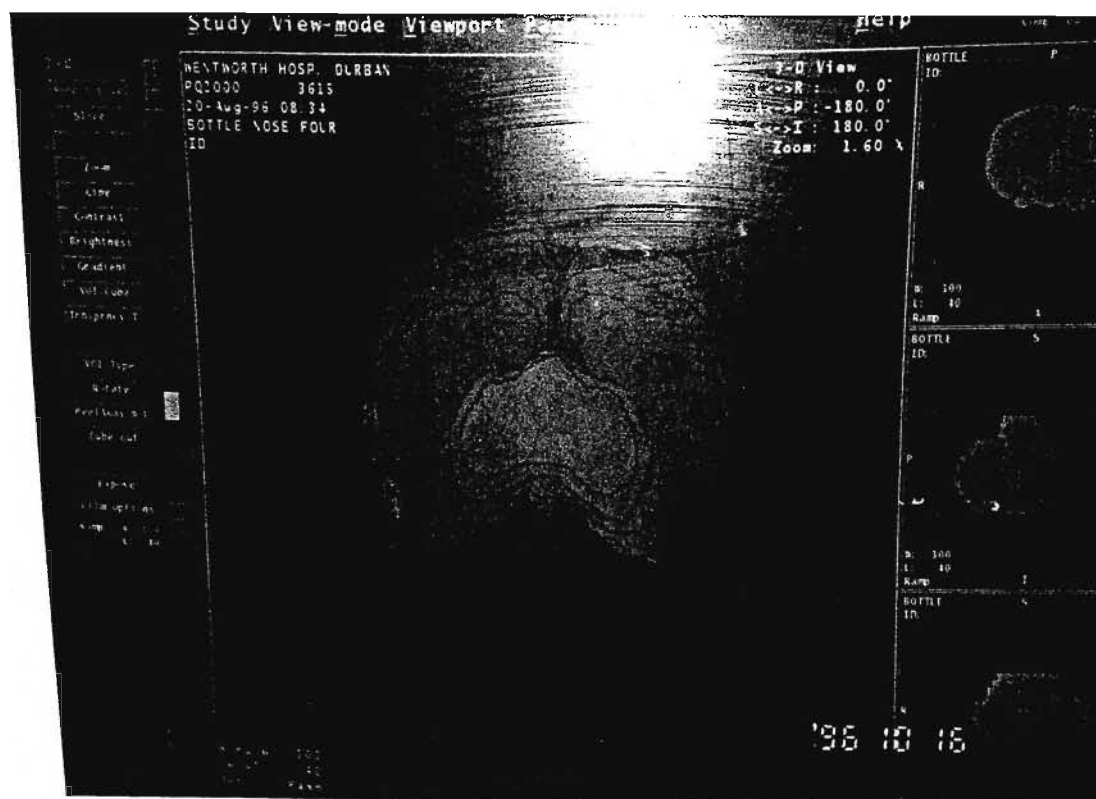
Figure 2. Picker PQ 2000 CT Scanner, Wentworth Hospital

The MRI procedures were performed on two different machines, the GE Sun Signa Scanner (1.5 Tesla unit) (Figure 3a) at Wentworth Hospital, Durban and the Siemens Magnetom Impact Scanner (1 Tesla unit) of Advanced Imaging Services (AIS) at St Aidan's Hospital, Durban (Figure 3b)
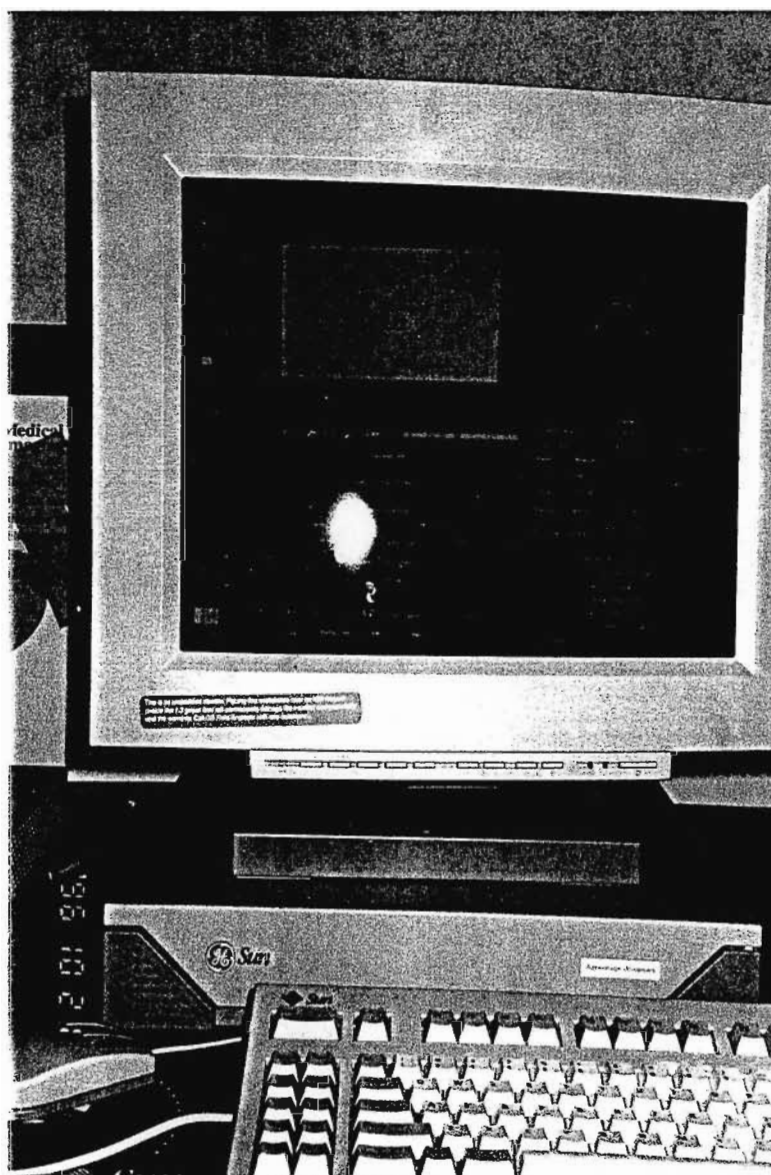
Figure 3a. GE Signa Sun MRI Scanner, Wentworth Hospital
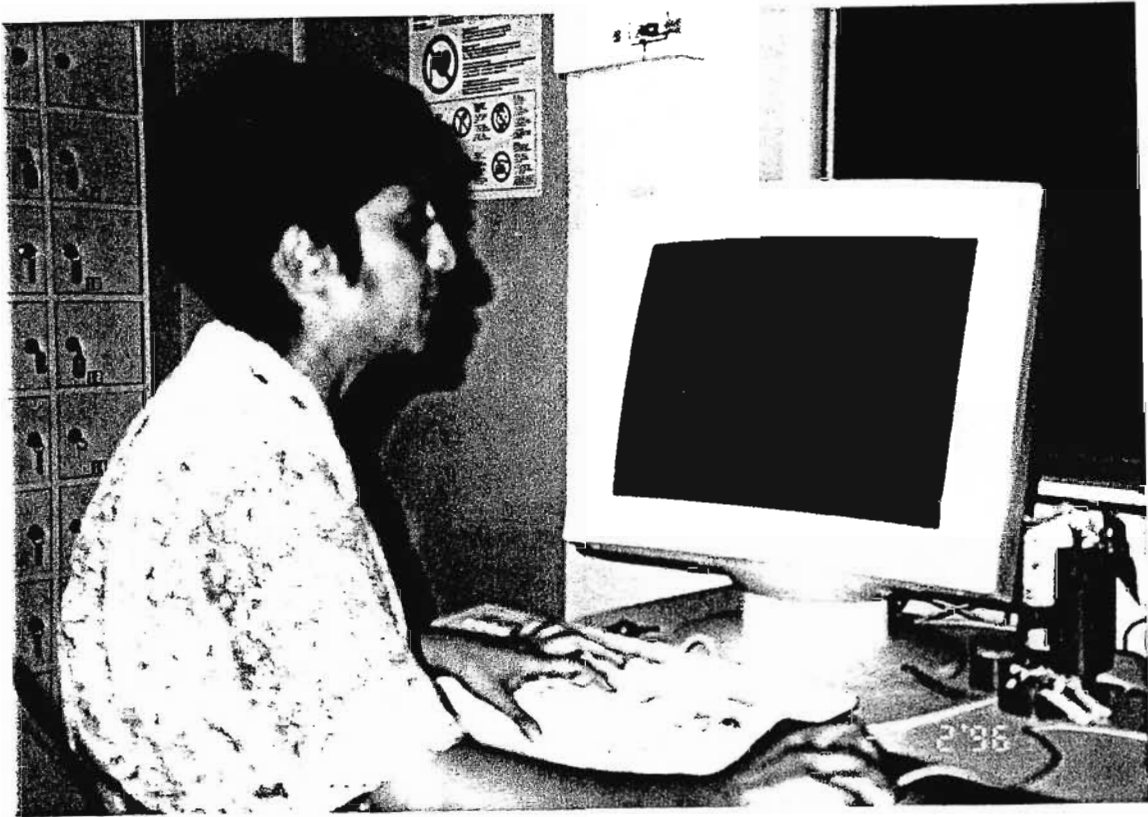
Figure 3b. Siemens Magnetom Impact MRI Scanner (AIS)

2.3. Procedure

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 are 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 (Walsh 1994).

MRI is vastly different to the above procedure and other conventional radiographic procedures, as it does not use X-rays. Instead, 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. 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. In MRI, gradient magnetic fields in three directions allow for spatial detection of data and a two-dimensional image to be formed (Palmer 1985: in Walsh 1994). Both the techniques of CT and MRI have their merits and disadvantages and these are discussed subsequent to observation of the results obtained via their use.

The specimens were weighed, measured and dissected on their arrival at the SB headquarters in Umhlanga. The heads were severed and scanned while fresh or stored in the freezer at -20°C until scanned, some of which were subsequently defrosted and scanned (see Table 2). The specimens were placed in sealed plastic bags to prevent contamination of the scanners and transported to the scanning units. 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 and infra tentorium) (Figure 4) were calculated by tracing each slice with a digitiser. The former area houses the cerebral cortex, while the latter contains the posterior fossa. A 3-D statistical measurement was applied using the Picker Voxel Q applications package to calculate the volumes of respective areas. The tentorial areas were combined to calculate overall brain volume (BV). Cranial volume (CV) was also calculated from these slices through the inclusion of fluid and ventricular volumes.
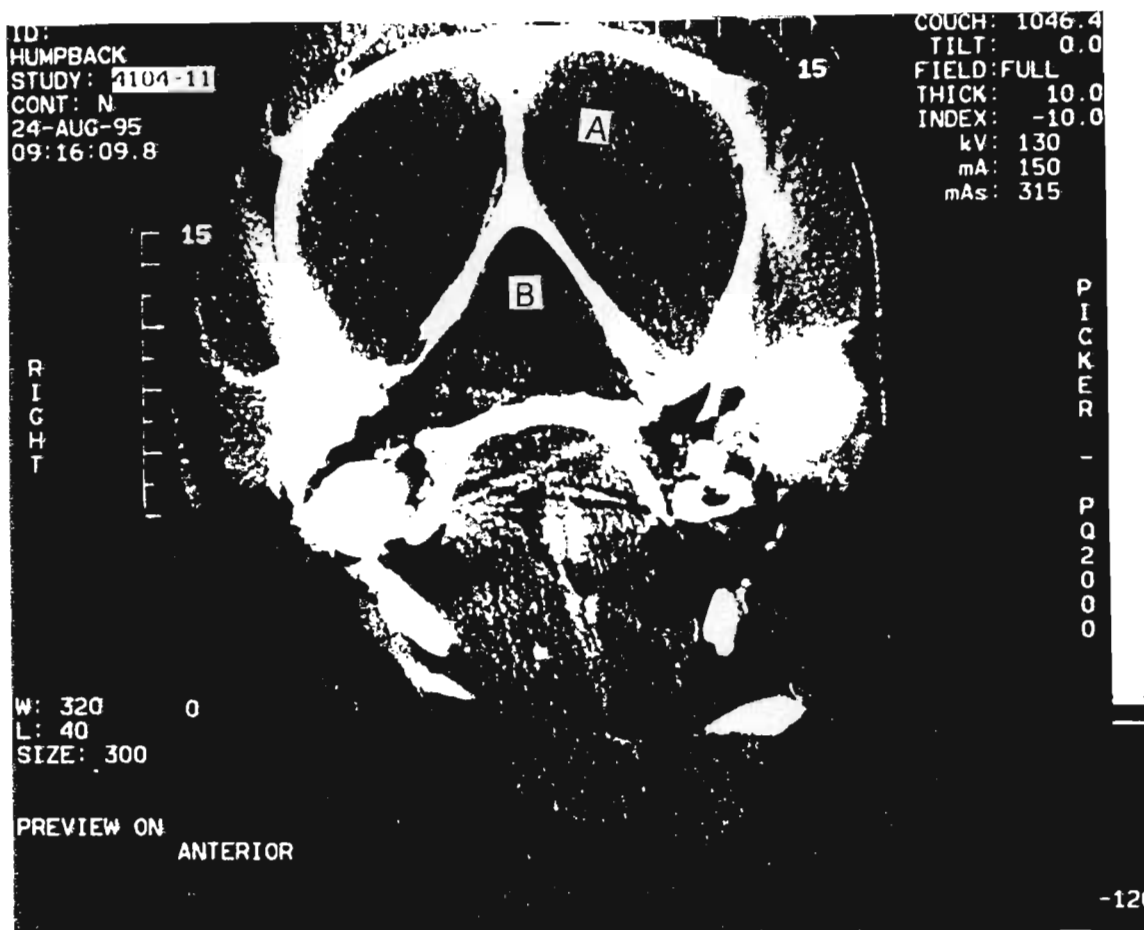
Figure 4. CT scan image   (A= supratentorium, B= infratentorium)

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, axial, coronal and sagittal (Figure 5 a,b,c).
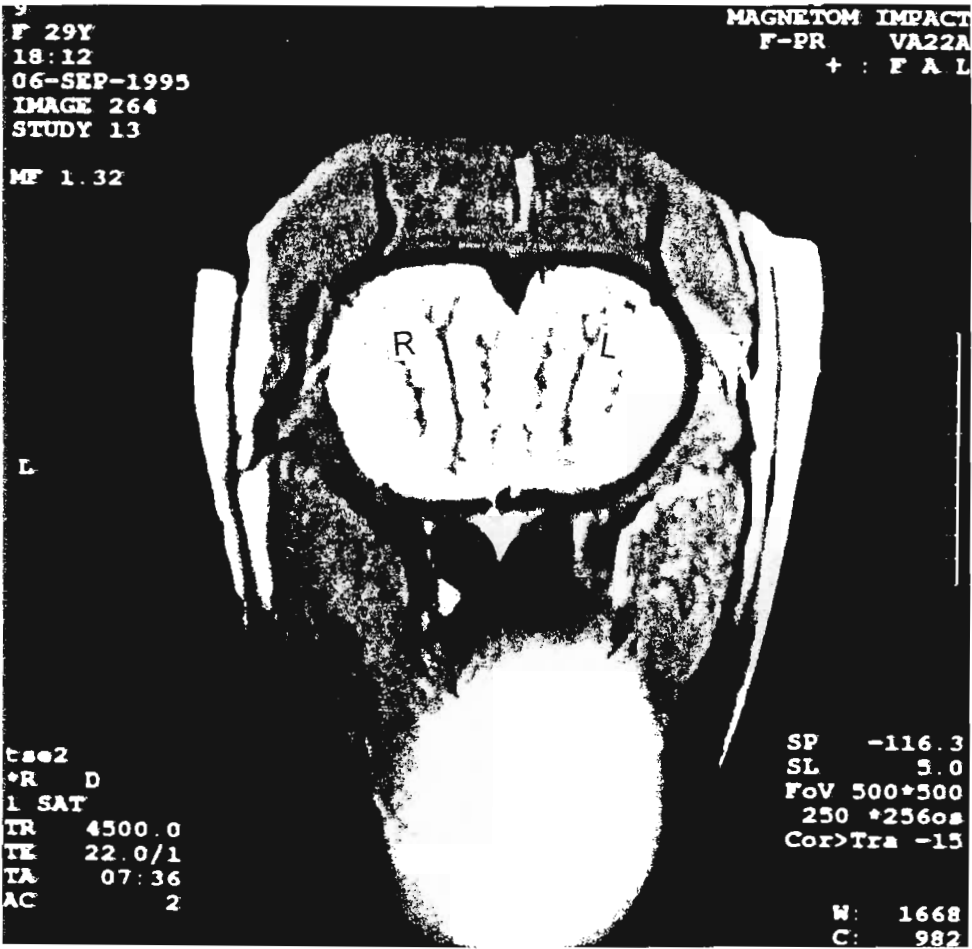
Figure 5a. MRI axial image   (L= left hemisphere, R= right hemisphere)
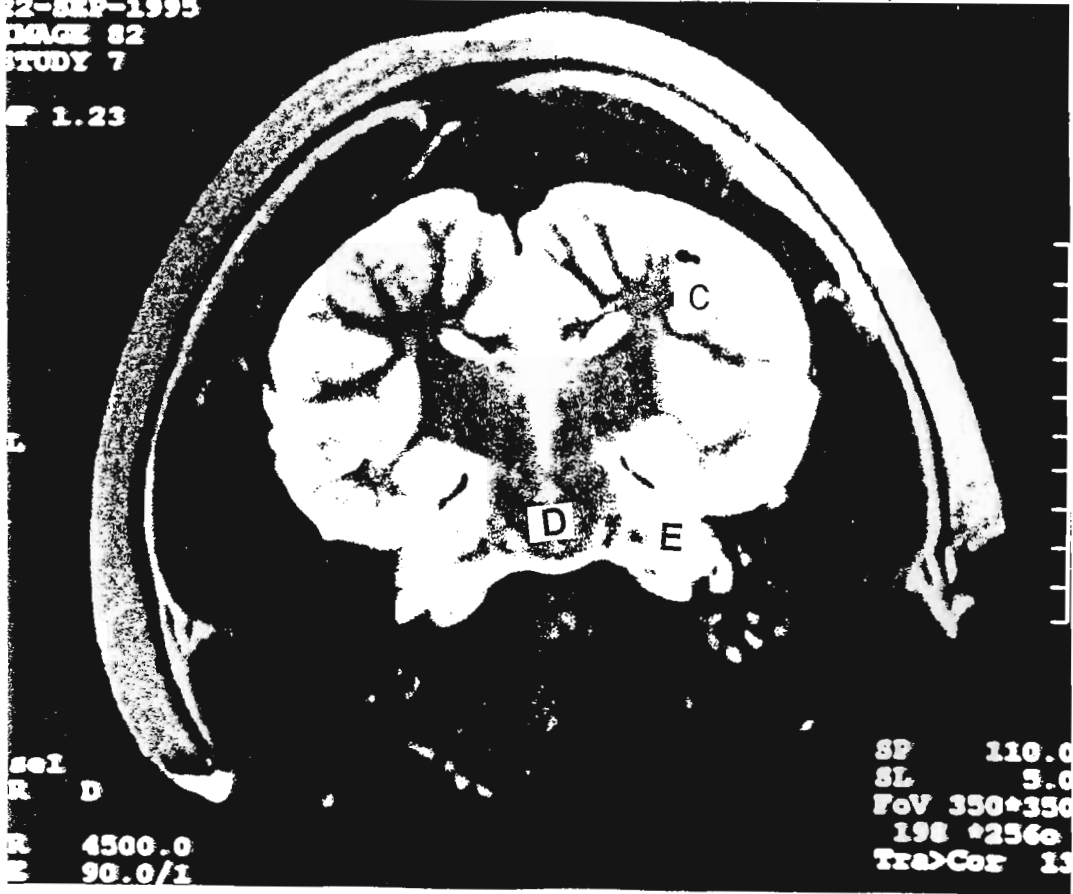
Figure 5b. MRI coronal image (C= cerebral cortex, D= brainstem, E= cerebellum)

Figure 5c. MRI sagittal image (F= medulla oblongata, G= corpus callosum)

For comparative purposes, only the coronal images are analysed. The cerebral cortex, mid-brain and cerebellum were traced on both MRI machines, using a digitiser. At Wentworth, the Advanced Windows software package 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 (1) whereby the separate slices were added before multiplying slice areas by slice thickness added to interslice gap:

modified Cavalieri Principle:

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

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 (NR) (2) was calculated from the following equation (Dunbar 1992):

(2) NR = NV/ (TV - NV)

where NV = neocortex volume (cerebral cortex volume, cf Passingham1982); TV = total brain volume;

CT and MRI display different types of images of the brain, with the respective images presented above in Figure 4 & Figure 5 a,b,c. 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 CT only allows discrimination between the supratentorial and infratentorial cortical volumes (Figure 4, marked as A and B respectively), MRI permits distinction between cerebral cortex (C) and the posterior fossa, comprised of the brainstem (D) and the cerebellum (E) (Figure 5b). MRI viewing in sagittal and axial planes, in addition to coronal imaging (the only plane possible using CT) allows for the detection of finer structures, for example the medulla (F) and corpus callosum (G) from the sagittal plane (Figure 5c) and the differences between left and right hemispheres (Figure 5a, marked as L & R respectively).

The differences in image quality were revealed by consideration of the condition under which the specimen was scanned (Figure 6), either fresh (6a), frozen (6b) or defrosted (6c).
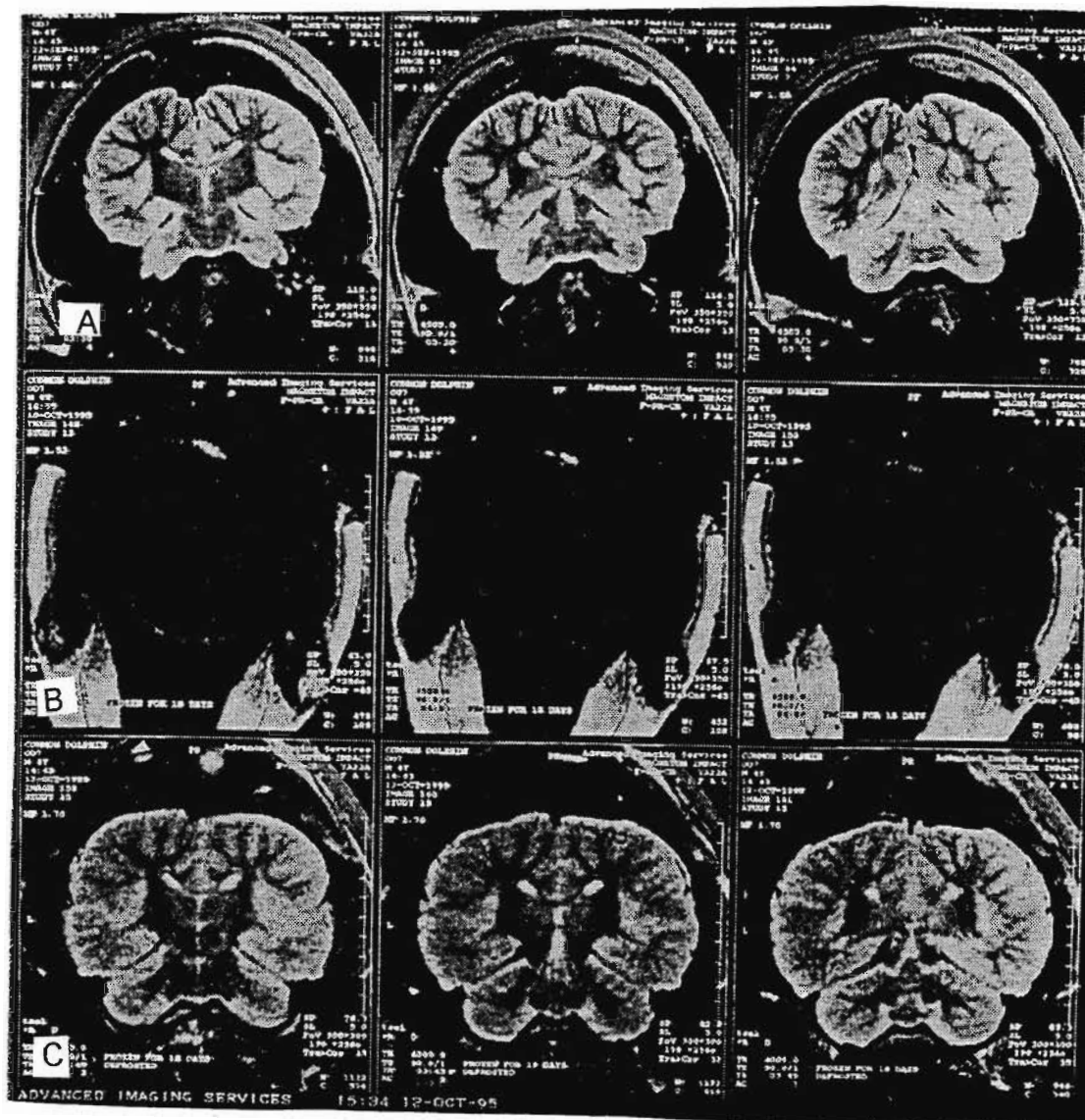
Figure 6. Image quality according to condition of specimen. (A= fresh, B= frozen, C= defrosted)

3. RESULTS

The results are presented in three major sections, namely the brain volumetric relationships from CT and MRI (including CT and MRI results, effects of freezing and CT- MRI relationships), measures of relative brain size in dolphins (incorporating interspecific comparison and RBS in relation to sociality) and finally a comparison between primates and dolphins in relation to relative brain volume and group size relationships). Regression analyses have been included for several significant relationships to permit estimation of one variable from values of the other.

3.1. CT and MRI brain volume relationships

3.1.1. Brain volumes and relationships from CT scans

The volumes of the supratentorial and infratentorial regions of the brain were measured from CT scans of 4 bottlenose dolphin specimens. These volumes were analysed in relation to total brain volume and cranial volume. The latter volume is only measurable using CT, as MRI cannot detect bone. The different volumes were calculated (Table 3) and analysed using regression analysis. As the study sought to establish a correction factor from CT to MRI for brain volumes and as bottlenose dolphins were the most commonly available animals, this species was selected to provide the greatest sample size. However, potential interspecific differences may result in the need for different species' equations.

Table 3. Supra- & Infratentorial Volumes, Total Brain Volume and Cranial Volume from CT scans.

SPECIMEN	SUPRATENTORIAL VOLUME	INFRATENTORIAL VOLUME	TOTAL BRAIN VOLUME	CRANIAL VOLUME
BOT 3	900.34	262.35	1162.69	1166.55
BOT 4	1052.51	242.27	1294.78	1298.41
BOT 5	1053.44	320.87	1374.31	1392.37
BOT 6	1190.23	299.58	1489.81	1514.24

As Total Brain Volume (TBVC) and Cranial Volume (CRV) are almost perfectly correlated (r = .9996, n= 4, P < 0.05), it is possible to calculate total brain volume from cranial volume, as the latter measure is more accessible. A regression analysis between these two variables reflects a highly significant relationship, ($F_{1,2}$ = 2275.37; p < 0.001; R^2 = 99.91%), resulting in equation (3):

(3)   TBVC = 75.21 + 0.93(CRV);

As this study is specifically concerned with the cerebral cortex, it would be of value to be able to estimate cortical volume from cranial and/or total brain volume. Cranial volume and supratentorial volume (SV) are strongly

correlated and a regression between these variables yielded a highly significant relationship ($F_{1,2}$ = 27.98; $p < 0.05$; R^2 = 93.33%) resulting in equation (4) (below).

