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Understanding Dolphin Intelligence Using Theories in Cognitive Neuroscience

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Abstract: *Bottlenose dolphins are widely accepted as intelligent creatures, so what about their brain and behavior contribute to their intelligence? Throughout evolutionary history, bottlenose dolphins have evolved and developed a large brain-size-to-body size ratio comparable to that of humans. Furthermore, they have particularly large cerebellums—which govern complex motor behavior—a fact that makes sense due to dolphins' complex skills such as echolocation and diving. To better understand dolphin intelligence, this paper will explore two different cognitive neuroscience theories, Jerison's Encephalization Quotient Hypothesis, and Dunbar's Social Brian Hypothesis. Furthermore, this paper will discuss how bottlenose dolphins both affirm and undermine these two theories from both a neuro-physiological and behavioral standpoint.*

Keywords*: Bottlenose Dolphins, Dolphin Intelligence, Dolphin Neocortex, Encephalization Quotient (EQ), Social Brian Hypothesis, Signature Whistles.*

I. INTRODUCTION

1.1 Background and Objectives

According to Jerison's Encephalization Quotient Hypothesis, the bottlenose dolphin's high Encephalization Quotient (EQ) should reflect an elevated intelligence. On the other hand, according to Dunbar's "Social Brain Hypothesis", intelligence and neocortex size correlates to the size and complexity of social groups. Bottlenose dolphins live in complex societies characterized by alliances and relationships that produced a need for higher cognitive processing demands. For bottlenose dolphins, there are aspects that both affirm and undermine both hypotheses. For instance, the Encephalization Quotient Hypothesis suggests that high encephalization suggests intelligence, however, the bottlenose dolphin's cortical expansion directly correlates more with their motor and processing skills instead of their intelligence. Similarly, while dolphins affirm the Social Brain hypothesis by exhibiting intelligent behaviors in a complex society, their neocortex physiology is inconsistent with the hypothesis. This paper will examine the truths and shortcomings of both hypotheses as well as discuss how dolphin intelligence can be demonstrated by their complex social behaviors.

1.2 Significance of the Study

Understanding the advantages and limitations of cogitative neuroscience theories like the Encephalization Quotient (EQ) and Social Brain Hypothesis can allow animal researchers to formulate more accurate models and predictors of animal intelligence. This knowledge can be used to design better experiments, interpret results more accurately, and make more informed conclusions about animal cognition. Knowing the advantages and limitations of animal cognitive neuroscience theories can also improve communication and collaboration between researchers working in different fields. By recognizing the strengths and weaknesses of different approaches, researchers can work together more effectively to advance the field of animal cognition.

Regarding a wider application, an understanding of the neuroscience of animals can be helpful for humans in several ways, such as improving our understanding of human brain function. Intelligent mammals like dolphins share many similarities with humans in terms of brain structure and function. By studying the brains of animals, we can gain valuable insights into the workings of the human brain. The neuroscience of different animal species can also elucidate the evolution of brain structure and function, and how different behaviors and cognitive abilities have evolved over time. Additionally, a specific understanding of dolphin cognitive neuroscience can help advance animal welfare: by understanding the cognitive neuroscience of dolphins, humans can gain a better understanding of their cognitive abilities, emotions, and behaviors. This can help develop more humane and effective methods for caring for and interacting with dolphins both in the wild and in animal theme parks.

Overall, understanding the advantages and limitations of animal cognitive neuroscience theories is crucial for advancing scientific knowledge, improving collaboration between researchers, promoting animal welfare, and informing ethical considerations.

II. ANIMAL INTELLIGENCE THEORIES

2.1 Encephalization Quotient Hypothesis

Is dolphin intelligence solely explained by brain expansion? According to Jerison's Encephalization Quotient Hypothesis, relative brain size correlates with a high intellectual capacity. Encephalization Quotient (EQ) is the ratio between actual brain mass and predicted brain mass for an animal of a given size, and the higher the ratio signifies higher intelligence. According to Marino (2007), bottlenose dolphins are highly emphasized mammals with an Encephalization Quotient (EQ) of 4.2, which is quantitatively closer to the human EQ of 7.0 than other that of many other animals (Fig.1). Their large brain size can originate from overall brain size or overgrowth of one particular area, such as the cerebellum. Hanson (2013) examined the brains of two bottlenose dolphins and found that the two largest cerebellar lobules, VIIb and IX, accounted for 20.1%/14.5% and 40.3%/40.5% of the cerebellar hemispheres (Fig. 2). In humans, these respective lobules only account for 8.6%, and 7.2% of the hemispheres (Fig. 3). In other species, these lobules have been linked to auditory function, and these lobule sizes in the dolphin are consistent with complex auditory skills in echolocation and whistling. However, even though Jerison suggests that high encephalization suggests intelligence, the bottlenose dolphin's cortical expansion directly correlates more with their motor and processing skills than their intelligence.