(4)   SV = 4.38 + 0.78(CRV);

SV is therefore also significantly positively correlated with TBVC and when SV is regressed onto TBVC, the result is a highly significant relationship ($F_{1,2}$ = 34.84; $p < 0.05$; R^2 = 94.58%), leading to equation (5):

(5)   SV = -65.07 + 0.84(TBVC);

3.1.2. Brain volumes and relationships from MRI

The brain volumes obtained from MRI scans are presented in Table 4. Values include cerebral cortex volume, brainstem volume, cerebellar vloume, and total brain volume.

Table 4. Relative brain volumes as calculated from MRI scans

SPECIMEN	CEREBRAL CORTEX VOLUME	BRAINSTEM VOLUME	CEREBELLUM VOLUME	TOTAL BRAIN VOLUME
BOT 1	1091.3	40.2	256.1	1387.6
BOT 2	1077.8	27.1	235.3	1340.2
BOT 3	868.4	33.5	173.4	1075.3
BOT 4	993.0	14.3	194.8	1202.1
BOT 5	1009.2	15.3	244.9	1269.4
BOT 6	1195.3	41.7	220.1	1457.1
COM 1	680.1	23.3	155.3	858.7
COM 2	714.8	21.1	168.3	904.2
COM 3	784.0	16.1	116.6	916.7
COM 4	749.4	15.2	140.0	904.6
COM 5	758.1	17.4	131.2	906.7
DWA 1	381.3	24.1	58.4	463.8
HUM 1	987.8	40.3	268.3	1296.4
HUM 2	949.0	38.4	243.0	1230.4
SPO 1	439.3	25.6	97.5	562.4
SPO 2	784.2	42.1	178.9	1005.2
STR 1	525.4	43.8	96.6	665.8

As with CT scans, it is valuable to assess the relationship between total brain volume and regional brain volumes, namely cerebral cortex volume (CCV) and cerebellar volume (CBV), in order to permit estimation of the latter volumes from the former. The following two equations reflect these relationships.

TBVM and CCV are strongly correlated with a regression analysis of these variables yielded a highly significant relationship ($F_{1,15} = 1172.95$; $p < 0.001$; $R^2 = 98.74\%$), resulting in equation (6):

(6) $CCV = 14.31 + 0.79(TBVM)$;

Of interest is the finding that the above equation has a similar slope to equation (4), the CT estimate of cerebral cortex volume. However, CT overestimates this volume, as is evident from its higher Y- intercept.

From an analysis of cerebellum volume (CBV) and total brain volume, where the cerebellum is the dependent variable, a significant relationship was found ($F_{1,15} = 111.17$; $p < 0.001$; $R^2 = 88.11\%$) yielding the equation (7):

(7) $CBV = -32.52 + 0.2(TBVM)$;

3.1.3. Impact of freezing on CT and MRI volumetric calculations

After being scanned in a fresh state, bottlenose dolphins BOT 5 and BOT 6 were frozen and defrosted in order to determine whether or not this process had a significant influence on CT and MRI volumetric analysis of regional and total brain volumes. (Table 5).

Table 5. Defrosted brain volumes from CT and MRI

SPECI MEN	SUPRA TENTO RIAL VOL.	INFRA TENTO RIAL VOL.	BRAIN VOL. CT	CRANI AL VOL. CT	CEREBRAL CORTEX VOL. MRI	BRAIN STEM VOL. MRI	CEREB ELLAR VOL. MRI	POSTE RIOR FOSSA VOL. COMBI NED MRI	BRAIN VOL. MRI
BOT 5	1058.9 (76.1)*	333.0 (23.9)	1392.0	1514.2	999.9 (78.9)	35.6 (2.8)	232.2 (18.3)	267.8 (21.1)	1267.7
BOT 6	1240.7 (79.7)	316.2 (20.3)	1556.9	1581.2	1169.4 (79.4)	95.4 (6.5)	207.6 (14.1)	303.0 (20.6)	1472.4

* Values in brackets represent regional brain volumes as percentages of total brain volume.

The supratentorial volume was greater after defrosting in calculations of both specimens using CT images. However, cerebral cortex volume on MRI decreased for both specimens (Figure 7). Defrosting also increased the infratentorial (posterior fossa) volume calculated from CT images, but increased the posterior fossa volume for MRI (cerebellar volume decreasing and brainstem increasing in both specimens) (Table 5; Figure 7. And see Table 6).

cerebral cortex (STV)
77.25

cerebral cortex
80.75

brainstem
2.05

posterior fossa (ITV)
22.75

cerebellum
17.2

(CT fresh)

(MRI fresh)

cerebral cortex (STV)
77.9

cerebral cortex
79.15

brainstem
4.65

posterior fossa (ITV)
22.1

cerebellum
16.2

(CT defrosted)
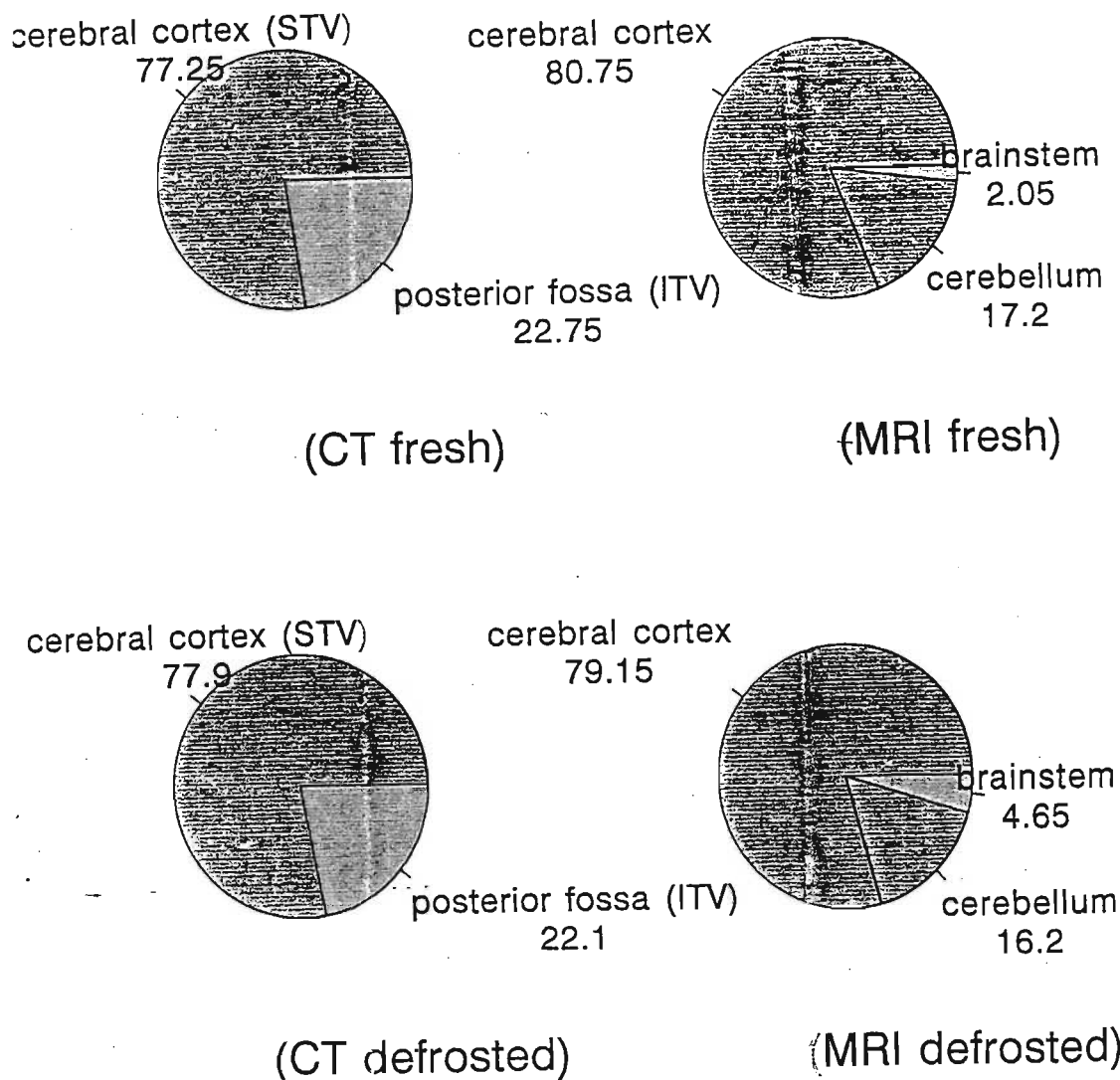
(MRI defrosted)

Figure 7. Comparison of Total Brain Volume Composition (%) for fresh and defrosted Bottlenose Dolphin Skulls

Ratio values for scans of defrosted animals were also calculated (Table 6). While the brain volume- body mass ratio (BRM), neocortex ratio (NR) (CT) and higher cortical ratio (HCR) remained the same as for fresh scans, the neocortex ratio NR (MRI) and the grey-white matter ratio (GWR) decreased. Because of the lack of differentiation between grey and white matter after defrosting, the GWR could not be measured using the same settings as for fresh animals (using a restricted range of pixel intensity- GWR1). The use of a wider range of pixel intensity (GWR2) resulted in a more similar reading to fresh values (Table 6. And see Table 8).

Table 6. Defrosted ratio values from CT and MRI

SPECIMEN	BRAIN VOL-BODY MASS RATIO	NEOCORTEX RATIO CT	NEOCORTEX RATIO MRI	GREY-WHITE MATTER RATIO 1	GREY-WHITE MATTER RATIO 2	HIGHER CORTICAL RATIO
BOT 5	6.1	3.2	3.7	0.1	0.7	4.3
BOT 6	7.7	3.9	3.9	0.1	1.0	5.6

3.1.4. CT- MRI relationships

The different volumes calculated from CT and MRI (Table 3 and 4 above) were converted to proportions of total brain volume to permit comparison between the two techniques (Table 7). For cerebral cortex measurements, CT yielded a lower value than MRI for all bottlenose dolphins under comparison (for example, Figure 7). Whereas MRI permitted a separate reading of the brainstem and cerebellum, which together comprise the posterior fossa, this was not possible using CT. The MRI values of posterior fossa were therefore combined to allow for comparison with CT values. Even so, it is evident that CT provides a higher value for the posterior fossa than MRI (Figure 7).

Table 7. Cortical volumes as a percentage of total brain volume

SPECIMEN	CEREBRAL CORTEX CT	CEREBRAL CORTEX MRI	BRAIN STEM	CEREBELLUM	POSTERIOR FOSSA MRI COMBINED	POSTERIOR FOSSA CT COMBINED
BOT 1		78.6	2.9	18.5	21.4	
BOT 2		80.4	2.0	17.6	19.6	
BOT 3	77.4	80.8	3.1	16.1	19.2	22.6
BOT 4	81.3	82.6	1.2	16.2	17.4	18.7
BOT 5	76.7	79.5	1.2	19.3	20.5	23.3
BOT 6	77.8	82.0	2.9	15.1	18.0	22.2
COM 1	. . .	79.2	2.7	18.1	20.8	
COM 2		79.1	2.3	18.6	20.9	
COM 3		85.5	1.8	12.7	14.5	
COM 4		82.8	1.7	15.5	17.2	
COM 5		83.6	1.9	14.5	16.4	
DWA 1		82.2	5.2	12.6	17.8	
HUM 1		76.2	3.1	20.7	23.8	
HUM 2		77.1	3.1	19.8	22.9	
SPO 1		78.1	4.6	17.3	21.9	
SPO 2		78.0	4.2	17.8	22.0	
STR 1		78.9	6.6	14.5	21.1	

Several highly significant, positive correlations were found between variables of the CT and MRI techniques, including the relationships between cerebral cortex volume (MRI) and supratentorial volume (CT) ($r = .985$, $n = 4$, $P < 0.05$), total brain volume (MRI) and cranial volume (CT) ($r = .988$, $n = 4$, $P < 0.05$), cerebral cortex volume (MRI) and total brain volume (CT) ($r = .969$, $n = 4$, $p < 0.05$), the neocortex ratios from MRI and CT ($r = .959$, $n = 4$, $p < 0.05$) and finally between total brain volumes from MRI and CT ($r = .987$, $n = 4$, $p < 0.05$).

Regression analyses of the above variables generated highly significant relationships of value to future comparative analyses. The equations generated below are useful to those working with CT or alternatively with MRI, who wish to estimate volumetric values for the alternate technique.

Regression analysis of cerebral cortex (MRI) on supratentorial volume (CT) displayed high significance ($F_{1,2} = 63.41$, $p < 0.05$, $R^2 = 96.94\%$) and generated the following equation (8):

(8) $CCV = -159.21 + 1.12(SV)$;

The standard error of the co-efficient for the above relationship was 0.141 and the inflated CT values were expected as this technique includes fatty tissues surrounding the cerebral cortex as cortex.

The regression of total brain volume (MRI) on cranial volume (CT) revealed a relationship of high significance ($F_{1,2} = 78.88$, $p < 0.05$, $R^2 = 97.53$) and resulted in equation (9):

(9) $TBVM = -185.06 + 1.07(CRV)$;

A highly significant relationship resulted from the regression between cerebral cortex (MRI) and total brain volume (CT) ($F_{1,2}$ = 30.22, p < 0.05, R^2 = 93.79), leading to equation (10):

(10)   CCV = -246.43 + .95(TBVC);

Similarly, the regression of the neocortex ratio (MRI) on the neocortex ratio (CT) was highly significant, ($F_{1,2}$ = 22.82, p < 0.05, R^2 = 91.94) and resulted in equation (11):

(11)   NRMR = 1.58 + .74(NRCT);

Finally, the highly significant relationship from the regression between the total brain volumes from CT and MRI ($F_{1,2}$ = 77.9, P < 0.05, R^2 = 97.5%) (figure 8), yielded equation (12):

(12)   TBVM = -270.2 + 1.14(TBVC);
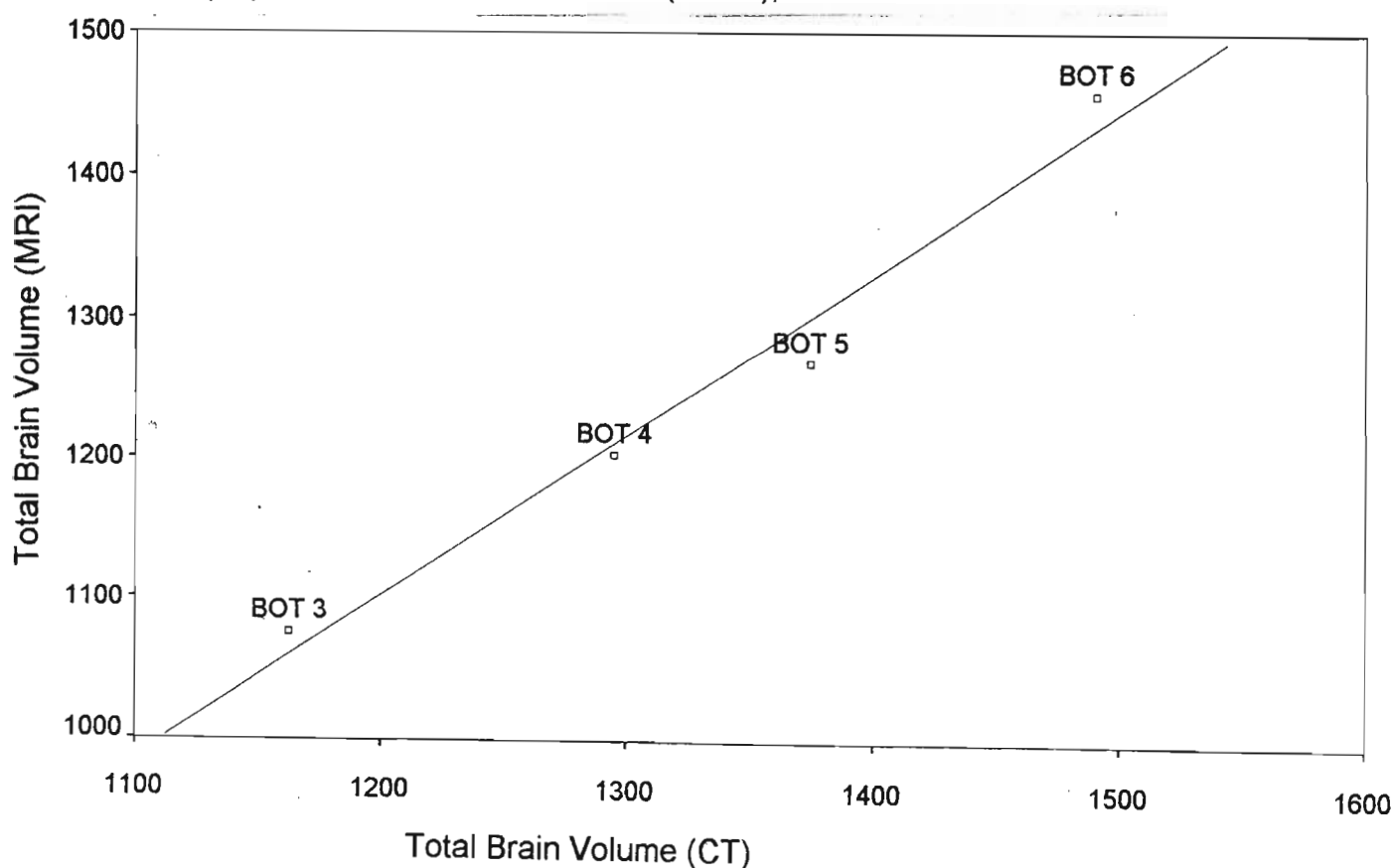
Figure 8. Regression of MRI on CT values for brain volume

3.1.2. Measures of Relative Brain Size in Dolphins

From the volumetric readings obtained from CT and MRI (above), it was possible to calculate different ratios of Relative Brain Size (RBS) (Table 8). These ratios provide an indicator of intellectual potential and allow for interspecific comparison in relation to sociality.

Table 8. Different ratios of RBS

SPECI MEN	BRAIN VOLUME	BODY MASS	BRAIN VOLUME-BODY MASS RATIO	NEOCORTEX RATIO CT	NEOCORTEX RATIO MRI	GREY-WHITE MATTER RATIO	HIGHER CORTICAL RATIO
BOT 1	1387.6	153	9.1		3.7		4.3
BOT 2	1340.2	160	8.4		4.1	1.9	4.6
BOT 3	1075.2	105	10.2	3.4	4.2	1.2	5.0
BOT 4	1202.1	80	15.0	4.3	4.7	0.8	5.1
BOT 5	1269.4	208	6.1	3.3	3.9	1.1	4.1
BOT 6	1457.1	190	7.7	4.0	4.6	1.2	5.4
COM 1	858.7	74	11.6		3.8		4.4
COM 2	904.2	58	15.6		3.8		4.2
COM 3	916.7	82	11.2		5.9	0.8	6.7
COM 4	904.6	120	7.5		4.8	0.5	5.4
COM 5	906.7	120	7.6		5.1	0.4	5.8
DWA 1	463.8	106	4.4		4.6		6.5
HUM 1	1296.4	100	13.0		3.2		3.7
HUM 2	1230.4	118	10.4		3.4		3.9
SPO 1	562.4	37	15.2		3.6		4.5
SPO 2	1005.2	80	12.6		3.5		4.4
STR 1	665.8	32	20.8		3.7		5.4

The ratios included are the brain volume to body mass ratio (BMR), the Neocortex Ratio (NR) from CT and from MRI (supratentorial volume to infratentorial volume and cerebral cortex volume to posterior fossa volume respectively). Two new ratios are also included, the first being the grey-white matter ratio (GWR) from MRI (based on differences in pixel intensity between grey matter, GM, and white matter, WM) (equation 13) allowing for an indication of higher functions in relation to basal ones. Finally the Higher Cortical Ratio (HCR), which relates cerebral cortex (CCV) to cerebellar cortex (CBV), from MRI (equation 14) is included, as it is proposed that this reflects a more direct measure of brain input versus output or processing capacity than alternative ratios.

(13)   GWR= GM/WM;

(14)   HCR= CCV/CBV;

In addition to the cross-technique neocortex ratio (CT-MRI) (above), only the higher cortical ratio and neocortex ratio (MRI) were significantly related with a regression of HCR on NRMR revealing a highly significant relationship ($F_{1,15}$ = 44.44, $P < 0.001$, R^2 = 74.77), generating the following equation (15):

(15)   HCR = .49 + 1.06 NR,

3.2.1. Interspecific Comparison of Dolphin Brain Volumes & Composition

Mean values of Delphinid brain volumes and ratios from different species, obtained from MRI scans, are presented in Table 9. The data presented are taken from sexually mature animals only.

Table 9. Mean values of Delphinid brain volumes and ratios from MRI scans of mature animals

SPEC IES*	CEREBRAL CORTEX	BRAIN STEM	CEREB ELLUM	TOTAL BRAIN VOL.	BRAIN VOL.-BODY MASS RATIO	NEO-CORTEX RATIO MRI	GREY-WHITE MATTER RATIO	HIGHER CORTICAL RATIO	GROUP SIZE
BOT	1048.4	31.6	226.0	1306.0	8.0	4.1	1.4	4.6	67
COM	763.8	16.2	129.3	909.3	8.8	5.3	0.6	6.0	300
HUM	968.4	39.4	255.7	1263.4	11.7	3.3		3.8	7
SPO	784.2	42.1	178.9	1005.2	12.6	3.5		4.4	94

* Mean values combine male and female data, except for the spotted dolphin values, which are based on male data only.

To permit interspecific comparison of brain composition, mean volumes of cerebral cortex, brainstem and cerebellum were calculated (Figure 9). From visual examination of Figure 9, one might expect cerebral and cerebellar cortex to be positively correlated. However, this was not the case ($r = .8483$, $n = 4$, $p > 0.1$), although the correlation co-efficient may not be reliable in this instance, as a result of the small sample size.
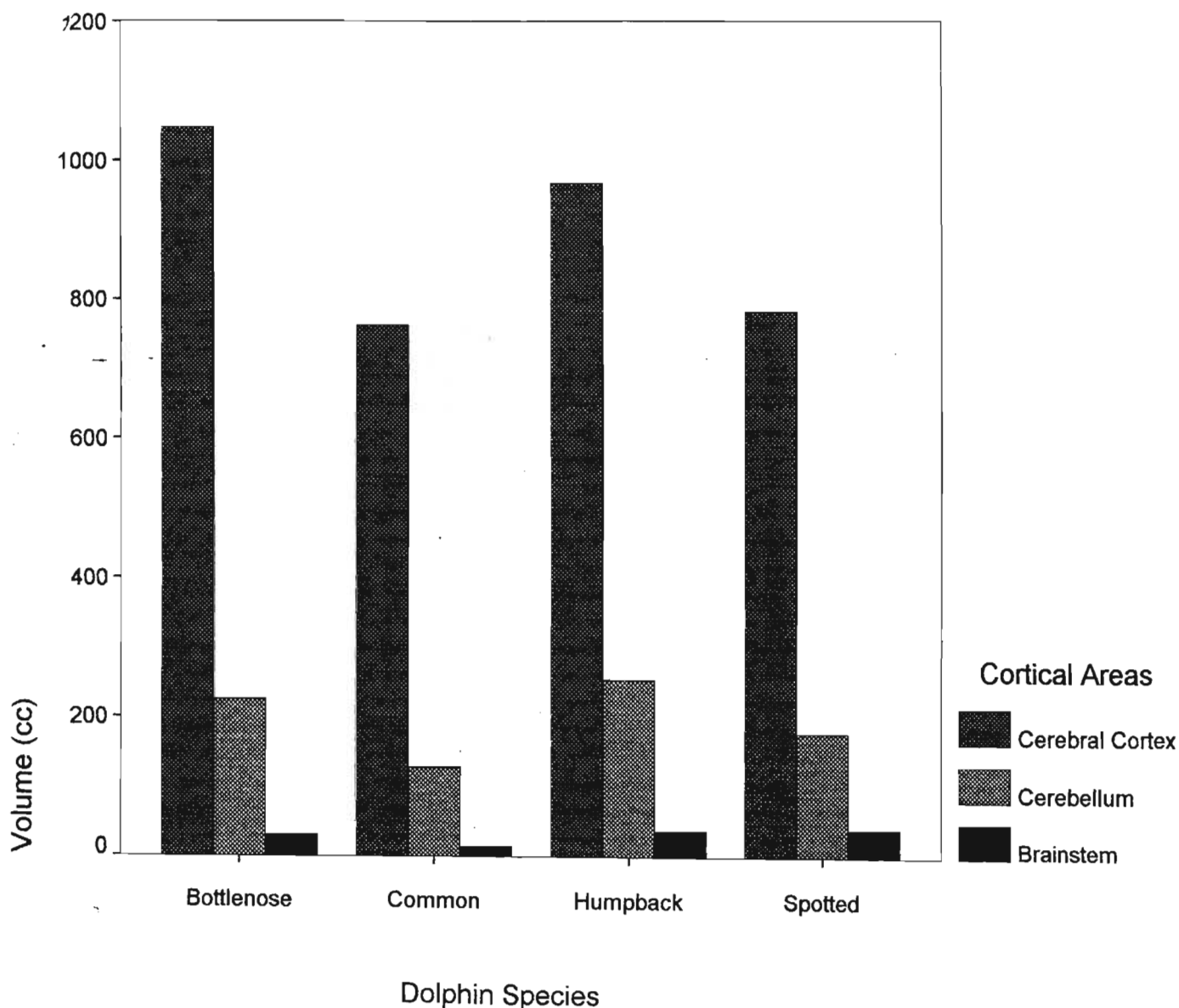
Figure 9. Regional brain volumes of dolphin species from MRI

Mean brain volume-body mass ratio, neocortex ratio and higher cortical ratio were determined for the different species (Figure 10). As determined above, a strong positive correlation was evident between the higher cortical ratio and the neocortex ratio ($r = .979$, $n = 4$, $p < 0.05$). As previously mentioned, the higher cortical ratio is a more direct measure of processing capacity than the neocotex ratio, as it focuses on cerebral cortex relative to cerebellar cortex instead of the rest of the brain.
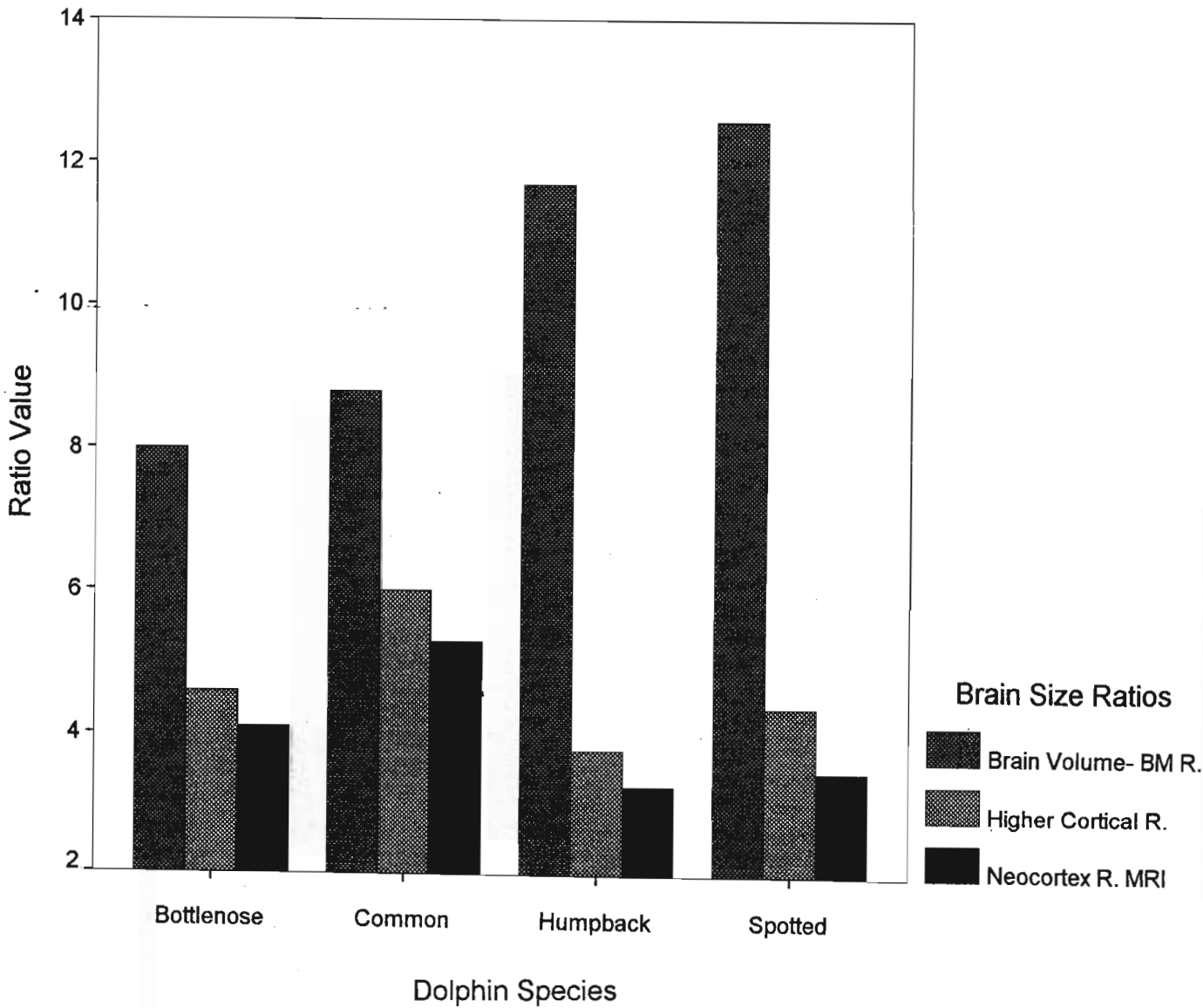
Figure 10. Relative Brain Size ratios of dolphin species calculated from MRI. (BMR=brain volume-body mass ratio; NR=neocortex ratio; HCR=higher cortical ratio)

3.2.2. RBS and sociality in Dolphins

Although this investigation utilised a small sample size, differences in mean volume values of different odontocete subfamilies, namely the Steninae and Dephininae were tabulated, as these subfamilies have different forms of social organisation (Table 10).