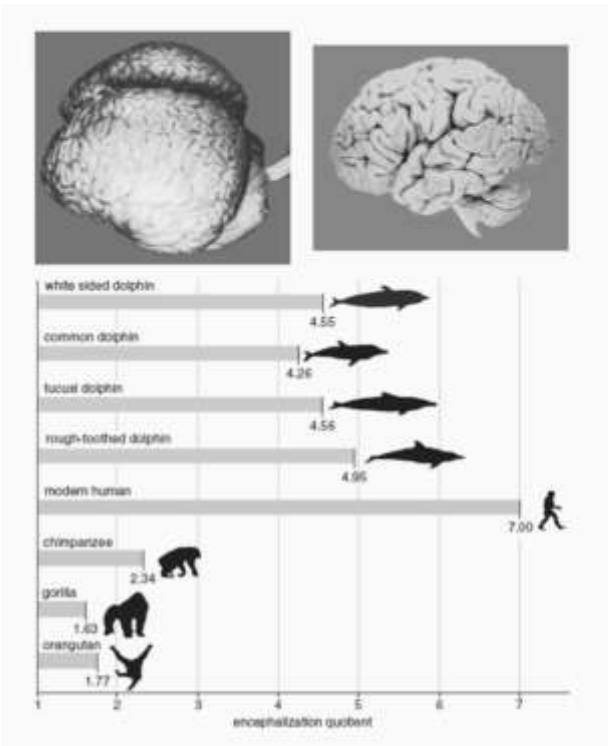

Figure 1. *Encephalization quotient of dolphins compared to other mammals*

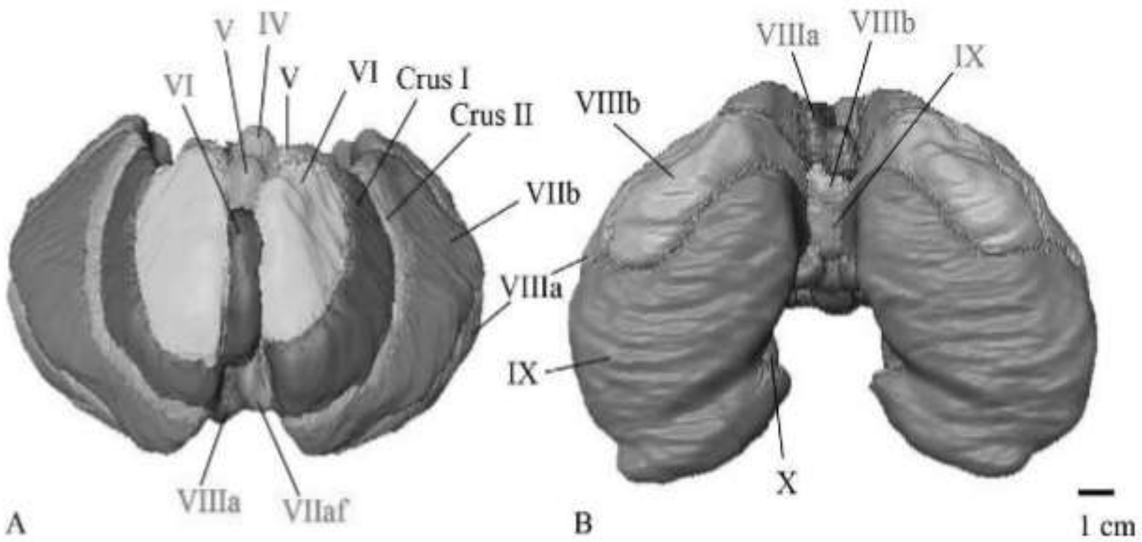

Figure 2. *Bottlenose dolphin cerebellum: reconstruction of Ventral (A) and dorsal (B) aspects; hemispheric lobules are labeled in black, while vermal lobules are labeled in light gray.*