Table 10. Mean Relative Brain Size values for mature dolphins in the suborder Odontocetes

	CEREBRAL CORTEX	BRAIN STEM	CERE BELL UM	TOTAL BRAIN VOL.	BRAIN VOL- BODY MASS RATIO	NEO- CORT EX RATIO MRI	HIGHER CORTICAL RATIO
superfamily: Delphinoidea family: Dephinidae	916.9	34.7	216.9	1168.5	10.1	4.1	4.8
subfamily: Steninae	968.4	39.4	255.7	1263.4	11.7	3.3	3.8
subfamily: Delphininae	865.5	30.0	178.1	1073.5	9.8	4.3	5.0

While the Steninae appear to have a larger brain volume to body mass ratio, cerebral cortex, posterior fossa and total brain volumes (Figure 11), the Delphininae have higher neocortex and higher cortical ratios.
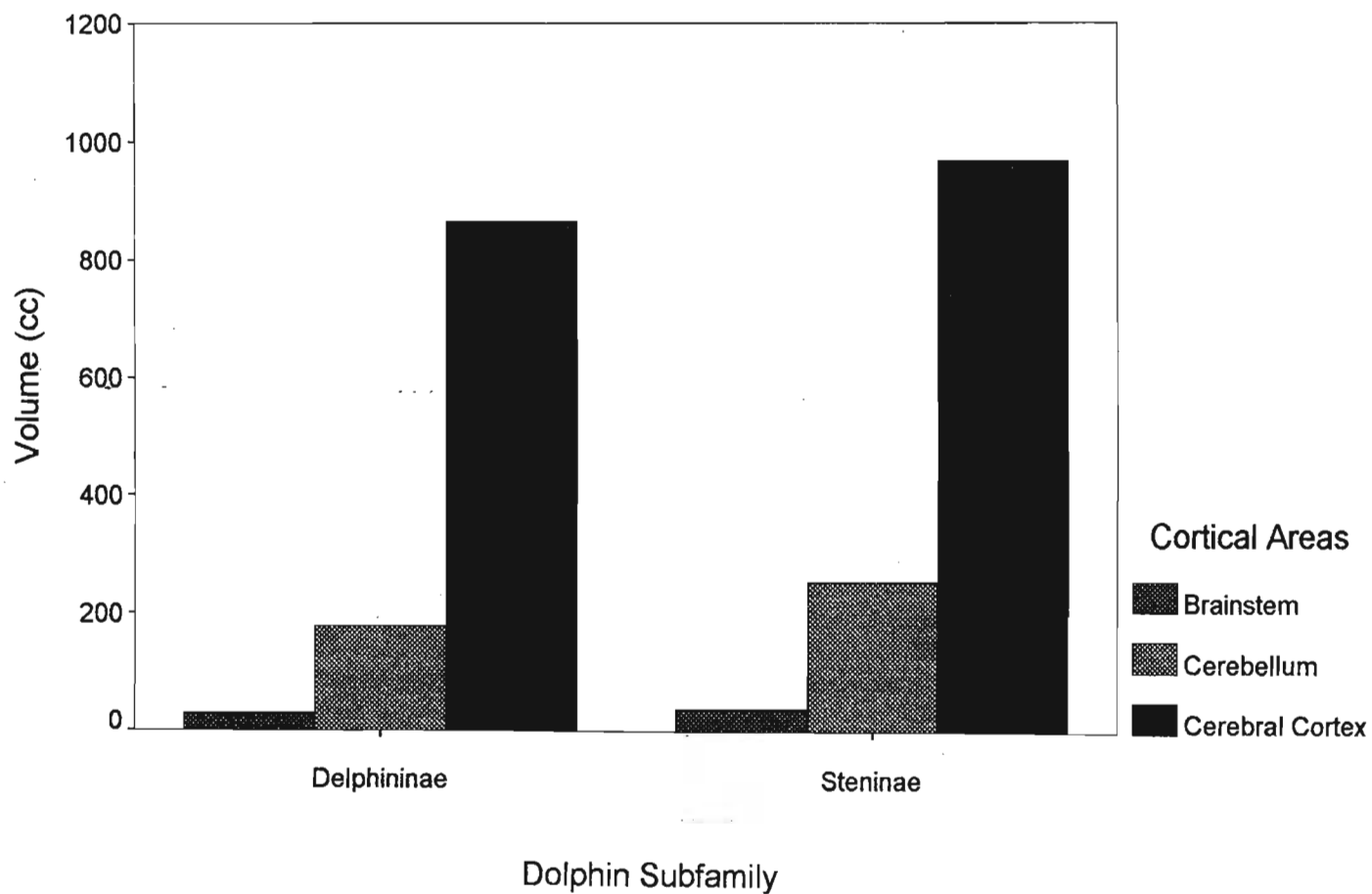
Figure 11. Comparison of brain composition between the two dolphin subfamilies Steninae and Delphininae

From the interspecific comparison, it is apparent that only the higher cortical ratio was significantly related with two other variables, mean group size (r = .981, n = 4, p < 0.05) and neocortex ratio (r = .979, n = 4, p < 0.05).

As a standard for comparison to the correlation of RBS and sociality found in this study, dolphin EQ values from Worthy & Hickie (1986) were tabulated against mean and maximum group size for these species (Findlay 1989) (Table 11). No significant relationship was found between EQ and mean or maximum group size.

Table 11. Delphinid EQ in relation to Mean Group Size and Maximum Group Size

SPECIES	MEAN GROUP SIZE	MAXIMUM GROUP SIZE	EQ
Globicephala scammoni	7.33	120	1.4
Orcinus orca	5.33	11	1.5
Physeter catodon	15.6	115	0.3
Platanista indi	1	5	1.4
Tursiops truncatus	76.2	1500	2.8

The relationship between the neocortex ratio and mean group size for the different dolphin species in this study is presented in Figure 12. It is evident that common dolphins, who live in the largest groups, have the highest neocortex ratio, while the solitary humpback dolphins have the lowest neocortex ratio.
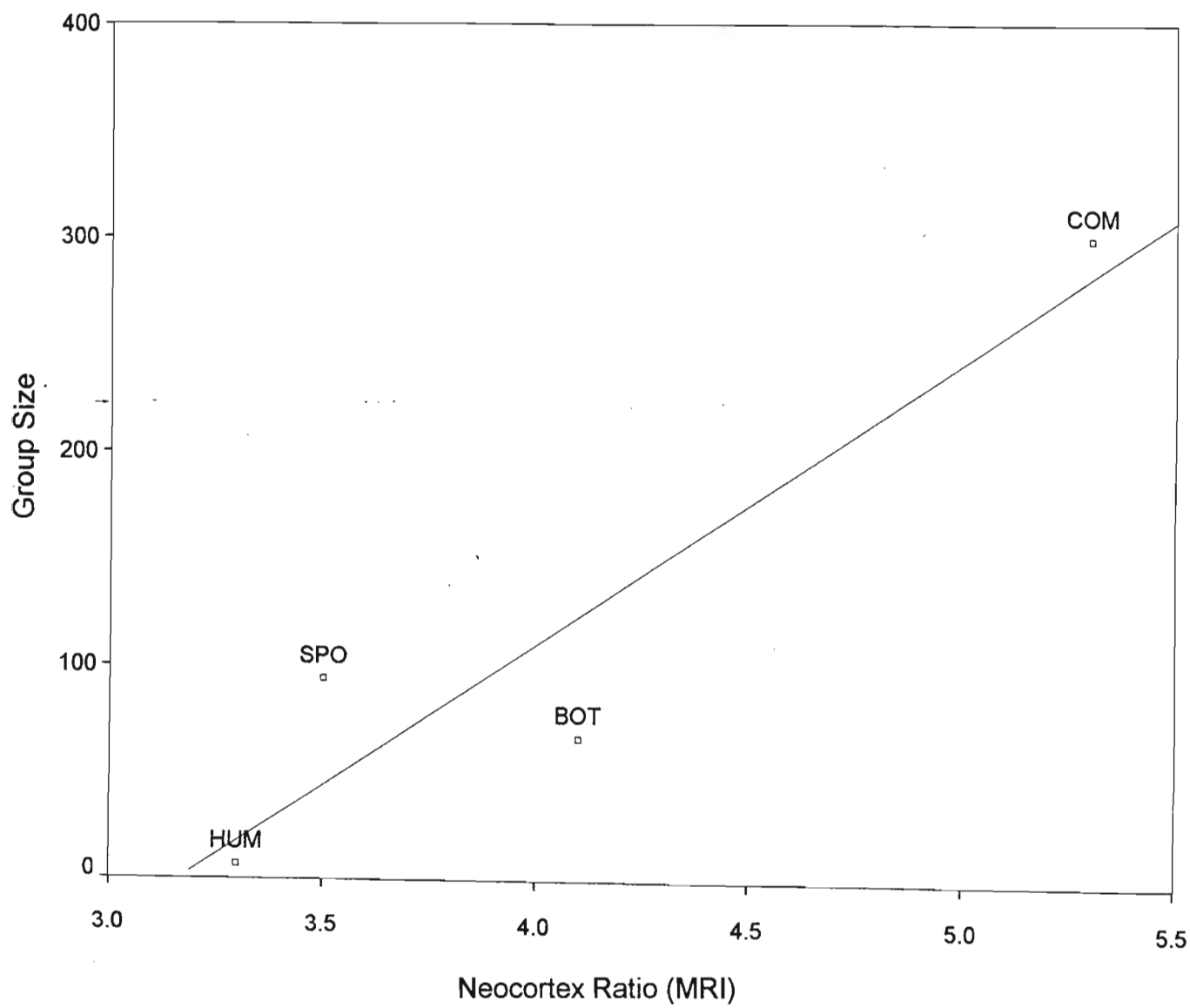
Figure 12. Dolphin Neocortex Ratio in relation to Group Size

3.3. Comparison of Delphinid and Primate Brain Volumetric relationships

The final result presented in this study (Table 12) compares the values obtained for dolphins to the relevant primate data from Dunbar (1992). This is the case as Dunbar found a correlation between group size and neocortex in primates and this study has found a similar relationship in dolphins. In addition, as dolphin RBS values have not been previously analysed in comparative data sets, the primates present the best order for comparison, as most documented data relates to this order.

Table 12. Comparison of Dolphin Brain Volumes to Primate Volumes (Dunbar (1992).

SPECIMEN	BODY MASS	NEOCORTEX VOLUME	TOTAL BRAIN VOLUME	NEOCORTEX RATIO	MEAN GROUP SIZE
Cheirogaleus	0.31	1.040	4.667	0.8	1
Microcebus	0.05	0.740	1.680	0.79	1
Lepilemur	0.92	3.282	7.175	0.84	1
Lemur	2.20	13.750	25.910	1.23	9.5
Avahi	1.07	4.628	9.461	0.96	2
Propithecus	3.48	13.170	25.194	1.1	5
Indri	6.25	20.114	36.285	1.24	4.3
Daubentonia	2.80	22.127	42.611	1.08	1
Loris	0.322	3.524	6.269	1.28	1
Nycticebus	0.80	6.192	11.755	1.11	1
Perodictus	1.150	6.683	13.212	1.02	1
Galago	0.372	2.810	5.794	0.94	1
Tarsier	0.125	1.768	3.393	1.09	1
Callithrix	0.28	4.371	7.241	1.52	8.5
Cebuella	0.14	2.535	4.302	1.43	6.0
Saguinus	0.38	5.894	9.537	1.62	5.2
Callimico	0.48	6.476	10.510	1.61	7.3
Aotus	0.83	9.950	16.195	1.59	3.8
Callicebus	0.90	11.163	17.944	1.65	3.3
Aloutta	6.40	31.660	49.009	1.82	8.2
Ateles	8.00	70.856	101.034	2.35	17
Lagothrix	5.20	65.873	95.503	2.22	23.4
Cebus	3.10	46.429	66.939	2.36	18.1
Saimiri	0.66	15.541	22.572	2.21	32.5
Macaca	7.80	63.482	87.896	2.6	39.6
Cercocebus	7.90	68.733	97.603	2.38	15.4
Papio	25.00	140.142	190.957	2.76	51.2
Cercopithecus	4.85	47.550	67.035	2.44	23.9
Miopithecus	1.20	26.427	377.760	2.33	65.5
Erythrocebus	7.80	77.141	103.167	2.96	28.1
Pygathrix	7.50	48.763	72.530	2.05	-
Nasalis	14.00	62.685	92.797	1.75	14.4
Procolobus	7.00	50.906	73.818	2.22	35
Hylobates	5.70	65.800	97.505	2.08	3.4
Gorilla	105.00	341.444	470.359	2.65	7
Pan	46.0	291.592	382.103	3.22	53.5
Homo	65.0	1006.525	1251.847	4.1	148.4
Sousa ch.	109.0	968.4	1263.4	3.3	7
Stenella c.	80.0	784.2	1005.2	3.5	94
Tursiops	163.2	1048.4	1306.0	4.1	67
Delphinus	107.3	763.8	909.3	5.3	300

3.1.1. Group size- neocortex ratio relationships in primates and dolphins

Total brain volume, neocortex volume and the neocortex ratio for dolphins were compared with primate data (Dunbar 1992). As human mean group size was not evident in Dunbar (1992), the mean value for human group size from Dunbar (1993) was used. The values for Pithecia were excluded as they were inaccurate (R.I.M. Dunbar pers. comm). The dolphin values for group size- neocortex ratio have been plotted on the primate regression of log GS on log NR ($F_{1,34}$ = 143.68, P < 0.001, R^2 = 80.87%) according to equation (16) and represented in Figure 13.

(16)   log (GS) = .17 + 3.05 log (NR)

This result is the most significant finding of this study. Visual examination of Figure 13 reveals that the human is the only primate within the dolphin range of neocortex ratio. Furthermore, humans do not even fall midway into the dolphin range of neocortex ratio (human NR = 4.1), from solitary humpback dolphins at a NR of 3.3, to common dolphins at a NR of 5.3. This serves as a most compelling reason to question data supporting a "natural scale" of brain evolution with humans at the pinnacle and encourages further comparative investigation of different grades of adaptation.
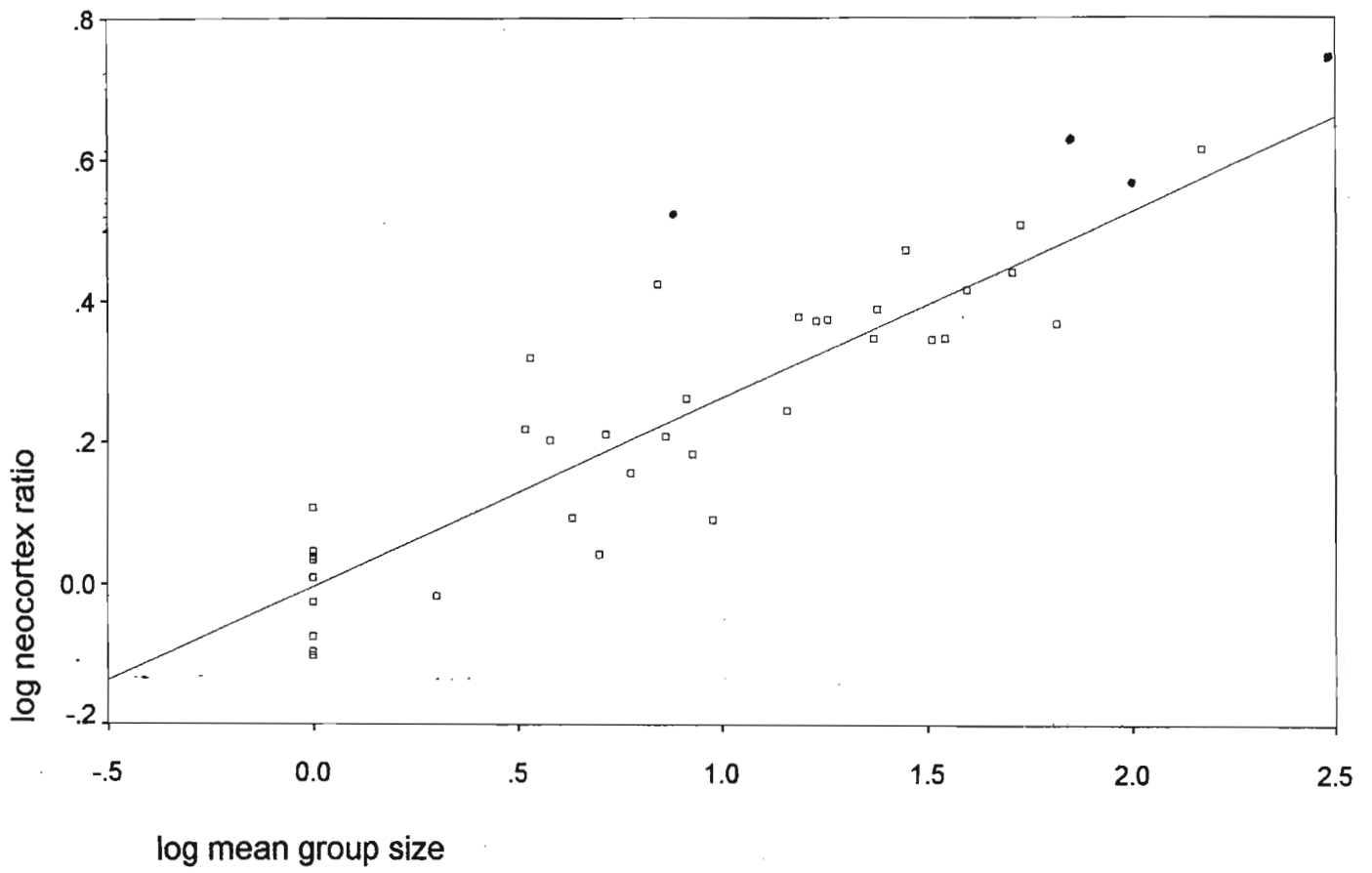
The values for different dolphin species on the logarithmic plot illustrated below are indicated by the filled dots.

Figure 13. Neocortex ratio in relation to group size for primates and dolphins

4. Discussion

Analysis of the values obtained using CT revealed that total brain volume is highly correlated with cranial volume in cetaceans. Investigations of the cranial volumes of skulls of rare species and fossils may therefore be undertaken using cranial volume and the values corrected according to equation (3) to obtain total brain volume. The study also found strong correlations between supratentorial volume and cranial volume and between supratentorial volume and total brain volume. An important finding is that an estimate of cerebral cortex volume can thus be obtained from cranial volume or total brain volume, using equations (4) and (5) respectively. As the above findings, in addition to the ratio of cerebral cortex volume to total brain volume, are integral to studies of relative brain size, in relation to the hypothesis under consideration, the above findings form an essential base for further investigation.

Whereas CT only permits differentiation between supratentorial volume (containing cerebral cortex) and infratentorial volume (housing the posterior fossa), MRI allows analysis of cerebral cortex in addition to the brainstem and cerebellum, which together constitute the posterior fossa (Hurribunce, pers. comm). MRI scans indicate that cerebral cortex and cerebellar volumes are both strongly correlated with total brain volume. With total brain volume, one can thus estimate the volume of cerebral and cerebellar cortex from MRI, according to equations (6) and (7).

Although CT scans overestimate total brain volume and posterior fossa volume, they appear to underestimate cerebral cortex volume as evidenced in the comparative findings of CT and MRI. This confirms the value of MRI for volumetric analyses of the cerebral cortex undertaken in this study.

The condition under which the specimen was scanned was found to have an important effect on volumetric readings, which in turn, if distorted, would affect the nature of the relative brain volume- sociality relationship . Freezing and defrosting had significant effects on regional and total brain volume readings. While both frozen and defrosted specimens could be scanned using CT, only defrosted specimens could be studied using MRI, as this procedure depends on the movement of hydrogen protons- which cease to move upon freezing, thereby providing an extremely weak signal.

Both procedures yielded higher total brain volumes after defrosting, while the cerebral cortex volume increased on CT and decreased on MRI. Although the posterior fossa volume increased on both procedures, the cerebellum decreased while the brainstem increased on MRI. Following defrosting, the brain volume to body mass ratio, the neocortex ratio (CT) and the higher cortical ratio remained the same as for fresh readings (as overall changes in volume were minimal), while the neocortex ratio (MRI) and the grey- white matter ratio decreased. Additionally, as a result of the decreasing differentiation between grey and white matter, where the same range of pixel intensity was used for defrosted specimens as for fresh specimens, the grey- white matter ratio appeared significantly reduced. The range required extension to allow for some differentiation between the two types of brain matter.

Freezing not only affected readings of regional and brain volumes, but also increased cranial volume. During the process of slow freezing, the cells become altered, with ice crystals forming and penetrating through layers of cells, rupturing these. On defrosting, water occupies the space previously occupied by the ice crystals and this results in a distorted volume (Rijkenberg, pers. comm). In addition, where brain solutes are concerned, brain volume is altered as membranes tear away during defrosting. The

solute balance of cells subsequently changes and the osmotic pressure of cells is also altered, therefore affecting water content in the tissue, altering density and volume (Rijkenberg, pers. comm).

Further factors affecting volumetric analyses may include tissue death, which increases over time, replacement of cerebrospinal fluid with air and finally the cause of death. Royston (pers. comm) notes that a telling sign of death by asphyxiation in humans is the loss of differentiation between grey and white brain matter. As almost all of the specimens used died as a result of asphyxiation, this may explain the lack of differentiation between grey and white matter, with further degeneration occurring through freezing and during defrosting. However, where species are rare, or captured in regions without access to neuroimaging facilities, it is encouraging to note that the margins of error between defrosted and fresh animals are not vastly significant for values of brain volume, CT estimates of neocortex ratio and MRI estimates of the higher cortical ratio.

There are several highly significant correlations between CT and MRI variables for estimating brain volumes. These include the relationship between cerebral cortex (MRI) and supratentorial volume (CT), total brain volume (MRI) and cranial volume (CT), cerebral cortex volume (MRI) and total brain volume (CT), the neocortex ratios from MRI and CT and finally total brain volume from MRI and CT. This has serious implications for researchers working in locations with CT facilities, but without MRI, as correction factors may be implemented to arrive at MRI values from CT values (equations 8-12) thus allowing access to a wider range of species.

In comparison to MRI, CT appears to overestimate total brain volume and posterior fossa volume, possibly through reading soft tissue surrounding the

cortex as cortex. Although MRI provides higher precision and differentiation capabilities for volumetric analysis, CT enables calculation of cranial volume, which is not possible using MRI (as it does not register bone).

Another benefit of MRI is that it provides images in all three planes; however, for the purposes of this study only the coronal images were analysed. Investigations of structures such as the pons, medulla and corpus callosum are made possible by analysis in the sagittal plane; axial images promote research into the differences between hemispheres, which may be interesting in the context of language and communication.

It may be concluded that MRI and CT both have their merits and shortcomings as techniques. While MRI provides higher resolution images with more precise readings of specific brain structures than CT, it may only be used on fresh or defrosted specimens. CT may be used to scan an animal in any condition, fresh, frozen or defrosted. And while not as accurate as MRI, CT does have the advantage of allowing measurement of cranial volume. This study found a highly significant correlation between the two techniques and the high cross- technique correlations on several measures served to illustrate this. The value of the cross- technique correlations lie in the fact that results obtained on CT can be accurately corrected to reflect equivalent MRI readings for comparative analysis.

The values obtained from CT and MRI analysis were used to calculate a variety of relative brain size ratios, including (1) measures relating brain volume to body weight (pseudo- relative measure), (2) a relative measure of neocortex (the neocortex ratio from CT and MRI) and (3) the newly devised ratios of grey-white matter ratio (equation 13) and cerebral to cerebellar cortex (higher cortical ratio) (equation 14).

While the neocortex ratio was documented by Dunbar (1992) and its utility verified by Dunbar (1995) in relation to group size, the two new measures of relative brain size proposed in this study require further investigation. This applies especially to the higher cortical ratio, which is not only strongly correlated with the neocortex ratio (equation 15) but also with group size (equation 16). It is proposed that both of these measures provide a more direct measure of brain input and output. The grey- white matter ratio should provide an indication of processing capacity, as it is believed that the processing capacity of the brain relies strongly on the relationship of grey to white matter (Jerison 1982a). Furthermore, cerebral cortex and cerebellar cortex provide the values for the type of ratio sought by Passingham (1982) to relate input to output of brain "traffic". In addition, the contemporary view is that cerebellar cortex may be viewed as "basal" cortex, required for basic functional integration, while cerebral cortex may be described as "higher" cortex, as it is responsible for the performance of "higher" cognitive functions, such as attention, perception and memory (Luria 1973, 1982), although some sensory cerebral cortex performs basic functions and cerebellar cortex appears engaged in motor memory and attentional processes (D. Perret, pers.comm). According to the prevailing view, a ratio holding cerebral cortex relative to cerebellar cortex should therefore provide some insight into the degree of higher cortical functioning. Application of such ratios to a greater range of cetacean and primate species should verify or dismiss this hypothesis.

This study has verified the hypothesis that, for the species of bottlenose, common, humpback and spotted dolphins, a relationship is in existence between the neocortex ratio and group size, as is the case for primates. Of interest is the finding that the only measure significantly correlated with both group size and the neocortex ratio in the cross species comparison was the higher cortical ratio, which not only indicates the usefulness of this measure,

but which provides further evidence that examination of its efficacy is required.

In accordance with the hypothesis under investigation, namely that the relative size of neocortex is related to social complexity, as measured by group size, (verified for primates by Sawaguchi & Kudo 1990; Dunbar 1992, Dunbar 1995), humpback dolphins score the lowest neocortex and higher cortical ratios, as expected for solitary animals. Although the spotted dolphins have a larger mean group size than bottlenose dolphins, the latter have larger neocortex and higher cortical ratios than the former. It is essential to note that group sizes for coastal and pelagic dolphins vary tremendously, which may explain this phenomenon. Although uncertainty exists in relation to group size for marine and terrestrial mammalian species, which may be viewed as increasing the difficulties of describing qualitative relationships, fluctuations in group size may be viewed as more socially complex. Common dolphins are acknowledged as living in the largest groups of all the species under study and as such obtained the expected highest values for neocortex and higher cortical ratios. While the Steninae (including humpback dolphins) have bigger average, absolute values, it is interesting to note that the Delphininae (including bottlenose, common and striped dolphins) have higher relative measures of brain size, suggesting that social complexity is related to increasing RBS in dolphins.

No previous study has found a correlation between RBS and sociality in cetaceans. For example, no correlation was found between EQ and sociality (as evidenced by group size) in dolphins, following an analysis of EQ data from Worthy & Hickie (1986) and relevant group size data from Findlay (1989).

The four dolphin species studied were analysed with primate data on neocortex volume, neocortex ratio, body mass and group size from Dunbar (1992). The comparative analysis was conducted in terms of relating group size to the neocortex ratio.The major finding of this study pertained to the positioning of cetaceans in relation to primates comparative analysis mentioned above. All non-human primates fell outside the range of dolphin neocortex volume, with the human neocortex ratio occurring only midway into the dolphin range. Of interest is the fact that according to Aiello & Dunbar (1993) earlier hominids, including Neanderthals, and early modern *Homo sapiens*, had larger neocortex ratios than living humans. They also had larger groups than extant humans according to Aiello & Dunbar (1993), which may explain their higher neocortex volumes. However, one may question the accuracy of group size estimates, as it could be argued that humans live in "groups" extending into the millions (D. Perret, pers. comm). Even earlier hominids, however, do not surpass the midpoint value of the neocortex ratio for dolphins calculated in this study.

Although Ridgway (1990) notes that interspecific brain volume variation among dolphins is vast, this study has established a range of neocortex ratios displaying the variation for dolphins of four species of differing social structure. Although these results have been based on MRI values for sexually mature animals, a larger sample of species could even reveal stronger correlations.

Milton (1988) proposed that increased relative brain size is related to ecological complexity. However, subsequent research has dismissed this notion for primates by supporting evidence to show that social complexity drives the evolution of a larger amount of brain and neocortex (Sawaguchi 1990; Sawaguchi & Kudo 1990; Dunbar 1992, 1995). This has been linked to the concept of social or "Machiavellian" intelligence (Byrne & Whiten 1988,

Byrne 1995) with the suggestion that neocortex is perhaps the best indicator of intellectual potential (Byrne, pers. comm). (For a comprehensive review of RBS and its correlates refer to Appendix A). However, the alternative hypothesis, namely relating ecological complexity to brain size, must still be tested for marine mammals.

A different grade of adaptation may be responsible for the high development of the cetacean neocortex ratio in relation to other animals; this study has found a strong relationship with sociality, but has not dismissed ecological complexity as a possible selective mechanism. One fact is striking, the *scala natura*, which always implicitly places primates (and ultimately humans) above other animal species, is shattered by the extremely high positioning of dolphins (especially the social species) in relation to primates, (especially humans) on the neocortex ratio- group size measure. This alone indicates the serious need to engage in further comparative brain analysis, not only for Delphinid species, but also for species belonging to different mammalian orders.

4.1. Implications of findings and future research

The findings of this study emphasise the need for comparative investigation of terrestrial and marine mammalian brains, to further our comprehension of brain evolution, comparative anatomy and the selective pressures behind increased relative brain size and its correlates, whether ecological, social, cognitive or behavioural. The findings pertaining to dolphin relative brain size in this study present a powerful display of the possibilities of parallel evolution. The new measures of relative brain size described in this study are applicable to primate, mammalian or vertebrate species' analyses and will hopefully develop through continual exposure to different species of different orders. The use of cranial volume to ascertain brain and cerebral cortex volume allows for the use of museum collections of the skulls of rare or fossilised species, not only for cetaceans, but for primates, carnivores and ungulates. In addition, the ability to estimate correction factors from CT to MR volumes and from defrosted volumes to fresh volumes will permit the accurate determination of brain volumes or permit the freezing of rare specimens until arrival at appropriate scanning facilities. Aside from the interesting findings pertaining to dolphin relative brain size in relation to primates and to sociality, it is hoped that the value of the neuroimaging techniques utilised will be recognised and used to reconceive the study of the brain, its regions, evolution, size, correlates and functions for all mammals.

The following still need to be achieved and refined to bring the work to its full potential:-

More subjects are required to improve estimates across species;

A larger range of species (both extinct and extant) must be investigated, possibly through the use of cranial volume measurements and refined equations developed in this study;

A more detailed comparison with other cetacean groups and mammalian orders, with information on specific brain structures being related to testing the hypothesis of social complexity driving brain evolution in addition to an investigation of the alternative hypothesis of foraging and ecological complexity driving brain evolution.

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Appendix A:

Relative Brain Size and Evolutionary Neuroanatomy in Mammals

From the vast amount of research into the structure of the brain, researchers have developed measures of brain size, either absolute or relative (Von Bonin 1937; Jerison 1973; Passingham 1982; Sawaguchi & Kudo 1990; Dunbar 1992). From such measures of brain size, inferences have been drawn about the correlation between cortical size and intelligence, and whether increased intellectual capacity stems from ecological or social pressures. Comparative analyses can be made from the phylogenetic reconstructions permitted by evolutionary neuroanatomy, (the study of comparative anatomy, embryology, ontogensis and palaeontology). Correlative neuroanatomy, a sub-discipline of evolutionary neuroanatomy, is of interest, as it relates the structural organisation of the brain to the functioning of different brain regions. This review focuses on absolute measures of encephalisation before providing the reasons for studying relative brain size (RBS) measures. Several measures of RBS are described and their advantages and limitations are discussed. The correlation between RBS and intelligence, social organisation, ecology and energetics and finally with cognition or behaviour are investigated. Following this, dolphin neuroanatomy is reviewed, under the areas of dolphin neural organisation in relation to other mammals and different measures of RBS in dolphins.

1. Why measures of relative brain size?

Absolute brain size (ABS) is not adequate for comparative analyses as it favours larger animals. The larger the animal, the bigger the organs must be

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 problems encountered with absolute brain size, 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 *et al* 1970).

Passingham (1982) noted that the larger the animal, the smaller the brain/body ratio, as an increase in brain size is relatively smaller than an increase in body size. This relative increase only allows valid comparisons between similar sized species. Although an alternative appears to lie in measuring brain size relative to spinal cord (Warden 1951) or medulla size, which provides an indication of additional brain tissue not required for sensory analysis or directed movement, the problem with this technique lies in the lack of such area measurements for different species (Passingham 1982).

To overcome the difficulties inherent with 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. Logarithms of the obtained values are used as points through which a regression line can be traced to derive the best line of fit between brain and body size for the group (see Figure 16). This permits interspecific analysis based solely on body weight (Passingham 1982). Although an improvement on absolute brain weight, brain weight relative to body weight may still be considered an absolute measure.

2. Different measures of Relative Brain Size

Several RBS measures are described below. These include the cephalisation coefficient (Von Bonin 1937), the encephalisation quotient (Jerison 1973) and its derivatives (Eisenberg 1981; Passingham 1982), comparative brain size (Clutton-Brock & Harvey 1980); processing capacity (Jerison 1982a); cranial capacity (Martin 1990); relative size of neocortex (Sawaguchi & Kudo 1990) and the neocortex ratio (Dunbar 1992, 1995).

Von Bonin (1937) formulated an equation known as the cephalisation coefficient, 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 relating the observed brain size of each species to the expected brain size of an average mammal similar in body weight. For example, human brain size may be compared to a hypothetical primate's by reading off the regression line the brain size predicted for a hypothetical primate of similar body weight. Human brain size is three times larger than expected for a primate of similar size according to this measure (Passingham 1982) (Fig. 16).

Jerison (1973) provides the equation for EQ (based on a slope of 0.67):

$$E = 0.12 \ W^{0.67}$$

(where E = brain weight in grams & W = body weight in grams). EQ is calculated by ascertaining expected brain size relative to body size (E_E) and then relating this to actual brain size (E_A) in the equation: $EQ = E_A / E_E$ (Martin 1990)

As the slope of 0.67 has been held to overestimate brain size in large mammals and underestimate it in small mammals (Martin 1990), it is appropriate to consider Eisenberg's (1981) redefinition of mammalian EQ in relation to a slope of 0.74: $EQ = 0.05\ W^{0.74}$

From this, the average mammalian EQ lies at 1.0. Where brain size is larger than expected, the EQ is greater than 1.0 and where smaller than expected, an EQ of less than 1.0. From Fig. 17, which provides values for several mammalian groups, three classes can be differentiated: insectivores and rodents have small brains relative to weight; ungulates, carnivores and prosimians have moderately sized brains, while simians and humans have large brains. Passingham (1982) notes that although the absolute brain size of the elephant is greater than primates, its EQ is within the range for ungulates and carnivores. From the research of Jerison (1973), it is apparent that only 3 out of 25 ungulates and 2 out of 15 carnivores hold an EQ within the range of 48 simian primates.

Passingham (1982) argues that the relation between brain size and body size is not as accurate as relatiing brain size to a more direct measure of brain inputs and outputs such as medulla size. Other forms of RBS therefore relate overall brain volume to volumes of specific brain and central nervous system structures, such as Passingham's example of brain volume relative to medulla volume (Fig. 18).

RBS measures relating overall brain size to different proportions of the brain require further discussion. The brain may be divided into three areas; these are, hindbrain, midbrain and forebrain. 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.

This neocortex, often vaguely referred to as cortex, covers the cerebral hemispheres. Neocortex can be distinguished from other types of cerebral cortex and, owing to its importance in higher functions, it forms the centre for interspecific comparison (Passingham 1982).

An interesting pattern is evident from comparative indices of different brain parts. The human pons and medulla are of an expected size for a primate of our size (Passingham 1982). There is a fair enlargement of the midbrain (mesencephalon), interbrain (diencephalon) and the striatum (in the telencephalon) compared to other primates with the greatest difference occurring in cortical areas such as the piriform cortex (palaeocortex), hippocampal cortex (archicortex), cerebellar cortex and neocortex. Finally, the "extraordinary development" of the human brain's neocortex and cerebellum best characterise its specialisation (Passingham 1982). Eccles (1973) recognises that these two brain components are closely related, with the neocortex receiving fibres from the cerebellum via the thalamus and returning fibres to the cerebellum via the pons.

Different neocortical areas perform specialised functions, such as sensory cortex receiving sensory information via the thalamus and motor areas controlling movement and association areas which appear essential to learning. 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. The human brain has the amount of sensory cortex expected, but is distinguished by the extent of the agranular cortex and the association areas, with the premotor cortex being especially large in the human brain (Passingham 1982).

Passingham (1982) suggests that the human brain is not merely a larger primate brain with unaltered regional proportions, as areas such as the cerebellum and neocortex are larger than for chimpanzees. Comparative values clearly indicate the difference between human and non-human primates in this regard (Fig. 19).

The proportion of neocortex to total brain size in primates increases as brain size increases (Fig. 20), with a regression analysis indicating that the size of the human neocortex is as expected for a primate of our size (Fig. 21). Similarly, 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. Where variance does occur, it is predictable in terms of the pattern expected for higher primates but not for mammals in general (Passingham 1982). Different regressions are used for different mammalian orders and sub-orders, as the rule relating brain size to neocortex size differs for these groups (Fig. 22).

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. Cell numbers are as expected for the observed neocortex size (Passingham 1973). It appears that cell density decreases as brain size increases in mammals, with humans having the predicted density in relation to brain size. In addition, it is apparent that all mammals share the same number of cells in similar cortical bands, indicating that all mammalian brains share the same basic building blocks (Passingham 1982).

Another relative measure of brain size is provided by Clutton-Brock & Harvey (1980) in an adaptation of Jerison's EQ. Referred to as comparative brain size (CBS) for a specific genus, the equation is as follows:-

CBS=log (brain wt) - [family elevation + family slope x log (body wt)]

Jerison (1982a) measures the processing capacity of the brain, based on the surface area of the cortex, where each square centimetre of cortex contains 2000 processing units or modules. A mouse with a $4cm^2$ cortex possesses 800 modules (processing units), a chimpanzee with $800cm^2$ has 1.6 million modules and a human with $2000cm^2$ cortex has 4 million modules.

Another measure of RBS, discussed by Martin (1990) is cranial capacity (CC), which is advantageous for investigations of skulls for which there exists no information on weight. CC can be measured using sintered glass beads or artificial endocast volume (latex mould of internal braincase contours) (Martin 1990). Alternatively, double graphic integration with the aid of X-rays may be used (Jerison 1973), where average height (h) and width (w) of the cranial cavity are superimposed on the braincasing's internal contours to obtain estimated cranial capacity: $C_{est}=$ ($\pi/4$ x w x h x l) where l = length of cranial cavity (in Martin 1990).

Martin (1990) notes that CC is highly correlated with brain weight ($r = 0.996$) (Fig. 23), although concerns about its limitations are discussed in section 4.2 below. The relationship between CC and brain weight (E) is virtually isometric, with CC thus providing an accurate indication of brain weight (in primates). Logarithmic plots of CC and body weights used by Martin (1990) (Fig. 24) have confirmed the original research of Bauchot & Stephan (1969), based on actual brain weights, that different grades of brain size exist-

"basal" insectivores, "advanced" insectivores, strepsirhines and haplorhines. As these formulae provide allometric values, the reader is referred to the limitations of allometry (see Byrne and Deacon, below).

The scaling equation for placental mammals is provided by Martin (1990), who notes that the previously used 0.67 slope is too low for such mammals, proposing that 0.75 is generally adequate. A species comparison is provided in Fig. 25 and orders are compared in Fig. 26 below:

$\log_{10} E = 0.76 \log_{10} W + 1.77$ $(r = 0.96)$

(where E = brain weight in mg; W = body weight in g)

Returning to cranial capacity, Martin (1990) has 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). In other words, ICC= C_A / C_E. For the four categories of mammals discussed earlier, the best slope appears to be 0.68. The ICC is assessed in sect 4.2 below.

Sawaguchi & Kudo (1990) have formulated a measure of relative size of the neocortex (RSN) to assess the degree of neocortical development in each superfamily of primates. RSN is based on the allometric relationship between neocortex volume (NV, in mm^3) and brain weight (E, in g) for each superfamily. This relationship is expressed as:

$NV = k \times E^a$,

where k and a are constants for the superfamily. It follows that,

$$\log NV = a \times \log E + \log K$$

Sawaguchi & Kudo (1990) used regression analysis to obtain the allometric equation for each superfamily as the correlation coefficient between neocortex volume and brain weight exceeded 0.98 ($p < 0.01$, t-test). RSN is independent of the effects of brain and body size (Sawaguchi & Kudo, 1990), where:

$$RSN \text{ (for a congeneric group)} = \log NV - (a \times \log E + \log k).$$

The final measure of RBS discussed is the Neocortex Ratio (NR) (Dunbar 1992) (Figure 27 a,b,c), obtained by dividing neocortex volume (NV) by total brain volume (TBV) minus neocortex volume, according to the equation:

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

The above measure aims to separate the rather loosely defined volume of neocortex from the rest of the brain, or hindbrain (Dunbar 1992), although there are problems associated with the definitions assumed in this study (sect. 4.2).

3. Correlations of RBS with:-

3.1 intelligence

Intelligence is a hypothetical concept and differing versions of what is perceived as intelligence exist (Worthy & Hickie 1986). For the purpose of this review, Jerison's (1973) definition of biological intelligence is adopted. He defined biological intelligence as the animal's degree of information-

processing capacity, or the integration of sensory-motor input and output. Worthy & Hickie (1986) note that brain size and RBS (cf. Jerison 1973) are often used to measure intelligence. More recently, Dunbar (1992) has calculated a neocortex ratio, which compares the neocortex volume to the volume of the rest of the brain for different species, building on the finding of Passingham (1982) that the significant difference between primates and other species is the vast expansion of neocortex. Although Dunbar's ratio is based on certain assumptions discussed by Byrne (1995) (sect. 4.2 below), its validity is evident as a result of its correlations with indices of behavioural complexity.

3.2 ecology

To reduce predation pressure on primates, the evolutionary response has been to increase the size of the social group (van Schaik 1983). Byrne (1995) proposes that this results in the increased fitness of individuals tending to group under threat of predation. It has been argued that a major concern of animals in groups, and one which may regard intellectual action, relates to the acquisition of food (Clutton-Brock & Harvey 1980; Gibson 1986).

Byrne (1995) observes that 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. He adds that range area or day range length have been used to measure such mapping, but that these underestimate environmental complexity. However, RBS and range size appear correlated (Clutton-Brock & 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. Milton (1988) notes that differences in gut size do not account for differences in brain size. However, Milton (1988) notes that based on the measure of CBS above (Clutton-Brock & 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) notes that primates requiring more complex foraging matrices have greater cerebral complexity. She further notes from research into cranial volumes by Eisenberg & Wilson (1978) that frugivores and nectarivores have larger cranial volumes than carnivores, insectivores or sanguivores, which indicates that an aspect of hyperdispersed, patchy and high-quality food resources stimulate increased brain size.

On the other hand, Milton (1988) contends that there is little evidence suggesting that social or breeding systems as such are related to primate or mammalian brain size, proposing that sociality in itself is not sufficient in explaining human brain size. She suggests that diet should not be excluded from study, as it is related to both RBS and sociality.

In research conducted on RBS in marine mammals, Worthy & Hickie (1986) show that species belonging to Sirenia, which forage on poor quality food, have relatively small brains, while odontocetes have large RBS, akin to primates. Milton (1988) thus notes that across different mammalian species, brain size (as well as sociality and breeding systems) correlates with diet.

3.2.1. Energetics

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. Without converting from a herbivorous diet, the brain and gut tissue could not both be enlarged, thus artefactually producing the above correlation (Aiello in Byrne 1995).

However 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.

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) with research suggesting that brain size may also scale to body size to the 3/4 power (0.73) rather than 2/3 power (Martin 1981, Hofman 1983a,b). 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 (as in Worthy & Hickie 1986).

The concern expressed by Martin (1981) (discussed in sect.4.2) that brain studies did not incorporate physiological considerations 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, noting that brain-body scaling may be determined by the following relationship: 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. What is interesting from Armstrong's study (1983) is that odontocetes are placed higher than primates in the relationship of metabolism to brain size. She concludes that "An analysis of the brain's energetics is necessary for a better understanding of the relation of brain to body" (1983:1304).

In a variation of Armstrong's (1983) conclusion, 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 to Armstrong's proposal that brain size is a function of metabolism, Hofman notes that it is 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.

Another energetic consideration deemed crucial to brain development (by determining gestation limits) appears to be the maternal metabolic supply to the foetus (Hofman 1983b). In addition, Hofman (1983b) found that two mammalian clusters exist in relation to neonatal indices: one for primates and certain cetaceans and the other for placental, non-primate mammals. The former group enjoy prolonged gestation, which Hofman (1983b) has suggested provides enhanced protection from environmental hazards, allowing optimal brain development to occur. In relation to the postnatal environment, Ridgway (1986a) noted that the longer gestation period in cetaceans might allow the neonate to be involved in complex activities requiring a more developed brain.

3.3 social organisation

It has been argued that the increase in RBS is a result of either ecological or social considerations. For an example of conflicting studies in this regard, Hemmer (1979) conducted brain studies with carnivores of different social structure and suggested that social species possessed larger brains than solitary species. Gittleman (1986) has opposed this view, noting from a much larger sample size that no such pattern exists. He suggests that increases in carnivore brain size stem from the complexity of foraging patterns. Although Milton (1988) has called for support of the relationship between brain size and ecological concerns, Dunbar (1992) has shown that neocortex ratio is not related to the environmental or ecological concerns of food acquisition, as evidenced by range area or day range. He has supported the view that increasing social complexity drives an increase in brain size (Figure 28), following research by Sawaguchi (1990) and Sawaguchi & Kudo (1990). Research has promoted the notion that social considerations, more significantly than ecological concerns, have selected for increased brain size in primates (Humphrey 1976, Byrne & Whiten 1988, Byrne 1995). For example, Dunbar (1992) found a correlation between group size and neocortex ratio only in haplorhines (monkeys and apes) but not in strepsirhines (galagos, lemurs and lorises).

Sawaguchi & Kudo (1990) investigated neocortical development in relation to primate social structure. They measured relative neocortex size allometrically (relating neocortical volume to brain weight for each superfamily), finding that "troop-making" congeneric groups had a larger amount of neocortex than solitary groups. Thus troop-size appears to be positively correlated with

relative neocortex size. In frugivorous anthropoids, polygynous groups possessed greater neocortex than monogynous groups. From this, Sawaguchi & Kudo (1990) concluded that the development of the neocortex relates to differences in primate social structure. This is evidenced by the fact that terrestrial primates have greater relative brain size than their arboreal counterparts and also by the positive correlation between group size and relative brain size in ceboid platyrrhines, but not in cercopithecoid catarrhines (Sawaguchi 1990).

Although many studies have proposed that the developing social structures in primates are linked to the evolution of neocortex and intellect, the Sawaguchi & Kudo (1990) study represents the first attempt to provide evidence that neocortical development relates to social structure. The divisions of social structure investigated included solitary, monogynous and polygynous species, these being classified in congeneric groups, where congeneric species shared social and ecological commonalities (Clutton-Brock & Harvey 1980). The relative size of the neocortex was found to be independent of the size of brain and/or body.

Neocortex is closely related to primate social structure, where the association is not the result of the relationship between neocortex and diet or activity timing (Sawaguchi & Kudo 1990). It was observed that polygynous monkey species had more fully developed neocortical areas than monogynous monkeys, which 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. 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 & 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 (Whiten & Byrne 1988, Byrne 1995) 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 & Kudo 1990).

Dunbar (1992) proposes that group size is a function of relative neocortex size, whereas ecological variables are not. He argues 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's 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). As any group's size is determined by ecological factors prevalent in the habitat, Dunbar (1992) proposes that species can only enter habitats requiring larger groups if they evolve greater amounts of neocortex, where neocortical volume is believed to be the best structural indicator of cognitive capacity. To reach these conclusions, Dunbar measured absolute neocortex size, the ratio of neocortex to hindbrain and the neocortex index (residual against body mass & rest of brain) against group size. This relationship between group size and neocortical size in primates has, more recently, been confirmed (Dunbar 1995). From the data provided by Aiello & Dunbar (1993), there does not appear to be a higher neocortex ratio for modern humans, who score lower than earlier hominids on almost all measures.

3.4 Cognition and Behaviour

Byrne (1995) suggests that a direct measure of intelligent behaviour is required to verify indirect measures such as group size, which only provides an index of the social problem, not an indication of the animal's intelligence or social complexity. Here he builds on the proposal of Humphrey (1976), that 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 & Byrne (1988) refer to this as "tactical deception", where tactical learning allows an individual to outsmart its conspecifics for resources. Tactical deception is thus the direct measure referred to above by Byrne (1995), who plotted an index of tactical deception against the neocortex ratio, finding that neocortex ratio predicts the frequency of deception (Fig. 29).

4. Assessment of studying RBS

4.1 Advantages

Studies of RBS reveal that the brain is the only organ better developed in simian primates than in other land mammals (Passingham 1982) and that other simian organs are not significantly different in their relative size, compared to other terrestrial mammals (Stahl 1965). From the investigations of relative brain proportions described above, it is evident that it is insufficient to merely regard brains as large or small. The expected and observed measures of RBS are important in that they display patterns for different groups, allowing for phylogenetic comparison. More recent measures of RBS, such as the neocortex ratio appear more accurate than relations of brain to

body size, although NR still relies on the assumption that intelligence is localised in the neocortex (sect 4.2).

Byrne (1995) notes that such measures of RBS are fruitful, as proof now exists that neocortex size, group size and deception are all correlated, indicating that for primates, intelligence is socially driven, while foraging concerns appear less significant to the growth of the cortex.

Another advantage of RBS measures is that parts of the brain may be calculated relative to each other and where the function of specific regions is known, the importance of the region in relation to the function served can be ascertained. (Sect. 5.1 provides a more comprehensive explanation, under correlative neuroanatomy.)

2. Limitations

Byrne (1995) notes that intelligence is often inferred from brain size, observing that scaling against body size is inappropriate as it promotes a "switchboard model" as opposed to an intelligent system of brain functioning. He proposes that ABS or relative neocortex size provide greater estimates of intellectual potential. The assumptions underlying the deduction of intelligence from brain size are discussed by Byrne (1995) and are highlighted below.

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 1995). Research by Barton et al (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.

Although ABS has been critiqued above, Byrne (1995) notes that brain size must be significant, as humans endure costs of enlarged brains. Being born with relatively large brains through an undersized birth canal has risks for the mother and/or infant and lengthened postnatal brain growth means an extended period of vulnerability for the infant. He proposes that increased intelligence is the major advantage which compensates for the costs associated with larger brains.

Allometric scaling, as used in relating brain size to body size, depends on a power relationship between the two variables for the species points to fall on a straight line (Byrne 1995). Although logarithmic plots provide straight lines for species groups, Byrne (1995), after Deacon (1990), suggests that the relationship may be a curvilinear function. In addition, Martin (1990) notes that allometry is based on the requirements 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 or deviation from the line of best fit were important- an animal placed above the line was brainier than expected and conversely, below the line, less brainy than expected. However, Byrne (1995) argues that there is no theoretical basis for the above reasoning, suggesting that this type of scaling makes strong assumptions about the functioning of neural tissue. He notes that two animals, one with a large (expected and observed) brain size and the other with a small (expected and observed) brain, are regarded as equally brainy. Although the brain does cope with sensorimotor inputs and outputs, like a

switchboard exchange, it also has additional processing capacity for computational intelligence and Byrne (1995) holds that this feature is marginalised in allometric studies.

The brain may be viewed as a super computer, with its vast interconnected network of neurons allowing its administration of executive functions (Byrne 1995). According to this proposal, Byrne (1995) suggests that larger neural brains make better computers, possessing more neurons and interconnections. He points out that the computer model contrasts with allometric studies, in holding absolute (not relative) size responsible for efficiency, thus making the models conflictual.

According to Byrne (1995), one must acknowledge that brain functioning includes both sensorimotor activity and computational intelligence and thus includes elements of both models. Jerison (1973) adopted this view in attempting to calculate the "extra neurons" available for computation by calculating the amount required for maintenance, somatic and vegetative purposes. Passingham (1982) calculated the other aspect of this integrated model, namely the sensory input and output (medulla volume) of the brain (above), although his work was limited by a lack of interspecific information on medulla volume or spinal cord area.

Dunbar's (1992) neocortex ratio (above) is based on the assumption that intelligence is localised in the cortex and Byrne (1995) is concerned that this underestimates the role of the hindbrain and subcortical structures in intellectual performance. In addition, Byrne (1995) notes that the relation of brain capacity to the resolution of problems requires a measurement of the complexity of the problems. Traditionally, issues confronting primates have been dichotomised into environmental or social categories, although Byrne

(1995) recognises that this distinction is artificial as animal societies are part of the environment and environmental problems are often solved socially.

Although Dunbar (1995) proposes that his neocortex ratio (neocortical volume to rest of the brain volume) provides the best fit to group size data, this represents a purely structural picture, as the other functional layers of cortex are not studied separately, nor are other cortical regions held in comparison with each other. Thus, for example, using this ratio the brain-stem and mid-brain are grouped together in relation to the neocortex, whereas they actually serve different functions. In addition, if we consider the brain as a functional system, it follows that more cortex will be dedicated to vital functions (Luria 1982). As brains are energetically expensive, the importance of different structures might be studied by considering the dimensions they occupy in the brain.

An issue of importance raised by Deacon (1990) and elaborated upon by Dunbar (1992) 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 larger cortical evolution. Although a behavioural requirement may cause a change in the brain, hypotheses are tested by regressing behaviour onto brain size, as behaviour of existing populations is restricted by current brain size (Dunbar 1992). It is evident that considerations of brain size cannot be avoided, if one wishes to comprehend the relationship between brain and behaviour. Once the cognitive processes behind the behaviour are unravelled and related to brain functioning, a stronger case may be made for comparative analysis.

Although numerous investigations have attempted to link brain size to intelligence among different species, certain problems are apparent. Firstly, according to Henneberg (1987) there exists no evidence to suggest that brain morphology is linked to behaviour. The other problem relates to an interspecific definition of intelligence. Byrne (1995) notes that in the absence of interspecific intellectual comparisons (no standardised intelligence test or uniform measures are available), brain enlargement is taken as reflecting intelligence, something he finds highly questionable. For example, ICC as a measure of RBS may be of value in assisting to distinguish between varying groups, but it is not adequate for the assessment of individual species (Martin 1990).

Due to the energetic costs of possessing neurons, a brain will not possess extra neurons if the costs exceed the benefits (Henneberg, pers. comm). From this, one may view extra neurons (Jerison 1973) or processing units as being adaptive. As the neuronal level of analysis is important, Henneberg has suggested that research should focus on biochemical processes and neuronal motor units, which can have several functions. One might note that this technique would be in direct contrast to one such as cranial capacity (Martin 1990), which, although not requiring brain weight to infer brain size from skull size, does not reveal anything of the finer structure and related functions of cortical regions. It is thus possible to remain sceptical about Dunbar's (1995) confirmation of his and Aiello's (1993) proposal of using cranial volume to predict the neocortex ratio. It *would* be a useful technique if proven to be valid and consistent. The issue is that neocortex is very difficult to measure, owing to its variation between individuals, populations and species. Aside from the variability of neocortex, there is the problem of incorrect definition of specific brain regions. For example, recent research

(Dunbar 1992) includes the mesencephalon and diencephalon as part of the hindbrain, whereas these areas actually lie in the midbrain and forebrain respectively (Kolb & Whishaw 1990).

An additional shortcoming of the RBS approach, as noted by Passingham (1982), is that interspecific comparisons have been based on crude measures of the size of particular areas, without recourse to finer measures of specific brain structures.

Another issue is that the function of the particular areas under study must be recognised. 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. The relationship between structure and function or anatomy and physiology is important. Kesarev (1971) pointed to a schism in research between the anatomy and physiology of the brain which appears to have remained in place. The relationship between structure and function is conceived of as "a complete if not ideal unity" (Kesarev 1971:52). If one analyses the brain from this perspective (cf Luria 1973, 1982), certain pitfalls of other measures of encephalisation become apparent. For example, the size of the brain and its components in itself become irrelevant, if one does not know the functions performed by the different cortical regions. However, once one begins to question how certain structures relate to function, the opportunities for adequate analysis fall into place.

5. Dolphin neuroanatomy

5.1 Basic neural organisation in relation to terrestrial mammals

Kesarev (1971) notes the increase in attention to evolutionary analysis, from where evolutionary neuroanatomy has arisen. As is noted by Kesarev, Haeckel's evolutionary triad is essential for any attempts at phylogenetic reconstruction, including those of the development of the brain. According to this triadic model, the findings of comparative anatomy, embryology, ontogeny and palaeontology must be brought together. Kesarev notes that the final element is the triad is not evident with respect to the brain. As a result of this, it is essential to compare the human cortex to the cortices of other related and unrelated species to understand the evolution of brain (Kesarev 1971). Histological or cytoarchitectonic methods have mainly been used to investigate structural complexities in comparative anatomical analyses.

The main cerebral areas of the human brain may be defined as follows: neocortex (new cortex), archicortex (old cortex), intermediate (transitional to the old periarchicortex), palaeocortex (primitive cortex) and peripalaeocortex (intermediate, traditional to the primitive cortex), (Kesarev 1971). Kesarev notes that directly contrasting features are traced between the oldest and youngest differentiated formations. He submits that paleocortex regresses during evolution, while the neocortex is the earliest to appear and the last to conclude its development in humans. It is the neocortex, the most phylogenetically recent cortex, that is associated with complex cerebral activity, or what Kesarev describes as higher mental functions, such as integrative and analytical functions, which are believed to be present only in humans.

There is a suggestion that the large development of the dolphin neocortex occurred as a result of the greater regulation required by their visceral and somatic functioning (Kesarev 1971). Ridgway (1986a) notes that while all cetaceans share common visceral and somatic functioning, not all share a high EQ, observing that higher dolphin values cannot merely be ascribed to somatic and visceral functions. He calls for a search for "other reasons for the large size of the dolphin brain" (1986:62).

Kesarev (1971) observes that quantitative considerations do not suffice for assessments of the level of brain complexity. He cites the dolphin as an example. As it possesses the greatest relative area of neocortex (humans included), one might 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). But as he subsequently mentions, a measurement based on a single factor cannot hope to realistically reflect the developmental state of the brain in mammalian evolution. To Kesarev, a more accurate measure was the index of maximal deviation (a ratio of the area of neocortex to palaeocortex). However, he submitted that limitations of this method existed, as volumes of certain cortical areas could not be measured.

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. This is referred to as correlative neuroanatomy by Kesarev (1971), owing to the focus on structure in relation to function.

From an evolutionary perspective, the development and formation of the mammalian neocortex occurred in an terrestrial environment, which varies

significantly from an aquatic environment (Kesarev 1971). The cetaceans are the only mammalian order to display a complete secondary return to water and this, in addition to their genetic relatedness to all terrestrial mammals, makes them highly significant in evolutionary terms. Deacon (1990) refers to cetaceans as being an exceptional case in brain evolution. Their evolution 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).

According to data from Kesarev (1971) and Ridgway (1986a) it is evident that the cetacean brain develops more rapidly than the human brain, and the growth is complete at an earlier stage of ontogenetic development. Thus, as Ridgway (1986a) notes, the brain at birth in cetaceans is half its adult weight, while in humans it is a quarter of the adult weight. The human only reaches the cetacean birth level at an age of six months and by age 18 months, while *Tursiops* has reached 80-85% of its adult brain size, the human has only 65-70% of its full brain size. Ridgway (1986a) and Kesarev (1971) both note that substantial human cortical development occurs postnatally, as opposed to lower primates, where cortical formation is almost complete at birth.

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 (Kesarev 1971, Glezer, Jacobs, Morgane 1988, Morgane, Jacobs & Galaburda 1986a, 1986b). The low amount of paleocortex in dolphins may be more than mere telencephalar organisation, as in dolphins the olfactory analyser, located in the paleocortex, may be totally absent. Kesarev notes that 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).

Cytoarchitectonically, dolphins display primitive neocortical organisation in comparison to primates. This is evidenced by the lack of differentiation between different cortical areas and zones, monotonous structure and predominantly simple neurons (Kesarev 1971). Additional evidence showing the low degree of cortical differentiation stems from the location of associative cortex. Whereas cortex with a largely organised associative function is located in recently evolved layers of the human cortex (layers II and IV), in dolphins these are situated in the older, functionally primitive layer (I) (Kesarev 1971). The same author notes that the simpler brain structure may result from the fact that an aquatic environment is considered less complex than an terrestrial environment in terms of homeostasis. In addition, he observes that cetaceans have no competitors at a similar CNS developmental level in the water.

Kesarev has omitted mentioning the physiological pressures of depth and diving on the dolphin, and thus, while being less homeostatically complex, they may face a barrage of pressures not encountered by terrestrial mammals. For example, Hofman (1983a) has noted that 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. Here, one cannot discard the aqueous environment of marine mammals and the fact that anaerobic respiration has been observed in cetaceans. In terms of cortical respiration, which is almost exclusively neuronal, and following the finding that the number of cortical neurons is a linear function of cortical surface area (Hofman 1982b), it may be safe to conclude that cetaceans,

with the greatest surface area, possess the largest number of neurons and thus engage in the greatest amount of cerebral oxygen intake.

Rather than considering the dolphin brain as adaptive or conservative, Deacon (1990) proposes that it should be held as a highly "derived" brain, one geared towards adaptation in its specialised environmental niche. This notion requires further investigation. Finlay & Darlington (1995) call for studies of species living in specialised niches, or of specific structures close to the sensory periphery which would allow for the most powerful test of developmental limits on the evolution of the brain. This type of analysis is readily applicable to sirenians and cetaceans and fits in with Jerison's (1986) study of the perceptual world of dolphins, which found them significantly different to the standard mammalian model.

Finlay & Darlington (1995) cite two hypotheses for consideration, namely one of developmental constraint and the other of adaptation. The first hypothesis holds that one can predict the size of any neural structure in any species by using a rule. The latter hypothesis opposes this view, holding that one cannot predict brain size from a specific formula. Using allometric information collected on volumes of different brain divisions, Finlay & Darlington (1995) set out to form a predictable measure of brain divisions, concluding that neocortex is highly predictable for almost all brain subdivisions (the first hypothesis). An additional finding of evolutionary interest is that marginal brain size changes result in a relatively large neocortical size change, implying that a marginal, initial divergence in RBS can result in markedly different neocortex volumes .

The cortical formations of the telencephalon hold the greatest evolutionary progression in the mammalian CNS. Where sensory and functional systems

have changed anatomically, they have transformed cortical formations with specialised functions. It has been proposed that a knowledge of the structural principles of organisation of sensory and associative systems, coupled to anatomical changes in functions related to ecological factors, would result in a theory of brain activity (Kesarev 1971). Kesarev has, however, omitted to mention the structural-functional changes in relation to *social* considerations (sect 3.3).

5.2 Relative Brain Size in Dolphins

Whilst a fair amount of encephalisation research has been undertaken with primates (Martin 1990, Clutton-Brock & Harvey 1980, Jerison 1973, 1979, Gould 1975), less work has been conducted with carnivores & ungulates (Gittleman 1986, Martin 1981). A relative shortage of research exists into the encephalisation of non-terrestrial mammals, specifically with respect to *cetaceans*. Aside from the work on cetaceans conducted by Elias & Schwartz (1971), Eisenberg (1986), Jerison (1986) and the contributions from Ridgway & colleagues (Ridgway *et al* 1966, Ridgway & Brownson 1984, 1982, 1979, Ridgway 1986a,b) and Worthy & Hickie (1986), not many other documented cases exist. This scarcity of research, combined with a lack of updated records, make for poor comparative analysis.

Dolphin scores are often excluded from or avoided in reported data sets which are examined for other, terrestrial, mammalian species. This may be as a result of their residence in a marine as opposed to terrestrial environment. However, dolphins are popularly regarded as extremely intelligent. Popular notions aside, several scientific findings (discussed below) indicate that dolphins are significant in comparative brain and intellectual studies.

Cetaceans, along with certain megaherbivores such as the elephant, posses the largest absolute brain size (Passingham 1982). The Delphinidae family incorporates species, such as the bottlenose dolphin, which hold the greatest brain to body size ratio amongst cetaceans (Ridgway 1990). According to Jerison (1982b) certain cetaceans, in common with humans, possess the highest relative brain size to body weight ratio.

Many other examples of cetacean superiority in different cortical measures are evident. These include, in opposition to Count (1947), the fact that cetaceans have the most convoluted brains of all species (Elias & Schwartz 1969), with Ridgway & Brownson (1984) noting that the average bottlenose surface area was 3745cm^2 as opposed to the human average at 2275cm^2 (Elias & Schwartz 1969). Certain cetaceans also have longer gyri as a function of brain size than humans (Elias & Schwartz 1971, Jerison 1982a, Ridgway 1986b). In addition, Martin (1990, 1982, 1981) proposes that in terms of cranial capacity, cetaceans, not simian primates, are the closest rivals to humans- the only primates with an exceptional brain size. If one were to include dolphins in certain comparative analyses, their significance would become apparent. For example, compared to the estimates in Jerison's (1982a) measure of processing capacity (above), the dolphin with a 3000cm^2 cortex would obtain the highest result, at 6 million modules.

Another important finding stems from the ratio of brain weight to spinal cord length developed by Ridgway et al (1966), who follow a proposal by Warden (1951) that such a ratio might allow for a standard of comparative intelligence across mammals. Whereas fish has a brain weight less than the cord, horses score approximately 2.5:1, cats 4 or 5:1, apes at 8:1 and the human at 50:1; the average brain-spine ratio for bottlenose dolphins is 40:1. What appears significant is the ranking of the odontocetes between humans and the apes (Ridgway et al 1966). Since this finding, subsequent studies have revealed

that this is a prominent pattern for the results of neural investigations involving cetacean comparisons.

Although the dolphins possess the most convoluted brain, they have only half the cortical thickness of humans (Kesarev 1971, Ridgway & Brownson 1982). The data cited by Ridgway (1986a) must be treated with caution as the specimen from which the estimate was drawn was immature. There is also significant interspecific variation within the cortical thickness of different cetaceans. Although 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 *estimation* from Ridgway (1986a). This estimation leads him to verify Haug's (1970) finding that *Tursiops* scores below humans, but above terrestrial mammals with high encephalisation. However, there is no explanation for how he arrives at this estimate.

It is evident from the above argument that cetaceans and specifically dolphins can neither be excluded from comparative studies, nor can they be neglected from such investigations. It is quite apparent from the consistently high scores of delphinids across several cortical measures that these species merit more attention than currently afforded. Bearing in mind the relative shortage of cetacean information throughout the comparative literature, it is possible to critically assess the available work on dolphin EQ and other measures of their relative brain size.

Stephan, Frahm & Baron (1981) have provided data on the volumes of different brain structures in certain mammalian species (primates and insectivores), noting that the size of the brain is strongly related to the size of the individual or species and its functional requirements. They note that the more complex the behavioural repertoire, the greater and more differentiated

the cerebral structures must be, proposing that size and progressive differentiation co-vary. Whilst differentiation can vary widely, size can only either increase or decrease, this leading Stephan, Frahm & Baron (1981) to submit that, for an interspecific comparison, considerations of size may lead to the determination of the functional significance of cerebral areas in different species. They chose the allometric method of relating brain size to body weight for interspecific comparison.

Of primary concern from the review is that many subsequent and contemporary research documents have been based on the above volumetric measures where, in the majority of cases, only 1 or 2 brains have been utilised per species. In addition, although Stephan *et al* (1981) include insectivores because of the phylogenetic origin of primates in insectivore-like ancestors in their analysis, no mention is made of data for other mammalian orders. Thus, for example, in terms of cetaceans, Ridgway (1986a) had to rely on previous measures from Kojima (1951) and Pilleri & Gihr (1971) in addition to taking his own measures (Ridgway & Brownson 1984). Once again, however, the number of specimens only exceeded three in 3 out of 10 species, *Tursiops (19), Physeter (16) and Delphinus (10).*

Ridgway (1986) notes that the data provided on cetacean EQ from Jerison (1973), Wood & Evans (1980) and (Ridgway & Brownson 1984) all concur in arriving at the conclusion that the EQ of small odontocetes rank higher than other mammals, including all primates, with the exception of humans, who outrank all other species. For dolphin EQ scores, refer to Ridgway (1986a) (Table 13) and Worthy & Hickie (1986) (Table 14).

Several important factors have to be considered when interpreting EQ values. Determining the exact age of cetacean specimens is impossible and

thus, without establishing a certain degree of maturation, it is very difficult to determine an appropriate EQ. A related issue is that immature animals have larger relative brain sizes than mature individuals (Count 1947) and it has been proven that EQ decreases as body length increases (Ridgway & Brownson 1984, Ridgway 1986a).

The logic behind EQ is that by using an allometric equation of brain-body weight in mammals, brain size is scaled to body surface area (Ridgway 1986a). Although, as Ridgway (1972) proposes, odontocetes have less body surface area than land mammals, they still rank higher when brain size is studied in terms of surface area (Ridgway 1986a) (Figure 30). Hofman (1982a) suggests a slope of 0.73 for the above EQ equation, derived from allometric studies of a wide range of mammals from differing orders. However, Worthy & Hickie (1986) have proposed a slope of 0.358 for cetaceans, with mysticetes at 0.360 and odontocetes at 0.546, these slopes being far removed form the mammalian slope discussed above (Figure 31 and Table 15).

Ridgway (1986a) notes that Hofman's (1982a) study placed the odontocetes between higher primates and humans (as did the Ridgway 1966 study), leading him to consider them unique in terms of encephalisation. Although regression analysis of brain weight against body weight for cetaceans is suggested by Ridgway (1986a), the reader is advised to recognise the shortcomings of this (sect. 4.2 above).

There is a large variation in brain size among delphinids, as Ridgway & Brownson (1984) have submitted. Their data ranged from a Delphinus neonate with a brain size of 442 grams to a mature Orcinus with brain size 6215 grams, and they note the weight range as being 14 times different

between biggest and smallest and in weight terms a difference of 344 times. However, neonates cannot be compared to adults if one is interested in understanding relative brain size and/or cortical development. Worthy & 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 (Table 14). They recognise that brain size in cetaceans is related more to phylogeny than to dive time, proposing that echolocation requirements may be responsible for large EQs.

In drawing the often diverse strands of the debate together, one must attempt to bind certain concepts to each other. The first of these is that, although there have been numerous investigations of the brain, most have been in absolute terms and as such, are absolute measures. From the above argument, it is evident that absolutes do not render as much value as do relative measures. A move has to be made in the direction of relative brain size. Different RBS measures have been discussed, including the different forms of the EQ, comparative brain size, cranial capacity, neocortex ratio and relative neocortex size. While these measures are an improvement on ABS, they will be more meaningful if related to functional areas. Unless structure and function are studied as a unity, further investigations will fall short of their potential. Evolutionary neuroanatomy provides the background for such contextualised brain investigations and deserves further research expansion. Within this method a shortfall is that the only tools of investigation have been provided by histology or cytoarchitectural analysis. As far as a comparative method is concerned, other highly adapted animals such as dolphins require further investigation. It is not sufficient to merely focus on humans and their nearest primate relatives, this excludes other orders of mammals with highly derived brain and social functioning. From the above review, it is evident that brain size is correlated with intelligence and cognition which in turn is correlated with social complexity. The development of the neocortex appears

related to social, more than ecological, pressure. While this has been confirmed for primates, no such research has been conducted with cetaceans. Studies of RBS in dolphins and their neural organisation in relation to other mammals have been undertaken and from the position held by dolphins in comparative studies it appears that they require urgent inclusion in comparative literature regarding relative brain size, intelligence and social complexity.
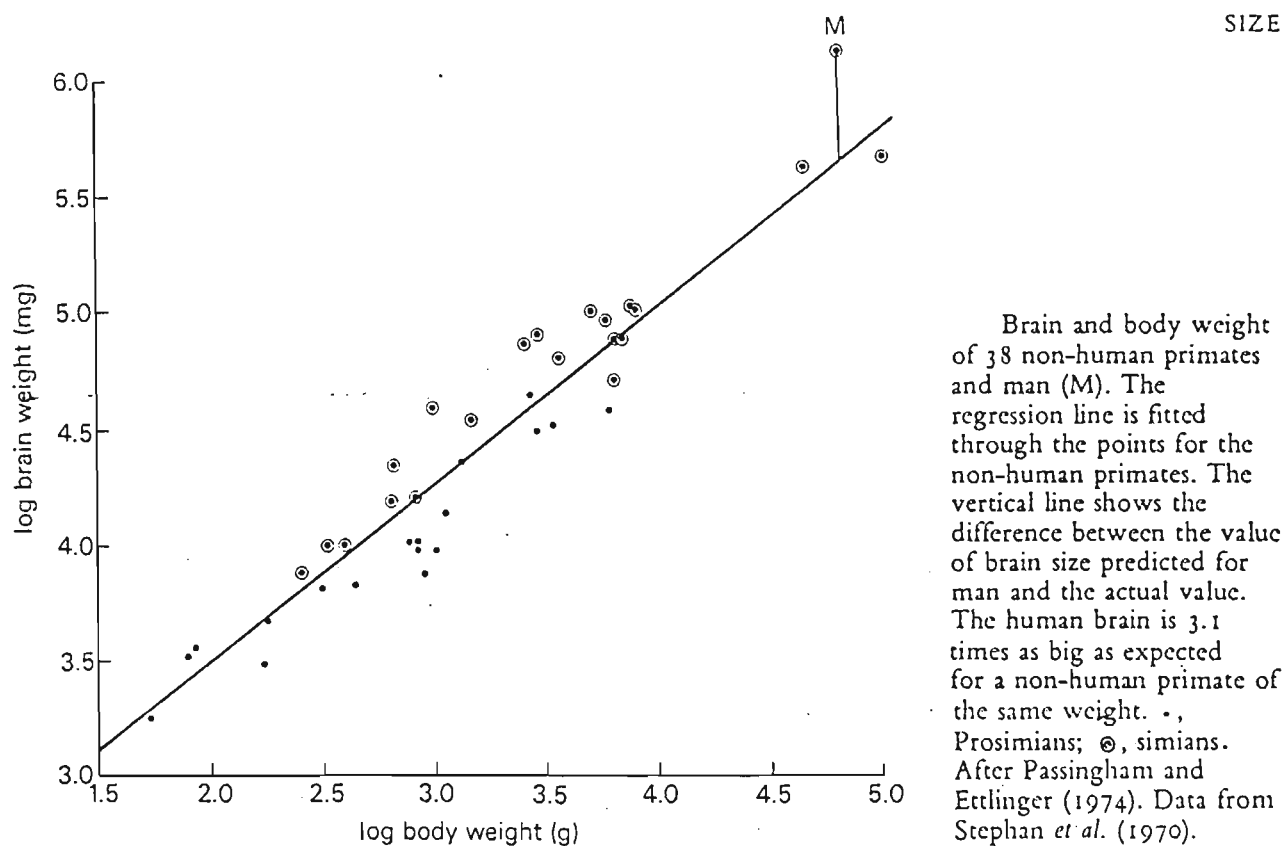
Brain and body weight of 38 non-human primates and man (M). The regression line is fitted through the points for the non-human primates. The vertical line shows the difference between the value of brain size predicted for man and the actual value. The human brain is 3.1 times as big as expected for a non-human primate of the same weight. •, Prosimians; ⊚, simians. After Passingham and Ettlinger (1974). Data from Stephan et al. (1970).

Figure 16. Log brain weight to log body weight for primates (Passingham 1982)

Encephalization quotient (EQ) in a variety of mammals. The mean is given by the dot and the range by the vertical lines. The dot above the carnivore range gives the value for a single carnivore. The upper range for the simian primates gives the values for two cebus monkeys. I, insectivores; R, rodents; U, ungulates; C, carnivores; P, prosimians; S, simians; M, man. After Passingham (1981a). Data from Jerison (1973).
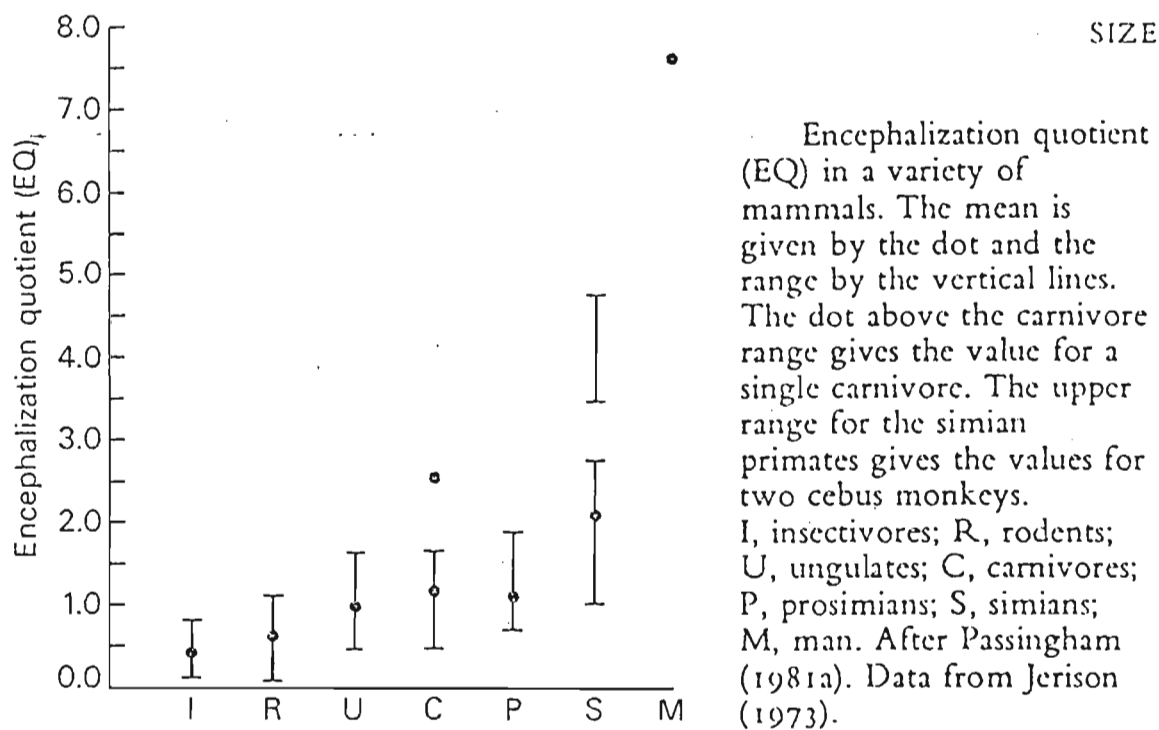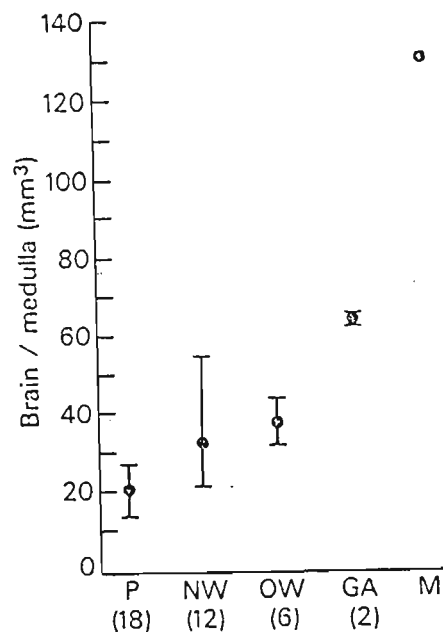
Figure 17. Encephalization Quotient for various mammals (Passingham 1982)

Volume of the brain (mm³) relative to the volume of the medulla (mm³) in primates. The mean is shown by a dot and the range by the vertical line. P, prosimians; NW, New World monkeys; OW, Old World monkeys; GA, great apes; M, man. The figures along the bottom give the number of species represented. Data from Stephan *et al.* (1970).

Figure 18. Brain volume relative to medulla volume in primates (Passingham 1982)
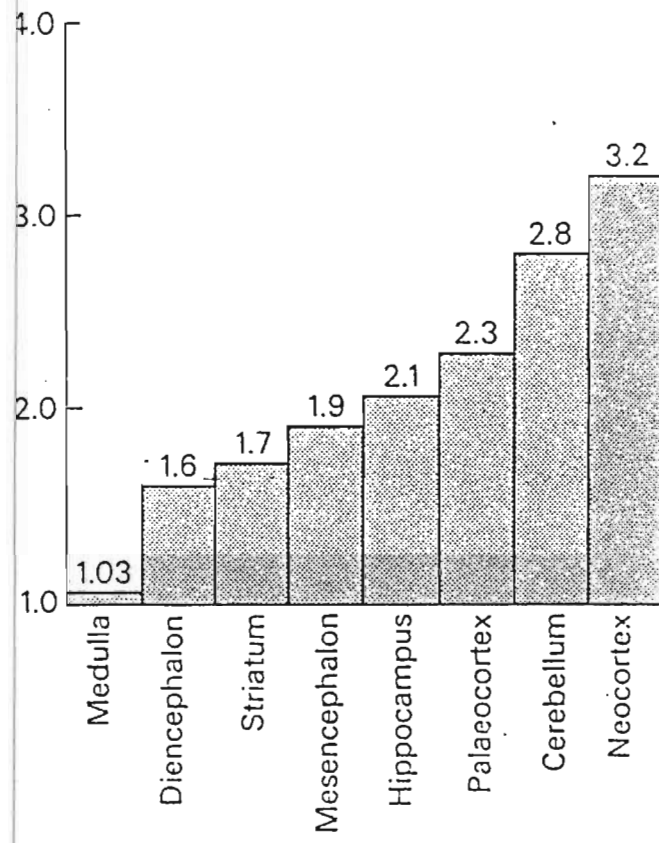
Indices showing the difference in size of each area of man's brain compared with the values predicted for non-human primates of the same body weight. The index is the obtained value/the predicted value. After Passingham (1975b). Data from Stephan et al. (1970).

Figure 19. Values of human brain areas compared to other primates (Passingham 1982)
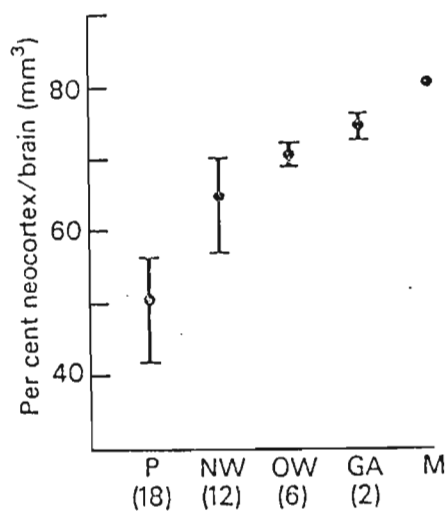
Volume of the neocortex (mm³) as a percentage of the volume of the brain (mm³) in primates. The mean is shown by the dot and the range by the vertical line. P, prosimians; NW, New World monkeys; OW, Old World monkeys; GA, great apes; M, man. The figures along the bottom give the number of species represented. After Passingham (1975a). Data from Stephan *et al.* (1970).

Figure 20. Neocortex volume as a percentage of brain volume in primates (Passingham 1982)
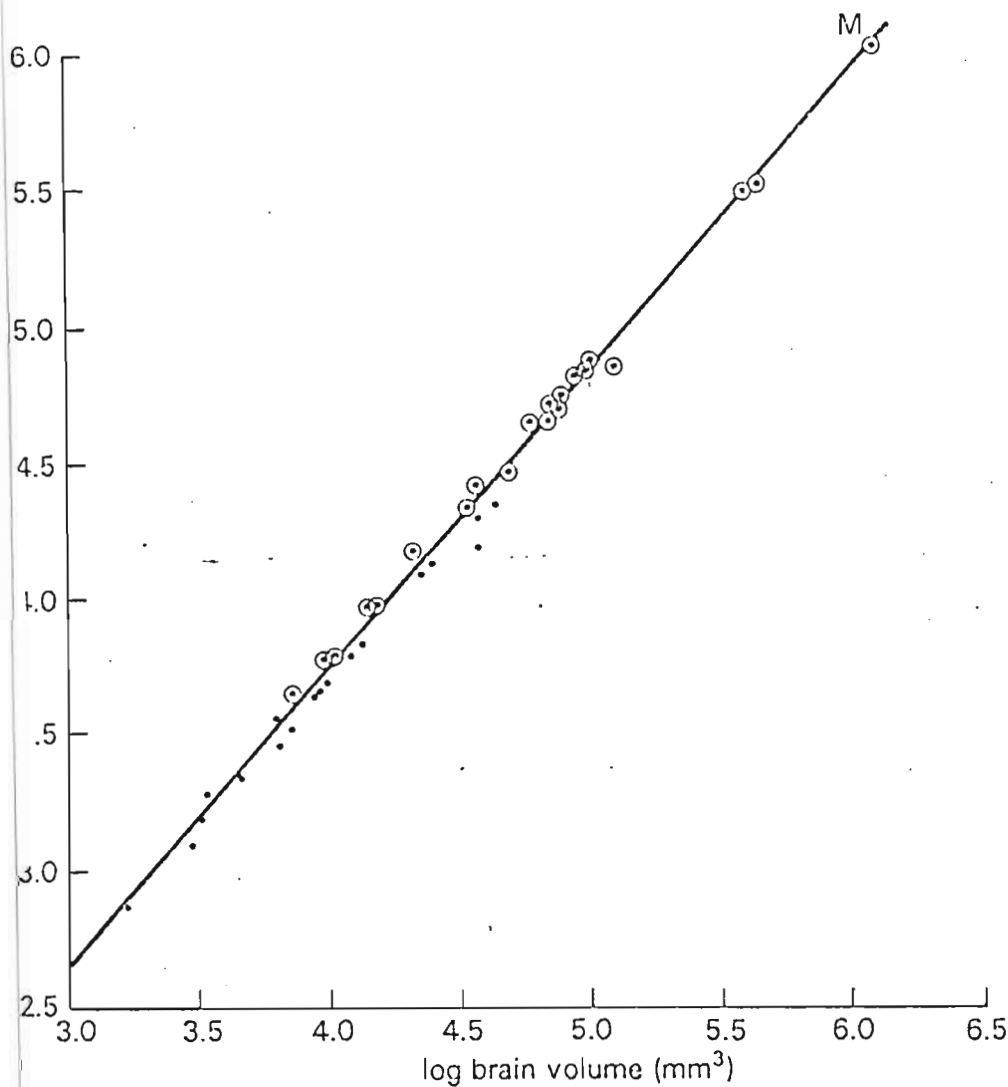
Volume of neocortex
(mm³) as a function of the
volume of the brain (mm³)
in primates. •, Prosimians;
⊙, simians; M, man. After
Passingham (1975b).

Figure 21. Neocortex volume as a function of brain volume in primates (Passingham 1982)

Volume of the neocortex (mm³) as a function of the volume of the brain (mm³) in mammals. ⊙, Marsupial; ▲, rodents; ▣, ungulate; +, carnivores; ×, prosimians; ◎, simians not including man. After Passingham (1981a). Data from Harman (1947).
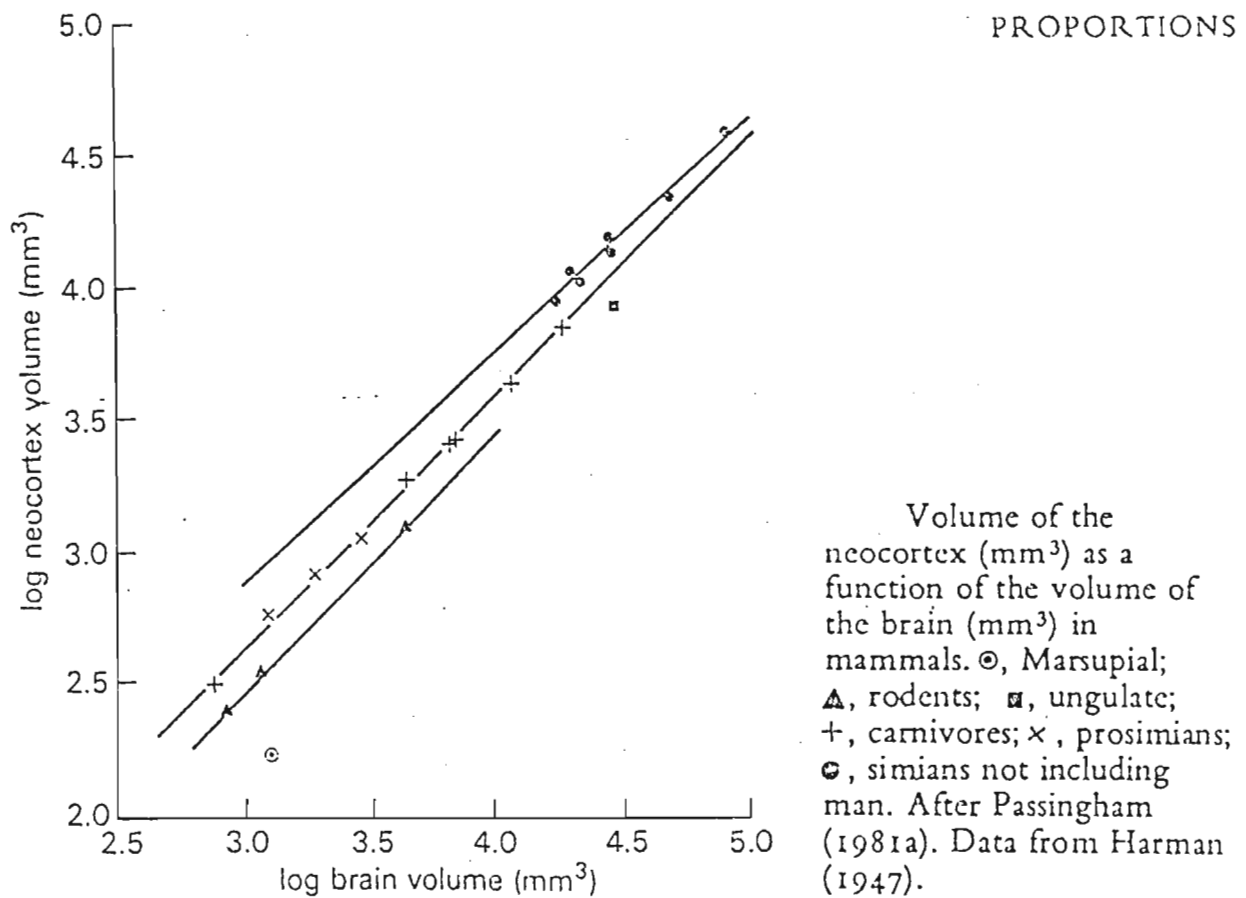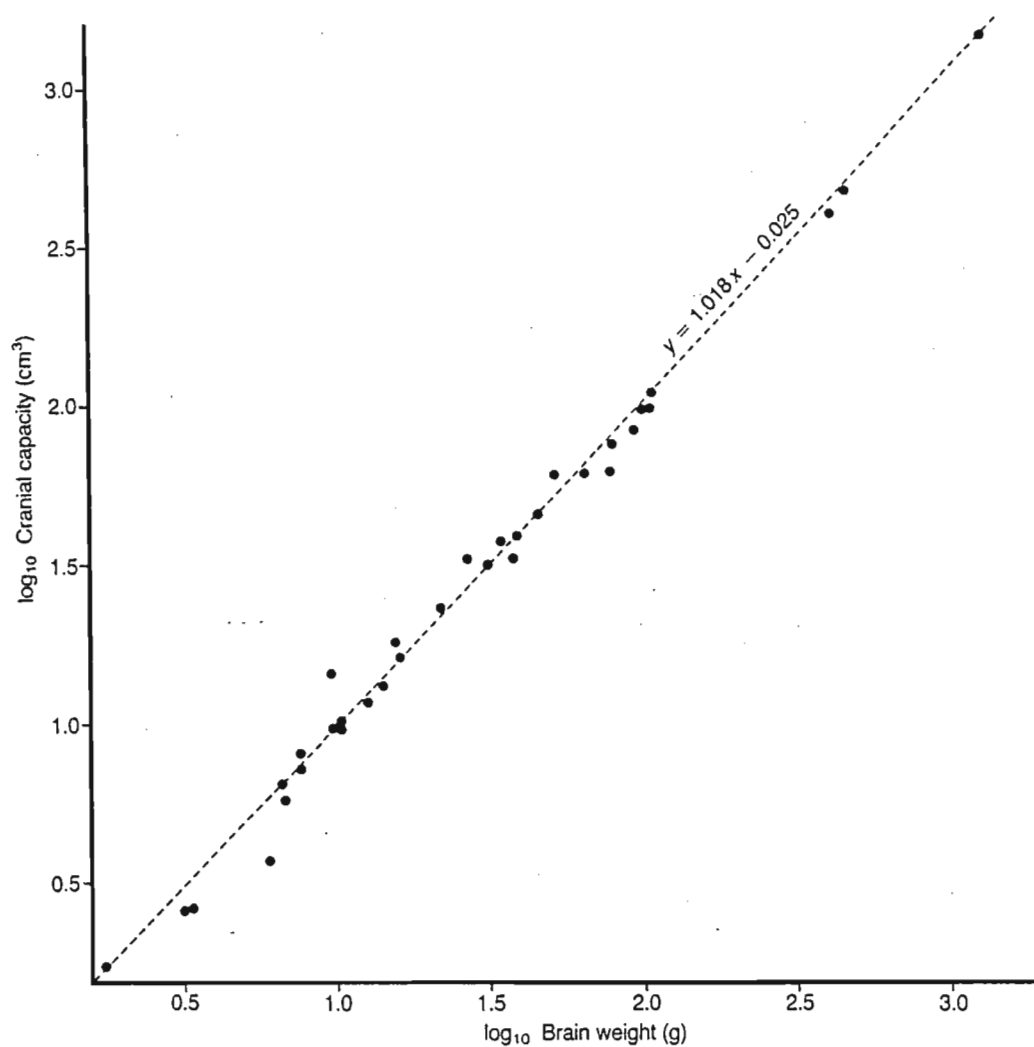
Figure 22. Neocortex volume as a function of brain volume in mammals (Passingham 1982)

Logarithmic plot of cranial capacity against brain weight for primates ($N = 33$ species). The best-fit line is the major axis, the equation for which is indicated. (Brain weights from Stephan, Bauchot and Andy, 1970; cranial capacities from Table 8.1.)

Figure 23. Logarithmic plot of cranial capacity to brain weight (Martin 1990)
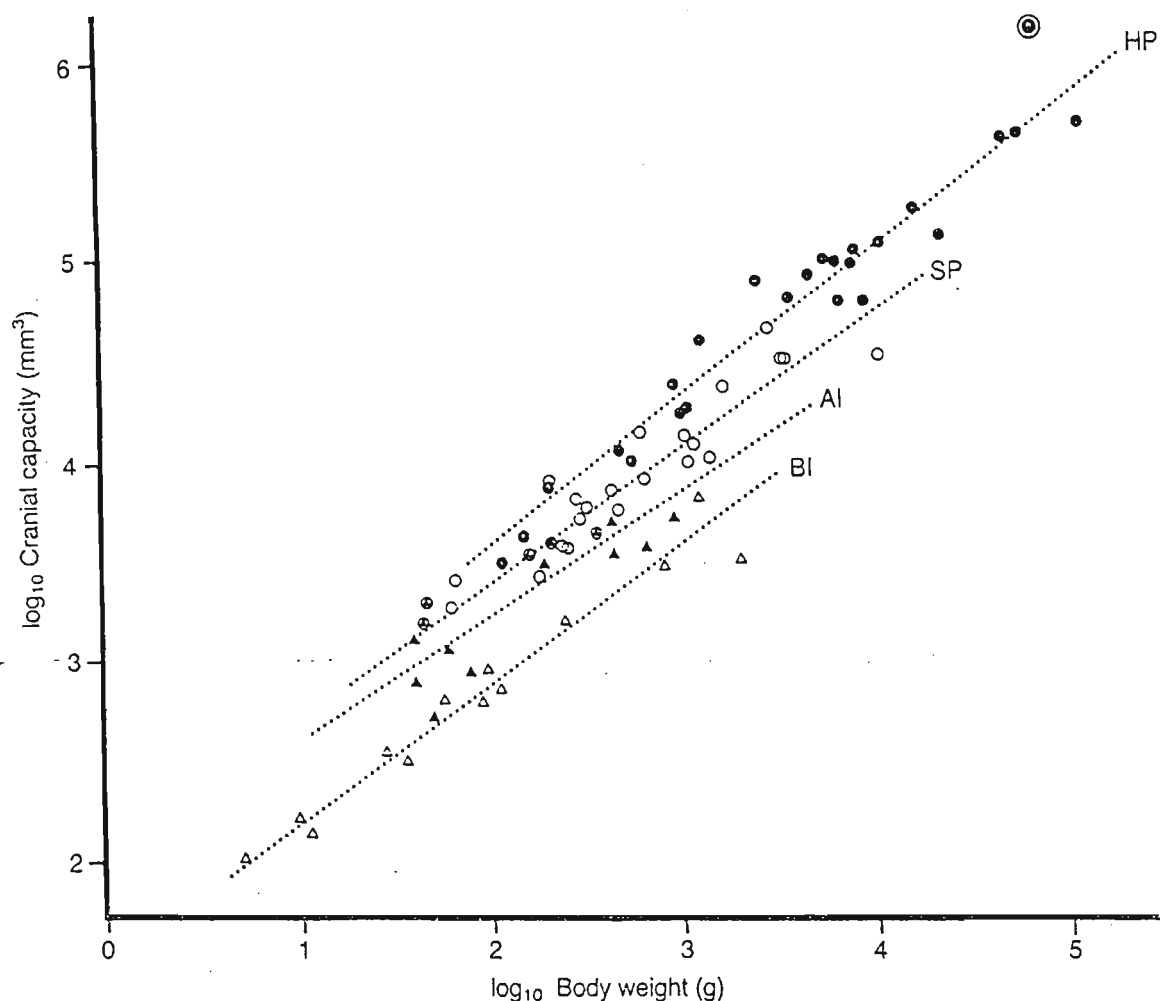
Logarithmic plot of cranial capacity against body weight for primates, tree-shrews and insectivores (data from Table 8.1). The best-fit lines are the major axes (equations given in text). Key: BI = 'basal' insectivores ($\triangle$; N = 13); AI = 'advanced' insectivores combined with tree-shrews ($\blacktriangle$ and $\textcircled{\blacktriangle}$, respectively; total N = 15); SP = strepsirhine primates – lemurs + lorises ($\bigcirc$; N = 22); HP = non-human haplorhine primates – tarsiers + simians ($\oplus$, N = 25; point for *Homo sapiens* is outlined). (Reprinted from Martin, 1983 with the kind permission of the American Museum of Natural History, New York.)

Figure 24. Logarithmic plot of cranial capacity against body weight (Martin 1990)
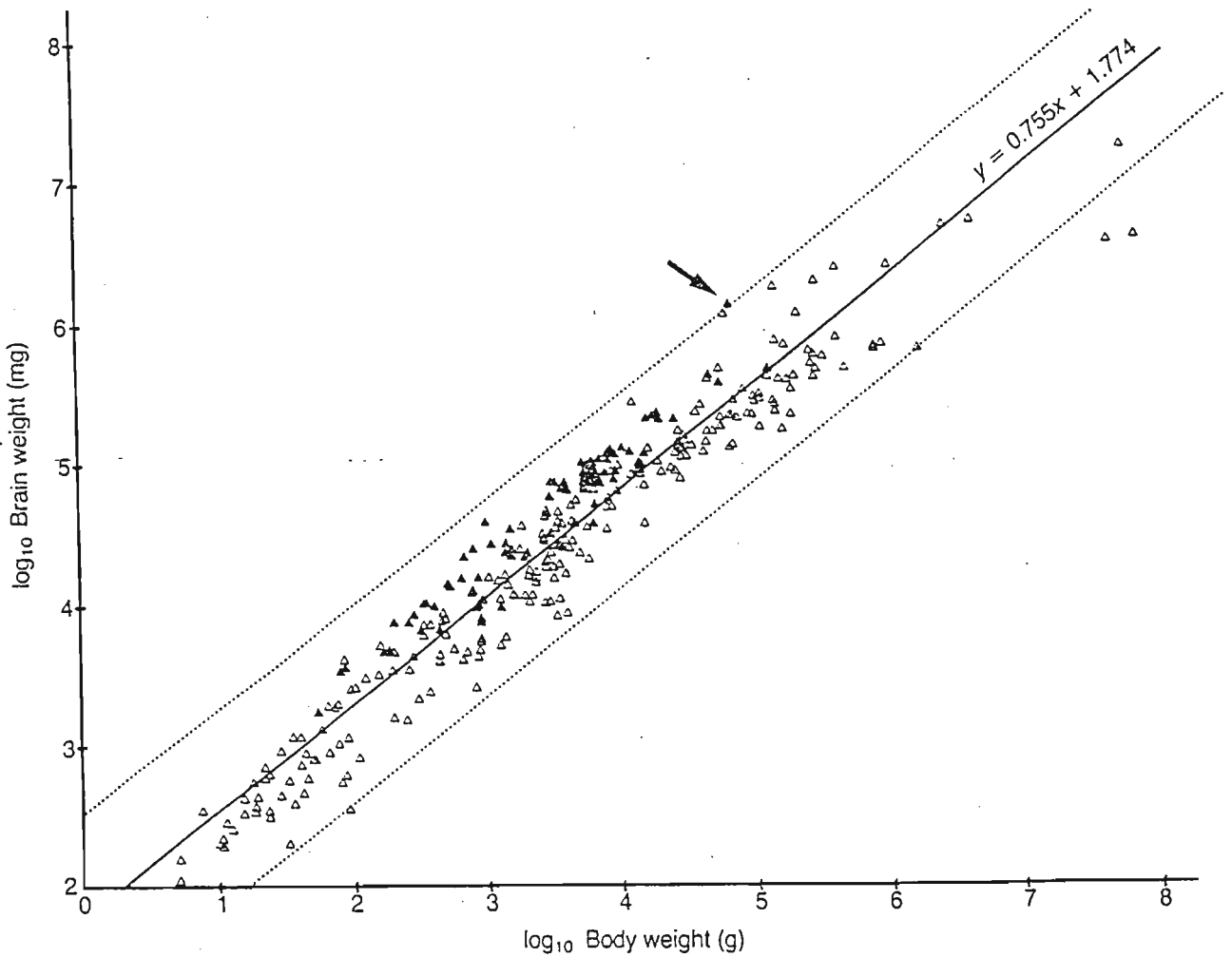
Logarithmic plot of brain weight against body weight for 309 extant placental mammal species: $\triangle$, non-primates; $\blacktriangle$, primates; arrowed point, *Homo sapiens*. The best-fit line (solid line) is the major axis for the entire sample. The dotted lines indicate fivefold variation on either side of the major axis. (Reprinted by permission from Martin, 1981c; *Nature* vol. 293, pp. 220–3. Copyright (C) Macmillan Journals Limited.)

Figure 25. Logarithmic plot of brain weight to body weight for placental mammalian species (Martin 1990)
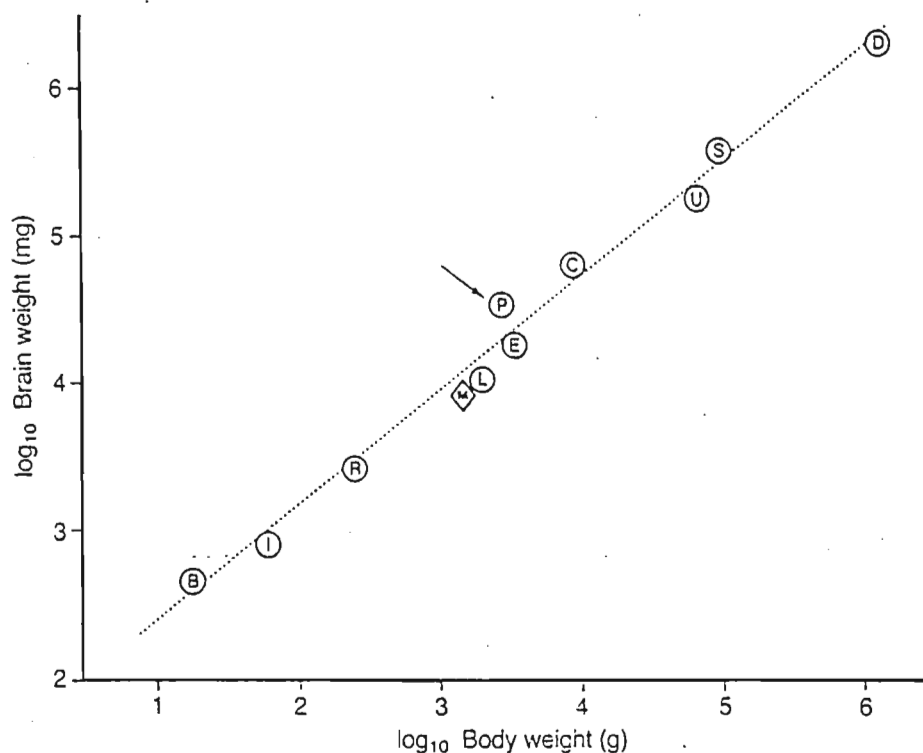
Plot of average logarithmic values for brain and body weights for 10 orders of placental mammals (circles) and for marsupials (diamond). The best-fit line (major axis) has been fitted to data for placental mammals only, and it is noteworthy that marsupials nevertheless lie as close to the line as rabbits and hares, contrary to the general belief that marsupials are 'primitive' mammals. Key: B. bats (Chiroptera); C, carnivores (Carnivora); D, dolphins and whales (Cetacea); E*, edentates (Edentata); I*, insectivores + tree-shrews (Insectivora + Scandentia); L, rabbits + hares (Lagomorpha); M*, marsupials: P, primates; R, rodents (Rodentia); S, seals and sea-lions (Pinnipedia); U*, hoofed mammals (Artiodactyla + Perissodactyla). (* Treated as single orders for purposes of analysis.) Note that the point for primates (arrowed) is the most prominent outlier above the line. (Reprinted from Martin, 1983 with the kind permission of the American Museum of Natural History, New York.)

Figure 26. Logarithmic plot of brain weight to body weight for placental mammal orders (Martin 1990)
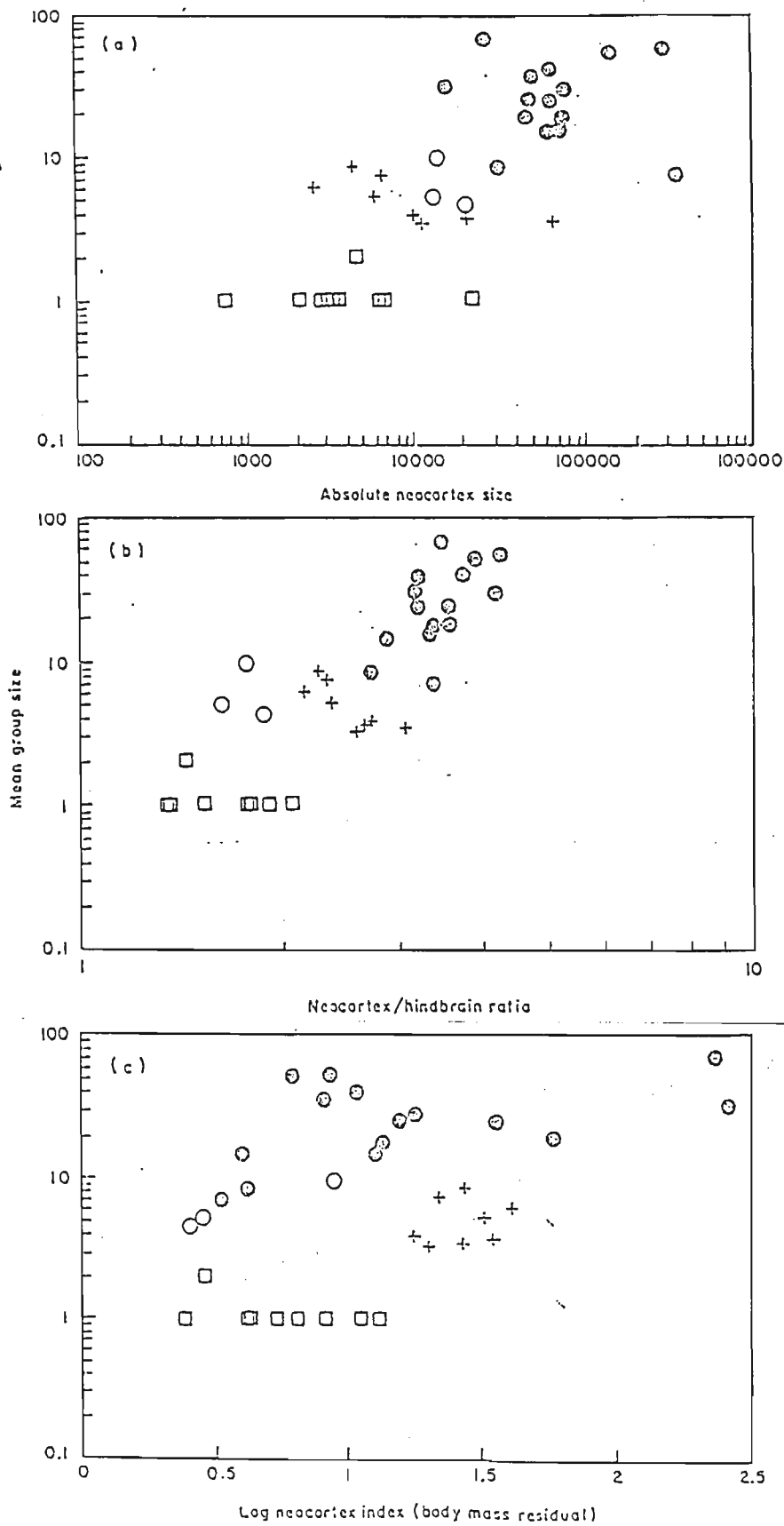
Figure 27. Measures of neocortex (Dunbar 1992)

NEOCORTEX SIZE AND GROUP SIZE
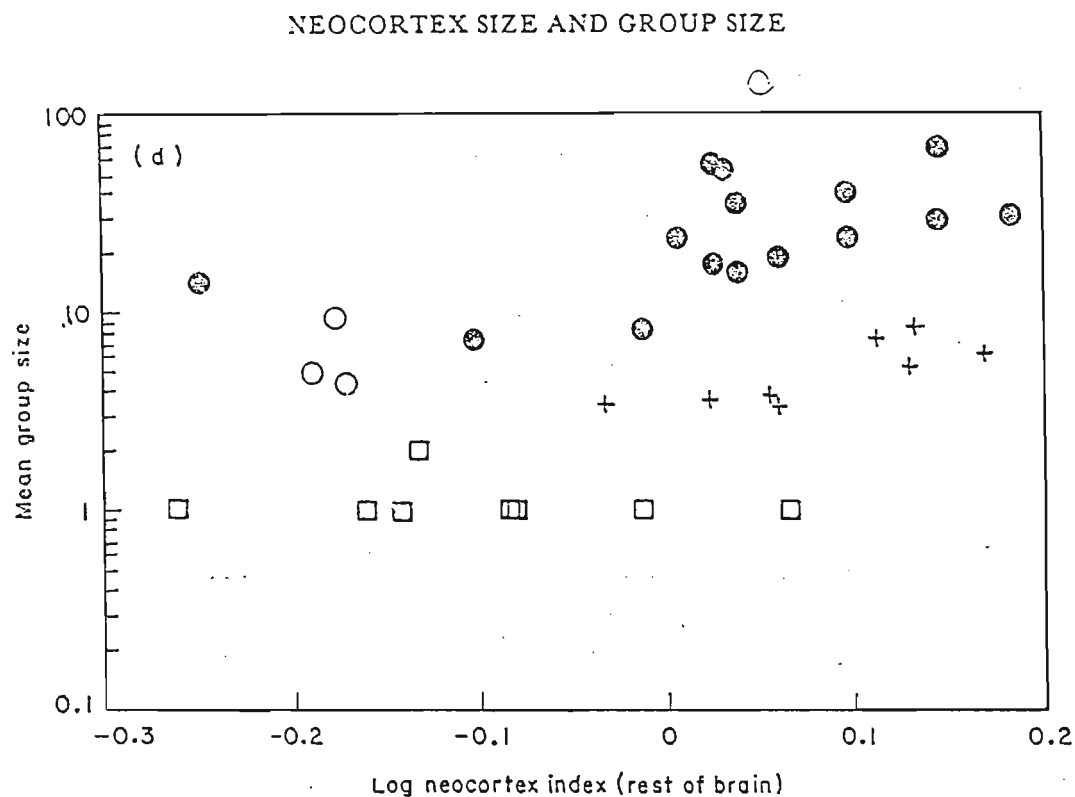
Figure 2d.

Mean group size for individual genera plotted against: (a) absolute neocortex volume, (b) neocortex ratio (relative to the hindbrain; i.e., medulla + cerebellum + mesencephalon + diencephalon), (c) neocortex index (residual against body mass) and (d) neocortex index (residual against rest of brain). Symbols and source as Figure 1.

Figure 28. Log of neocortex index to mean group size (Dunbar 1992)
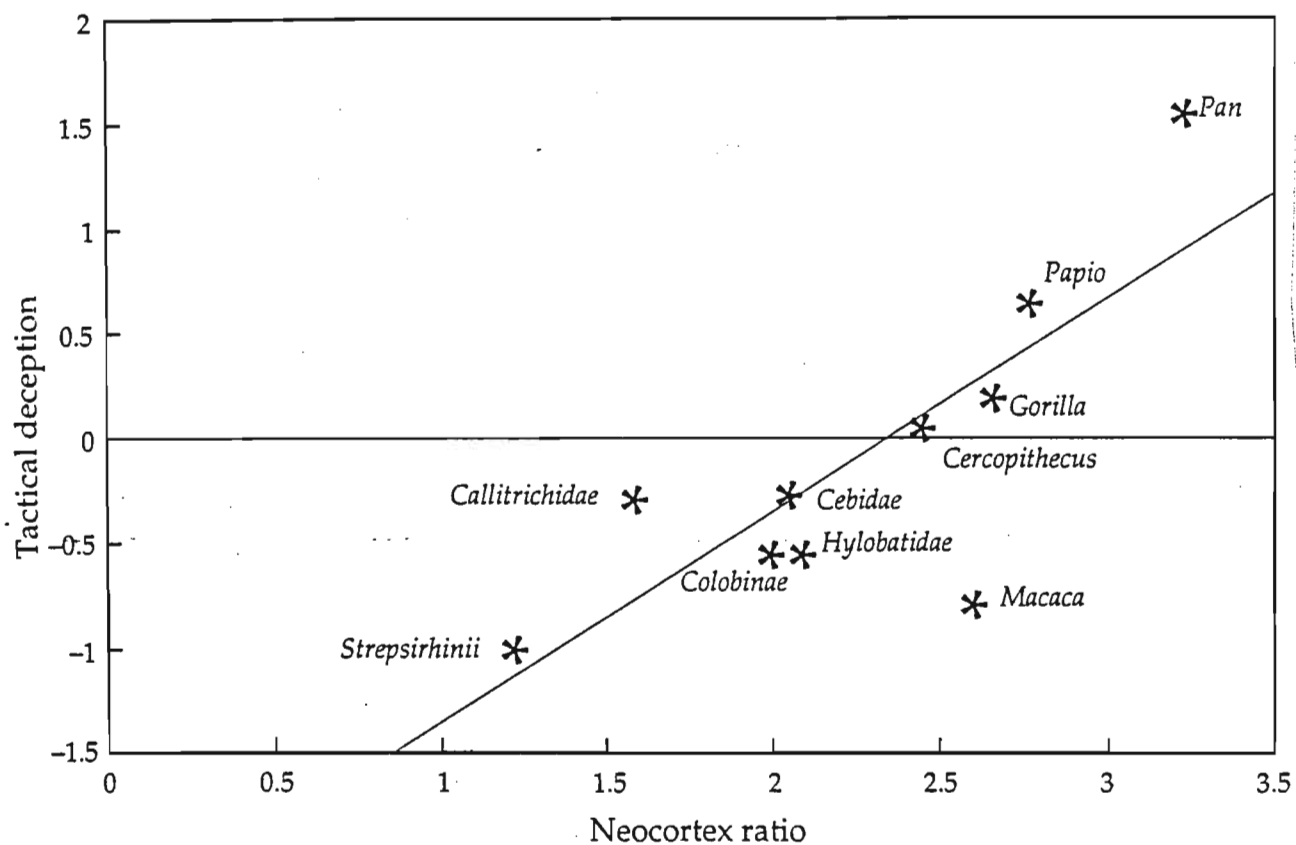
Neocortex ratio predicts deception frequency. Here, neocortex ratio is plotted against the frequency with which tactical deception is observed (corrected for the number of field studies) in wild primates, for 10 taxa of primates. This relationship is significant on one-way ANOVA (F(1,8) = 11.89, P < 0.01. Note that the great apes (Pan and Gorilla) overlap with monkeys (e.g. Papio) in neocortex ratio and index of deception.

Figure 29. Plot of neocortex ratio against tactical deception (Byrne 1995)
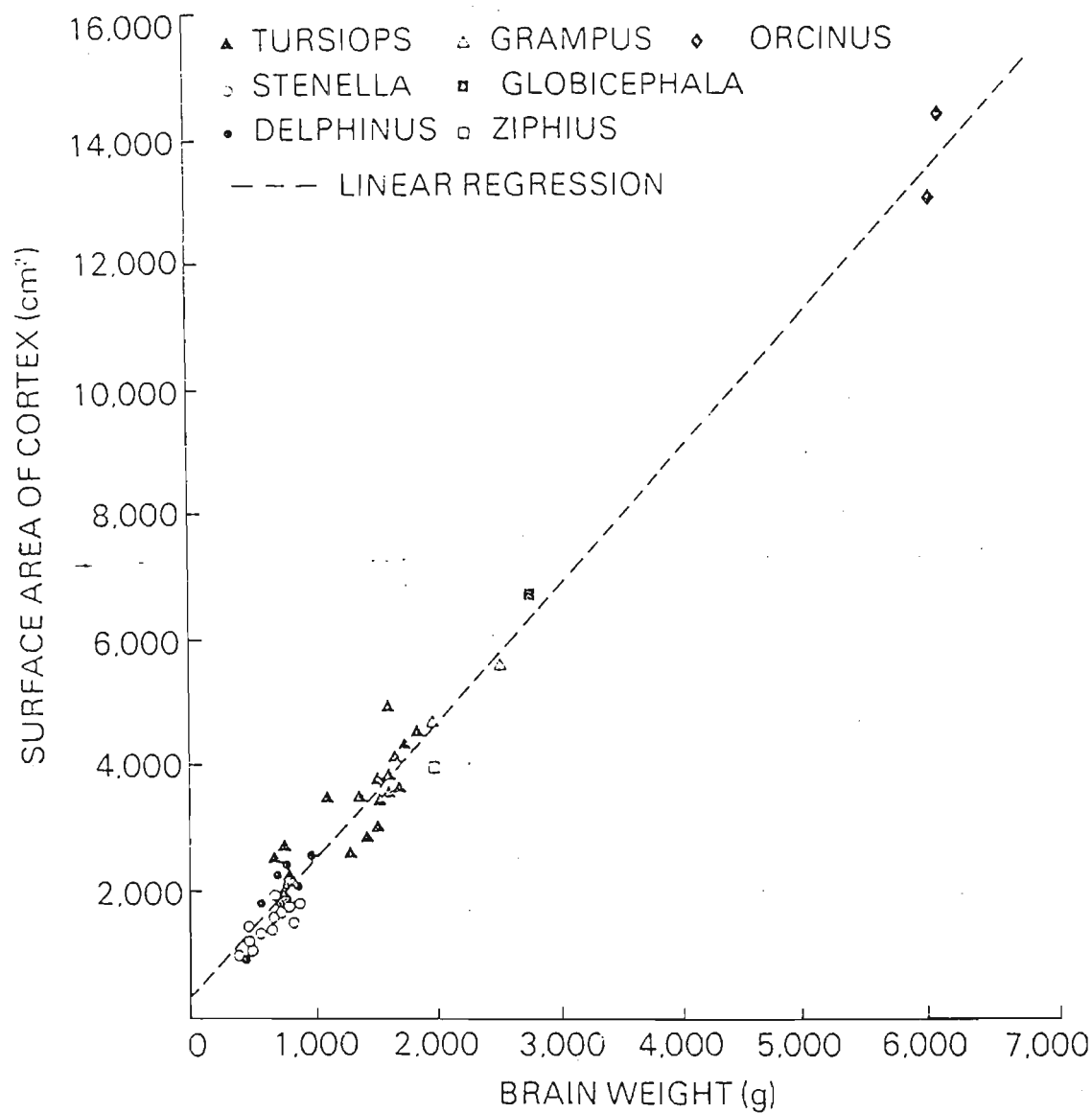
Surface area of the cerebral cortex plotted against brain weight. Linear regression of brain weight (W) in g vs. surface area of cortex in cm^2 (A) revealed $A = 330.4 + 2.17\ W$, with correlation coefficient $r = 0.98$.

Figure 30. Plot of surface area of cortex to brain weight (Ridgway 1986a)

Figure 31. Logarithimic plot of brain weight to body weight for different mammalian orders (Worthy & Hickie 1986)
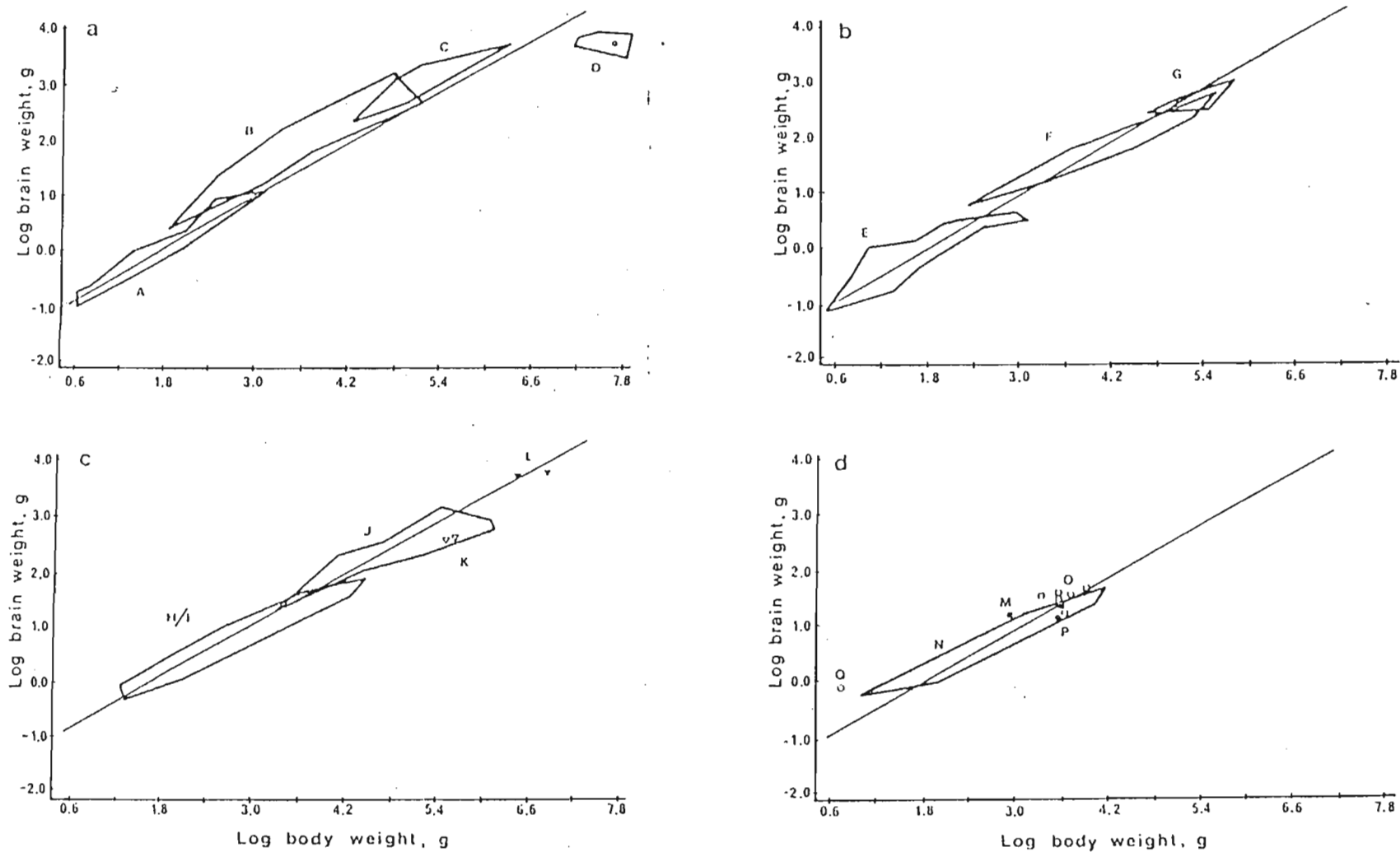
—Convex polygons enclosing the distribution about the overall relationship for the 16 mammalian orders and 4 suborders represented. *a*: *A*, Chiroptera; *B*, Primates; *C*, Cetacea—Odontoceti (*Physeter catodon*); *D*, Cetacea—Mysticeti. *b*: *E*, Insectivora; *F*, Carnivora—Fissipedia; *G*, Carnivora—Pinnipedia. *c*: *H*, Rodentia; *I*, Lagomorpha; *J*, Ungulata; *K*, Sirenia; *L*, Proboscidea. *d*: *M*, Hyracoidea; *N*, Marsupialia; *O*, Edentata; *P*, Pholidota; *Q*, Dermoptera.

Table 13. Dolphin EQ values (Ridgway 1986a)

Brain and body size of EQ for animals from ten genera of odontocetes. Only data from animals long enough to be mature were included. Measurements for one Orcinus, *five* Delphinus, *and one* Globicephala *were taken from Pilleri and Gihr (1971). The* Physeter *data are from Kojima (1951). All other measures are from Ridgway and Brownson (1984). All values are means except for those genera with only one specimen represented*

| Genus	N	Body length (cm)	Body weight (kg)	Brain weight (g)	EQ
Lagenorhynchus	2	207.5	99.5	1256.5	4.90
Tursiops	19	245.7	167.4	1587.5	4.40
Delphinus	10	193.1	67.6	835.6	4.20
Grampus	1	320.0	400.0	2551.0	3.92
Orcinus	3	555.0	2049.2	5617.7	2.90
Delphinapterus	1	340.0	636.0	2083.0	2.35
Globicephala	3	492.0	1061.0	2673.0	2.10
Kogia	1	320.0	248.0	999.0	2.10
Ziphius	1	549.0	2273.0	2004.0	0.97
Physeter	16	1538.8	37093.8	7818.8	0.60
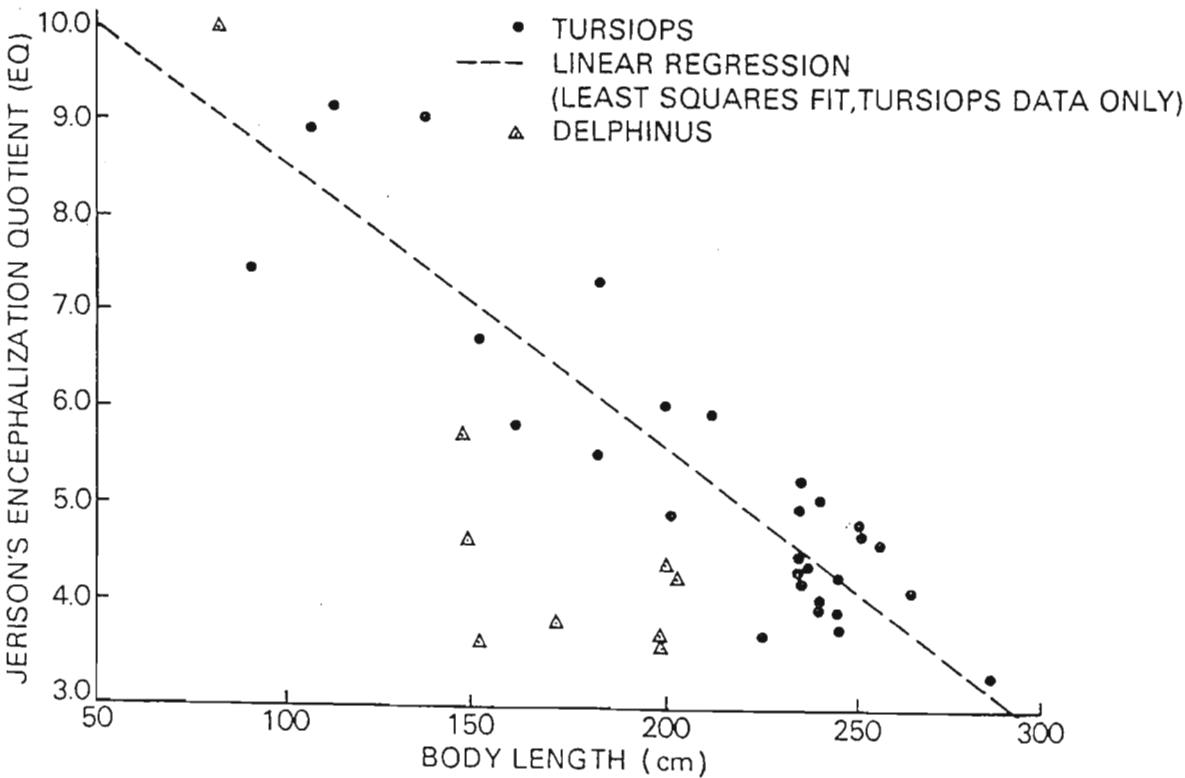
FIG. 4.1 EQ decreases with increasing body length. It is important to use only data from adult

Table 14. Dolphin EQ values (Worthy & Hickie 1986)

ENCEPHALIZATION QUOTIENT (EQ) AND AVERAGE AND MAXIMUM DIVE TIMES FOR A
VARIETY OF AQUATIC MAMMALS

Order and Species	Dive Time (min)		EQ	Source
	Average	Maximum		
Mysticeti				
Balaenoptera musculus		49	0.2	Harrison & Kooyman 1981
Balaenoptera physalus		20	0.2	Harrison & Kooyman 1981
Eschrichtius robustus		18	0.2	Slijper 1979
Megaptera novaeangliae		17	0.2	Slijper 1979
Odontoceti				
Globicephala scammoni		15	1.4	Harrison & Kooyman 1981
Lagenorhynchus obliquidens		6	5.1	Ridgway 1972
Orcinus orca		15	1.5	Ridgway 1972
Phocoena phocoena	0.25	4	2.6	Parker 1932; A. Read, pers. comm.
Phocoenoides dalli		8	2.5	Ridgway 1972
Physeter catodon	<30	90	0.3	Caldwell et al. 1966; Lockyer 1977
Platanista indi	1	2	1.4	Pilleri & Gihr 1970
Tursiops truncatus		5	2.8	Slijper 1979
Pinnipedia				
Callorhinus ursinus	<2	5	0.6	Kooyman et al. 1976, 1980
Halichoerus grypus		18	0.7	Harrison & Kooyman 1981
Leptonychotes weddelli	10	72	0.6	Robin 1973; Kooyman et al. 1980
Odobenus rosmarus		10	0.8	Harrison & Kooyman 1981
Phoca hispida		17	1.6	Ferren & Elsner 1979
Phoca vitulina	<5	20	1.3	Robin 1973; Harrison & Kooyman 1981
Zalophus californianus		8	1.1	Robin 1973
Sirenia				
Trichechus manatus	5	25	0.4	Harrison & Kooyman 1981; S. Innes, pers. comm.
Ungulata				
Hippopotamus amphibius	5	15	0.3	Slijper 1979

Table 15. Allometric relationship between brain weight and body weight for mammalian orders and suborders (Worthy & Hickie 1986)

RELATIVE BRAIN SIZE IN MARINE MAMMALS

ALLOMETRIC RELATIONSHIP BETWEEN BRAIN WEIGHT (g) AND BODY WEIGHT (g) FOR ALL MAMMALS AND FOR VARIOUS ORDERS AND SUBORDERS

Order and Suborder	b	a	n
Carnivora	0.641 ± 0.038	-0.77	62
Fissipedia	0.619 ± 0.044	-0.71	50
Pinnipedia	0.396 ± 0.207	$\div 0.55$	13
Cetacea	0.358 ± 0.064	$+1.07$	35
Mysticeti	0.360 ± 0.425	$\div 0.98$	11
Odontoceti	0.546 ± 0.175	$\div 0.15$	24
Chiroptera	0.822 ± 0.036	-1.40	192
Megachiroptera	0.777 ± 0.047	-1.22	27
Microchiroptera	0.805 ± 0.023	-1.40	165
Insectivora	0.685 ± 0.076	-1.25	51
Lagomorpha	0.587 ± 0.047	-0.91	15
Marsupialia	0.546 ± 0.001	-0.84	42
Primates	0.801 ± 0.048	-2.22	88
Anthropoidea	0.728 ± 0.052	-0.82	63
Prosimii	0.699 ± 0.097	-0.96	25
Rodentia	0.688 ± 0.033	-1.11	95
Ungulata	0.577 ± 0.082	-0.48	49
All mammals	0.755 ± 0.012	-1.27	648

NOTE.—The equation used is of the form log (brain weight) = b log (body weight) + a, where b is the slope and a is the intercept. The 95% confidence limits for the slope estimates are indicated (Sokal and Rohlf 1981).

Appendix B:

Odontocete Sociality and Ecology

This discussion outlines a general framework of odontocete sociality and ecology via a study of the function of cetacean schools and an overview of social ecology, prior to investigating the social organisation and ecology of some South African species. The species under investigation include the Common dolphin (*Delphinus delphis*), Indopacific Humpback dolphin (*Sousa chinensis*), Spotted dolphin (*Stenella attenuata*), Striped dolphin (*Stenella coeruleolba*), Bottlenose dolphin (*Tursiops Tuncatus*) and Dwarf Sperm Whale (Kogia simus).

1. Animal Order and Subdivisions

The order of cetaceans (whales, dolphins and porpoises) comprises the suborders of mysticetes (baleen whales) and odontocetes (toothed whales).

The suborder Mysticeti includes:

the families Balaenidae (3), Neobalaenidae (1), Eschrichtiidae (1) and Balaenopteridae, subfamilies Balaenopterinae (5) and Megapterinae (1).

The suborder Odontoceti includes:

the superfamily Platanistidae, family Platanistidae (2), family Pontoporiidae, subfamily Lipotinae (1) and subfamily Pontoporiinae (1) and family Iniidae (1);

the superfamily Delphinoidea, family Monodontidae, subfamily Delphinapterinae (1) and subfamily Monodontinae (1), family Phocoenidae, subfamily Phocoeninae (4) and subfamily Phocoenoidinae (2), family Delphinidae, subfamily Steninae (4) including Sousa chinenis, subfamily Delphininae (15) including Tursiops truncatus (bottlenose dolphin), Stenella attenuata (spotted dolphin), Stenella coeruleoalba (striped dolphin) and Delphinus delphis (common dolphin), subfamily Lissodelphinae (2), subfamily Cephalorhynchinae (4), subfamily Globicephalinae (6), and subfamily Orcaellinae (1);

the superfamily Ziphioidea, family Ziphiidae (20);

and the superfamily Physeteroidea, family Physeteridae, subfamily Physeterinae (1) and family Kogiidae (2), including Kogia simus (dwarf sperm whale) (Cooke 1991).

2. Sociality

There are important differences between the structure of dolphin and fish schools. Whereas fish schools do not have cohesive units of subgroups (Norris & Dohl 1980), dolphins have several kinds of units, discernible even during rest periods. Schools of fish and dolphins share the common features of having discrete boundaries to their schools, with school density not changing gradually, but rather altering abruptly. The most significant difference lies in internal school structure- in spacing, segregation of different classes and individual or group movement (Norris & Dohl 1980). The same authors note that the most obvious causal difference stems from the complex sociality of delphinids and the phylogenetic difference to fish schools, with the neural organisation of mammals being more advanced than that of

piscenes. It is thus that 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, Wursig (1986) notes that social mammals can transmit knowledge concerning prey, predators and the environment via social tradition and this may contribute to the phylogenetic difference in behavioural capacity and flexibility between mammals and fish.

A cetacean school may be defined as an aggregate regularly swimming together as a unit (Norris & Dohl 1980). This definition, which is broad, as a result of the variety of functions served by the school, may be compared to Gaskin's (1982) definition, where a school denotes a degree of social cohesion in the behaviour of animals in the unit. He notes that an "aggregation" describes a number of associated schools, travelling together in the same area or direction, but with distinctive spacing and varied feeding and movement. He reserves the use of the term "group" in a vague context, where it may or may not refer to a school. For the purposes of this paper, the wider definition of school, proposed by Norris & Dohl (1980) is used.

Cetacean schools function to allow social integration, with the school being viewed as an equilibrium system, composed of centrifugal forces (promoting school cohesion) and centripetal forces (factors spreading the school apart) (Norris & Dohl 1980). Thus different conditions result in drastic alterations to dolphin school size and spacing of animals and subgroups. Cohesive patterns include protection, fright, sleep or rest and associations (familial or habitual), 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 individuals' sensory information to promote relevant environmental

information to the group. Sensory integration is multi-faceted, relying on visual, auditory (active echolocation or passive listening) or taste sensation, temperature variation or tactile sensation. Sensory integration provides animals with more environmental information, freeing them to engage in various forms of activity (Norris & Dohl 1980).

It has been proposed that the formation of cetacean schools is due either to predation or as a result of foraging demands (Wursig 1986, Norris & Dohl 1980). Gaskin (1982) observes that most cetaceans either form schools when food sources are concentrated, as opposed to dispersed, or when cetaceans cannot be concealed in the environment. Norris & Dohl (1980) note that, as dolphins are highly socially advanced, 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 & Dohl 1980). Wells, Irvine & 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 in small groups, pelagic species reach aggregates of up to several thousand. However, most cetaceans are social (Wursig 1986), which confers an advantage to individual members of the group.

Certain cetacean species have segregated age and sex subgroups, including bottlenose dolphins, while most have mixed age-sex groupings (Wells, Irvine & Scott 1980). 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. Within bottlenose dolphins, the composition of the group may vary dynamically within a stable

herd, although subgroup associations display a greater duration (Wells, Irvine & Scott 1980).

3. Ecology

Within the large range of school sizes, cetacean schools have several functions including foraging, feeding, reproduction, individual development and learning, and predator protection.

3.1 Foraging

Cetacean schools feed primarily on schools of fish and squid species, many of which also exhibit aggregation tendencies. Norris & 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 & Dohl 1980). These formations, up to 1 kilometre wide, permit an area of 5km^2 to be scanned at a speed of 5 km per hour, increasing efficiency incrementally as opposed to single animal scouting (Wursig 1986, Norris & Dohl 1980). As the majority of food for pelagic dolphin species constitutes 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).

3.2 Feeding

School formation 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" (Norris & Dohl 1980). This involves initial heavy exploitation of a resource area, which is then left to reconstitute itself while another area is fished.

Methods of food capture are significantly different to search methods, with patterns of capture described as either spread school formations or cooperative capture methods (Norris & 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. 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 (Norris & Dohl 1980). 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 feeding schools have also been observed, where different species feed on similar types of food. The same authors note that dolphin species forming smaller moderate-sized schools appear to use more specialised kinds of food capture. For example, bottlenose dolphins herd and criss-cross to trap fish schools and Atlantic humpback dolphins and bottlenose dolphins often herd schools of prey into shallow water (Peddemors & Thompson, 1994). Norris & 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.

3.3 Reproduction

Norris & Dohl (1980) propose that 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. However, the same authors note that the cost of living in a group is incurred through sexual rivalry. Wells, Irvine & Scott (1980) believe that the school's function of bringing males and females together to mate is vital. Reproductive synchrony occurs primarily in migrant species, whereas tropical and sub-tropical cetaceans have broad, unseasonal reproductive modes (Wells, Irvine & Scott 1980).

3.4 Individual development and learning

The stage of an individual's development appears to determine the location within a school (Norris & Dohl 1980). Mother-young pairs are very common within schools and this dyadic relationship remains significant 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 & Dohl 1980). Odontocetes display a highly developed capacity for learning (Herman 1980). Norris & 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 & Dohl 1980). The complexity of dolphin schools may be the result of the dolphin's capacity for complex learning (Herman 1980) and its capacity to comprehend contingency patterns necessary for learning to occur (Norris & Dohl 1980).

3.4 Protection from predation

Sharks and killer whales prey on dolphins, whose typical reaction to environmental stress is avoidance and tightening of the group, with the peripheral animals engaging in most of the aggressive activity, while the young and vulnerable school members are protected by a "moving cup" of adults (Norris & 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, it makes sense for larger males to hold these positions, as they are better able to fend off predators (Norris & Dohl 1980). The same authors note that if the entire range of cetacean group size is considered, it becomes evident that variation in school size is as expected if predation were the propelling force behind schooling. Thus large whales are usually either solitary or form small reproductive units. Similarly, river dolphins form small groups or remain solitary, coastal dolphins form small to moderate schools, while pelagic dolphins form huge schools of up to several thousand members.

4. Social ecology

It is evident that 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 & 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 coordinated 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 coordinated foraging and feeding. Predation pressure also varies with habitat. Riverine species are almost free from predation, while coastal and pelagic species are preyed upon by humans, sharks and killer whales (Wells, Irvine & Scott 1980). Wells, Irvine & Scott (1980) note that inshore odontocetes form tight social bonds, evidenced by mass strandings and permanent family units, while riverine species appear to have territoriality as a possible dominance system.

5. Selective mechanisms influencing social systems

A wide range of adaptation is evident 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 & Scott 1980).

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 appearing correlated to school size (Johnson & Norris 1986). According to Wells, Irvine and Scott (1980), one cannot reduce the determining factor of group composition, stability or size to one environmental factor. They propose that the interaction of environmental factors of differing importance combine in determining group features. It appears that the ecological determinants of group size in larger delphinids are different than for the smaller delphinids, thus the larger the animal, the smaller the group (Johnson & Norris 1986). The threat of predation is less significant for larger animals, where prey density and size, in addition to predator mobility may be more important (Wells, Irvine & Scott 1980).

6. Sociality in mysticetes (baleen whales)

Baleen whale school structure does not generally resemble the tightly cohesive schools of odontocetes, with baleen whale schools being more widely dispersed or individuals living solitarily (Norris & Dohl 1980). This may be as a result of their capacity for long distance communication. However, these cetaceans do form large aggregates at breeding, calving or feeding grounds (Norris & Dohl 1980).

7. Parallels to terrestrial mammals

An interesting comparison has been made between inshore odontocete and terrestrial mammal social behaviour and structure (Wells, Irvine & Scott 1980). For example, dolphins and ungulates both display allomothering, care-giving behaviour, dominance hierarchies and group defense, for example, the African buffalo and bottlenose dolphins have herds and schools

of fixed home ranges, with slight overlaps, with the groups having mixed and fluid constitutions and displaying group defense (Wells, Irvine & Scott 1980). The same authors compare the social systems of bottlenose dolphins and primates, with the finding that bottlenose dolphins and baboons both form dominance hierarchies, mate via rotating consort relationships without permanent sexual pair bonds and both have group defense. Chimpanzees and bottlenose dolphins both have well defined, stable home ranges, with the fluid composition of subgroups within the group, dominance hierarchies and cooperative hunting and defense also occurring (Wells, Irvine & Scott 1980).

8. Social systems and 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, bottlenose dolphins have been found to target specific prey species in South African waters (Cockcroft & Ross, 1990). They mainly eat fish and feed cooperatively or individually. Bottlenose dolphins are occasionally preyed upon by sharks or killer whales (Wells, Irvine & Scott 1980, Cockcroft, Cliff and Ross, 1989). Individual feeding occurs on benthic & reef dwelling fish, while cooperative 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 50m deep and avoids turbid water (Peddemors, 1995). As mentioned above, cooperative and individual feeding techniques are used and a system of age and sex based resource partitioning has been shown off Kwazulu-Natal (Cockcroft & Ross, 1990).

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, Wells, Irvine & Scott (1980) note that Indian Ocean bottlenose dolphins have a group size of 100-200 animals, with a range from 3-1000 members, the groups displaying dominance hierarchies. These bottlenose dolphins' group characteristics include adult males, females and offspring; subadult males; subadult females; mixed males and offspring and fluid associations within a school (Wells, Irvine & 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).

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 & 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, this species eats 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 & Best, 1992). On the east coast, the prey are usually small, easily captured, pelagic shoaling species (Young & Cockcroft, 1994). Although supposedly opportunistic feeders, five prey species constituted 86.9% of the

dietary weight. There is also strong evidence for resource partitioning between sex and size groups (Young & Cockcroft, 1994).

In terms of sociality, common dolphins have been referred to one of the most gregarious cetacean species, occurring in large schools of up to several hundred and aggregates into the thousands (Leatherwood & Reeves, 1983).

Humpback dolphins are found in coastal or estuarine waters, with year-round residents following habitual inshore routes (Durham 1994). Opportunistic feeders, humpbacks prey on fish (mainly reef fish), hunt cooperatively and feed individually (Saayman & Taylor, 1979). They are occasionally preyed upon by sharks (Cockcroft, 1990). In Kwazulu-Natal, the humpback 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 & Thompson, 1994). They primarily feed on estuarine-associated and littoral fish species and cephalopods. Off the eastern Cape feeding increases during the rising tide (Saayman & Taylor, 1979). Elsewhere, the humpback moves onshore with the rising tide to feed in mangrove channels, sometimes incorporating purposeful beaching in pursuit of prey (Peddemors & Thompson, 1994).

The 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 & Scott (1980) note that humpbacks 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 & Taylor (1979) propose that humpbacks 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 than males (Durham, 1994).

Spotted dolphins have been sighted in the Mozambique channel and as far south as the Eastern Cape (Port St John's) (Peddemors, in press). 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, in press). 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).

Spotted dolphin groups range from 100-500+ members in size, with family units moving within larger, more flexible feeding aggregates (Gaskin 1982). Findlay (1989) notes that average group size for spotted dolphins in Southern Africa is 94 members, with a range from 200-300 individuals.

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 & 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 & Best, 1992).

Striped dolphin school size varies from four to several hundred members, with the average school size at 75 dolphins (Findlay, 1989). Miyazaki (undated manuscript) notes that large schools are often composed of numerous small schools, ranging from 20-200 dolphins. In small schools several females with a calf, pairs or several dolphins were observed. The range of school size captured was from 25 to 2327 animals, with the mean school size at 415 animals. Over 85% of the schools were composed of fewer than 500 dolphins, while only 4.2% had more than 1000 members. No seasonal variation was found in the size of captured schools caught in the Izu Peninsula. Groups were either composed of immature or mature members while some had mixed membership (Miyazaki, undated manuscript).

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. In terms of feeding data 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).

Conclusion

Although some researchers are sceptical about attributing functions to schools, cetaceans schools are noted as performing several important functions. These include the searching for and capturing of food, reproduction and growth, social integration, learning and protection from

predation. The movement and size of schools is largely determined by changing food sources and animal size respectively. It was also found that animals inhabiting areas further from the shore display greater school sizes, with a correlation between water depth and school size. It follows that riverine species have smaller groups than coastal species, which in turn have less members than pelagic, oceanic species. Sensory integration is believed to be vital to the coordinated survival efforts of the group's members and group living further allows social learning and development to occur. The transmission of knowledge via social tradition is an important feature of social mammals and one distinguishing them from fish schools. Social systems were discussed in relation to ecological considerations. It was noted that group size varies with habitat and foraging demands. In terms of selective mechanisms operating on group size, it was found that the interaction of differentially significant environmental factors determines group features. Animals of different sizes have different pressures driving group size, for example large animals with little threat of predation do not group owing to predation pressure. The social systems of marine and terrestrial mammals were briefly compared and many similarities proved to exist. Finally, the ecology and sociality of species migrating through or resident in South African waters were discussed. From the similarities and differences observed, it is evident that further research is required for comprehensive information on the issues of sociality and ecology.

Appendix C:

An assessment of the use of neuroimaging techniques in behavioural/psychological and neuroanatomical research.

Neuroimaging techniques, specifically computerized X-Ray tomography (CT) scanning and magnetic resonance imaging (MRI), have developed into powerful sources of investigation in several disciplines. Aside from the obvious value and applications of such techniques to the medical studies of pathology and surgery, there are additional and alternative utilisations for the above neuroimaging techniques. These less frequently used applications have much potential for inter-disciplinary investigations and as such form the substance of this paper. Breakdowns of the utilisation of neuroimaging units are mentioned, prior to illustrating the use of neuroimagery in behavioural, psychological and neuroanatomical research. These applications encompass diverse disciplines, such as psychiatry, psychology, anatomy and histology, physiology, pharmacology, biology, veterinary science and biomedical research. Where appropriate, mention of research in complementary disciplines is made. In essence, this investigation aims to prove the potential of neuroimaging for use in behavioural, psychological and neuroanatomical studies and seeks to show that up to this point, insufficient use has been made of such techniques in these fields. With further insight into the scientific wealth offered by such research tools, it is hoped that their capabilities will be brought to fruition.

CT scanning, as an enhanced and more evolved form of X-Ray tomography, 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; allowing for faster surgical intervention and reduced fatalities (McCort 1987). For reasons such as the above, the popularity of CT scanning increased throughout the 1980s, with Evens & Mettler (1985) reporting an estimated 5-5.5 million CT scans being performed in the United States during 1983. Steinberg, Anderson & Steinwachs (1987), noted a 59% increase in the use of CT at one institution between 1981 and 1984. As they note that MR has similar clinical applications to CT, it may be reasonable to expect an increase in MR units during the 1990s.

In terms of the statistics of MRI utilisation from 1985-1990, Evens & Evens (1991) note that the demand for MR is steadily increasing. The referrals for MR in Japan were half the number of those in the U.S. even though fees were substantially lower in the former country (Hisashige 1994). This scenario is mentioned as it is believed that neuroimaging techniques are unnecessarily overutilized in certain countries, when they could be put to alternate, more efficient usage in research.

From literature searches conducted on-line and on CD-Rom (where the search was for neuroimaging techniques, utilizations and applications in relation to medicine, behaviour and psychology), it was found that CT and MRI were used almost exclusively for the detection and diagnosis of pathology, injuries or in the assistance of surgical treatment. For example, out of approximately 20,000 articles on MRI from 1996-91 (using Ovid on-line/Medline), only 18 articles related to behaviour and 11 related to psychology (or rather in coping with psychological reactions when confronted with MRI). From the 1996-1991 search on MR and behaviour, almost all of the hits related to organic disorders, pre-,intra- and post-operative findings.

No topics related to behaviour *per se*, however this excludes fMRI, or functional MRI studies.

In another example, the search for MRI and behaviour and psychology for the period 1991-86 resulted in 19 articles for the former and 10 for the latter. Only 3 articles dealt with purely behavioural issues and MRI, whilst the psychology topics all related to anxiety, stress and patient's responses to MRI. (Two of the behavioural articles were by Kjaer et al, 1989, 1988 and deal with relaxation states in the human brain, the final one by Zimmerman & Hentschel, 1988, dealing with reproductive behaviour in mice). No cognitive or perceptual issues as such were dealt with. From mainstream searches such as the two examples described above, it is evident that very little use has been made of CT and MRI in behavioural and psychological research. An effort was made to assess the use of the two neuroimaging techniques in the above fields as well as in neuroanatomy via more directed and narrower literature searches.

Work with neuroimaging in related fields such as veterinary science may be of interest to those seeking alternative uses of such techniques. Although the majority of the articles in this field pertain to surgical treatment and the diagnosis of pathology (such as in tumour detection), some articles relate directly to neuroanatomy, such as the *in vivo* cephalic CT scanning of the chimpanzee, documented by Saban *et al* (1985). Research has also been conducted into the neurology of small animals by Lang, Huber & Vandevelde using CT (1988); principles of CT and MRI usage in such fields have been proposed by Wortman (1986) and the interpretation of such CT images is discussed by Stickle & Hathcock (1993).

Wolf *et al* (1992) demonstrated the successful application of a whole body magnetic resonance imaging system in providing images of a live rat. They discuss the advantages of the MRI technique as providing detailed information without incurring extra costs and allowing for longitudinal studies using anaesthesia, thus sparing the animals from death. Although their first proposal is debatable owing to the high costs of MRI, this method is the least invasive method available and the most humane for animal experimentation.

In terms of investigations of social behaviour carried out using CT (1980-96) and MRI (1985-96), all documented cases relate to psychiatric disorders. As they are concerned with psychopathology and the distinction between adaptive and maladaptive behaviour, they are not relevant to this discussion.

Regarding animal behaviour research and neuroimaging, all recorded cases using CT from 1980-1991 relate either to pharmacological effects on animals or to neurophysiological and neuropsychological experiments. MR investigations in this area from 1986 to 1996 have all related to lesions, surgical observations and chemical experimentation. Only one documented case exists relating to the actual behaviour of animals. This research, carried out by Ossenkopp *et al* (1986), pertains to the effects on behaviour of exposure to nuclear MRI. After administering repeated open-field and passive avoidance tests to rats, they concluded that there is no evidence for short or long term behavioural alteration in animals exposed to MRI. This has important consequences for those wishing to follow Wolf's (1992) suggestions regarding MRI with anaesthetized live animals and serves as a further compelling reason to employ this method of investigation with animals.

Studies involving mammals and neuroimaging from 1980 to the present were analysed and it was found that primate research in this area holds potential, although it is rare in the literature. Ruff (1989) suggests that image analysis, including computerized tomography, provides the following: new insight into studying the structural evolution of primate limbs, as it allows for improved estimates of body mass of fossils; displays the mechanical loadings of fore- and hind-limbs (reflecting dominance) and studies more 'subtle' behavioural differences intra- and inter-specifically from limb bone shapes. In addition, Ruff proposes that it also allows for a combination of diaphyseal and articular structural analysis, thus providing greater information on structural evolution of primate limbs. Studies of primate evolution stand to benefit from this technology.

Other notable research in the primate-CT scanning field includes imaging of the primate bony labyrinth, conducted by Spoor & Zonneveld (1995) and Spoor, Wood & Zonneveld (1994). The earlier text reflects an important shift from the usual functional analysis used to study the evolution of bipedalism in hominids. Here high-resolution CT scanning was used to produce cross-sectional images of the bony labyrinth for the examination of the vestibular system of certain extant and extinct primates. Using this method, it was found that the earliest species reflecting modern human morphology is *Homo erectus*, whilst the examinations of southern African crania attributed to *Australopithecus* and *Paranthropus* relate more closely to the contemporary great apes (Spoor, Wood & Zonneveld 1994). Spoor & Zonneveld, in subsequent work with CT and the primate bony labyrinth (1995), propose that as CT is 'non-destructive, fast and easy to perform, it is applicable to large samples and to rare or precious anthropological specimens'. Owing to their non-invasive nature, (MRI moreso than CT) these neuroimaging techniques may be referred to as 'choice methods' for studying (one or many) specimens which require preservation as well as quick, efficient examinations. The only

documented case of CT with non-primate, terrestrial mammals was conducted by Chen, Klein, Gamsu & Webb (1992) and related to an investigation of the mammalian lung. Specimens from the dog, pig, rabbit and sheep species were used to confirm that high resolution CT allows for differentiation between three distinct types of lungs.

MRI research in relation to primates from 1990-96 relates predominantly to the visual cortex, (Engel *et al* 1994, Rizzo *et al* 1992) or to pharmacological testing. As with CT in this field, such studies relating to behaviour or anatomy are extremely rare.

In relation to marine mammals, neuroimaging applications are even more scarce than for terrestrial mammals. Only four examples were found of such work. The first is the use of CT to observe acoustic structural anatomy in the forehead of spinner dolphins (Cranford 1988). CT has also been used in the determination of airsacs in the dolphin species *Lagenorhynchus albirostris* (Brouwers, Kaminga *et al*, 1990), as well as in observations of vaginal calculi in the dolphin species *Delphinus delphis* (Woodhouse & Rennie, 1991). The only case of MRI where dolphins have been included is presented by Sebes, Langston, Gavant & Rothschild (1991), where growth recovery lines in fossil vertebrae were analysed using MRI. Present research aims to prove that there is much potential for the use of neuroimaging with all mammals, marine and terrestrial.

Researchers such as Vannier & Conroy (1989) have called for the introduction, albeit cautiously, of imaging workstations into the field of computer-aided primatology and investigate the possibilities of usage of various types of workstations. These range from simple display systems and diagnostic reporting imaging-processing stations to manipulational systems,

entailing 3-D modelling and computer graphics applications. It is hoped that forthcoming studies will utilize the available technology and increase the popularity of neuroimaging in scientific investigations.

The final focus relates to the use of neuroimaging techniques and neuroanatomy. This is also the briefest section of the current literature review, as almost no work relates purely to neuroimaging and neuroanatomy, rather most accounts focus on anatomy in relation to pathology or surgery. For example, the only study in the last 5 years recorded by the Ovid on-line/medline search is that of the correlation between neuroanatomy and neuropathology in schizophrenia (Waldman, 1992).

As no general information appears to exist on neuroanatomy and CT/MRI, an attempt was made to study more specific categories such as investigations of the cerebral cortex and neocortex. All searches conducted covered the time period 1980-1996, and in all investigations relating to mammalian, primate and dolphin cerebral cortex and neocortex, it was found that no studies had been performed using CT or MRI.

From the above literature probes, it appears reasonable to conclude that a minority of studies into pure neuroanatomy have been carried out using neuroimaging techniques such as CT and/or MRI. An example of such a study is the volumetric measurement of the amygdala and hippocampus using MRI (Watson *et al* 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. Sergent (1994) notes that methods such as CT and MRI, in addition to other brain imaging methods, have

increased the capacity to visualize the brain at work and assist in establishing the link between specific cognitive functions and certain cerebral areas. In essence, the value of neuroimaging techniques is that they allow for a more detailed and precise understanding of the significant relationship between function and structure.

A final assessment of the application of neuroimaging techniques to behavioural, psychological and neuroanatomical investigation must include the following considerations. Since its inception more than two decades ago, CT scanning has proved to be invaluable to increasing the efficiency of radiology. Its surgical and pathological applications are as numerous as they are diverse. The popularity of CT was shown to rise during the last two decades, from investigations into its utilisation. Similar conclusions can be reached about the use and value of MRI, which, although more recently brought into use, is less invasive than CT and allows for more precise viewing of certain areas. MRI has increased vastly in its popularity and profitability over the last decade and along with CT holds much potential for future research. It is evident is that a profound shortage exists in the behavioural/psychological and neuroanatomical applications of CT and MRI. This is apart from studies of maladaptive behaviour and psychopathology, which form part of the surgical and pathological applications of neuroimaging. It was found that minimal studies had been conducted into social and animal behaviour using neuroimaging methods and that psychological research all related to psychological reactions by those confronted with CT or MRI or in connection with psychiatric disorders. Hardly any work has been conducted into cognition via CT or MRI. An important potential of neuroimaging techniques lies in their ability to aid in increasing our understanding of structural evolution. Only a few studies with marine and terrestrial mammals and more specifically with primates and dolphins have been recorded, with almost no purely behavioural or neuroanatomical focus. In terms of animal

research, it must be noted that MRI is the most favourable application, as it does not expose the animal to radiological effects, nor does it entail any behavioural changes. Furthermore, the animal does not have to be killed as it can be anaesthetised. Thus as MR is non-invasive and non-lethal, it should be considered above alternate, inhumane methods. The final theme examined was in relation to neuroimaging and neuroanatomy, where it was found that almost no work had been conducted into general neuroanatomy and more specifically into the cerebral cortex or neocortex. Finally, as CT and MRI are often unjustifiably used in superficial procedures, it is proposed that they should be implemented in alternate behavioural/psychological and/or neuroanatomic investigations when not utilized in their primary surgico-pathological role. Research being presently conducted with the use of CT and MR imaging should serve to substantiate the argument of this paper, which proposes that these techniques have vast and as yet unused potential for investigations of the brain and behaviour, with regard to function and structure. Neuroimaging can improve the accuracy and validity of research and it can only serve to widen the vision of future scientific investigations.