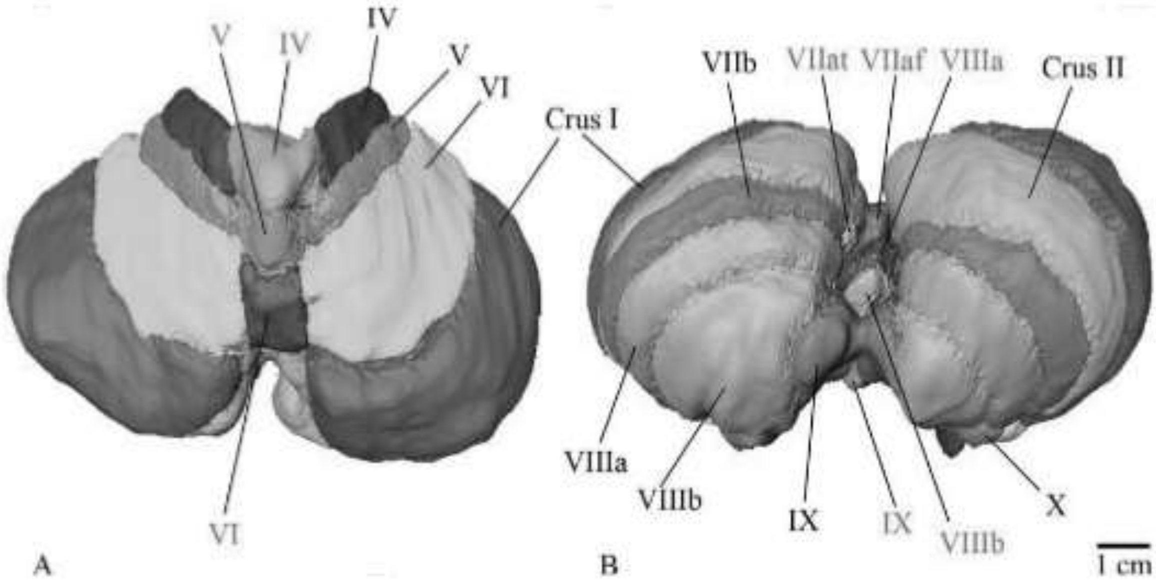

Figure 3. *Human cerebellum: reconstruction of Ventral (A) and dorsal (B) aspects; hemispheric lobules are labeled in black, while vermal lobules are labeled in light gray. Lobule 1X and IIb are significantly smaller in human cerebellum*

2.2 Social Brain Hypothesis

Dunbar claims that a large brain size, or more specifically, a large neocortex size, reflects a greater number of social relationships, an increase in information-processing demands, and ultimately greater intelligence. However, even though the dolphin's relative brain size is large, its neocortex is not. Huggenberger (2008) shows that the dolphin's neocortex is relatively thin, with a low neuron density and granulation that contradicts Dunbar's claim. Nevertheless, the dolphin neocortex still exhibits a high gyrification, high synaptic density, and a high absolute number of synapses similar to that in humans which is worthy of consideration (Huggenberger, 2008).

Thus, why does the bottlenose dolphin, known to be very intelligent, not display a complex neocortex? What does it even mean for a neocortex to be complex? Not much is understood about how the neocortex structure relates to intelligence since it is very difficult to obtain brain samples from dolphins, and most dolphin brain samples used in papers are obtained from dolphins deceased due to unnatural causes. Furthermore, there is a paucity of research demonstrating the correlation between neocortex size and intelligence and more evidence is needed to support brain size's effect on complex motor behavior. Therefore, is Dunbar necessarily incorrect about his Social Hypothesis? While there is more research on the neocortex and intelligence required, there is, however, research regarding complex societal relationships and intelligent behavior in bottlenose dolphins that supports Dunbar.

Dunbar's Social Brain hypothesis argues that when the size and complexity of a social group increase, the number of different relationships in the group may increase, and thus more intelligence on behalf of the animal is required to navigate this complexity. Connor, (2007) researched group complexity and cognitive intelligence by observing bottlenose dolphins in Shark Bay, Australia. The author observed a large and complex society with over 600 dolphins in their 200 km-squared study area as well as a classic fission-fusion structure—a society in which individuals associate in small groups that frequently change the composition. The fission-fusion grouping pattern is very complicated and thus poses significant cognitive challenges. Social relationships are very dynamic and constantly changing and there is uncertainty in the knowledge of third-party relationships even with known individuals due to constant changes. Thus, bottlenose dolphins exist in a very complex group structure that requires them to possess a very intelligent brain. However, is Dunbar's Social Brain Hypothesis, namely that animals with larger neocortexes are more intelligent, sufficient? Dolphins exhibit many forms of social intelligence as demonstrated by behaviors that will be mentioned in the next section.

III. DOLPHIN SOCIAL INTELLIGENCE

3.1 Alliance Relationships

Intragroup and intergroup relationships exist when males form distinct levels of alliance within their social network. The first level alliance is the formation and maintenance of relationships with female consorts, which usually involve two or three males and one female. The second level alliance or a "super-alliance" is the cooperation between first-order alliances in either taking or defending attempts to take females from alliances, and the size of the second level is from 4-14 or more males. Together, members of this "super alliance" helped each other find females to herd and mate with, and they help steal females from other dolphins as well as defend against any "theft" attempts from rivals.

Furthermore, there is even evidence of a third level of alliance formation because some second-order alliances associate regularly and amicably with other groups. According to Connor (2001), males in super alliances can participate in 5 to 11 different alliances and with 5 to 11 different alliance partners in the super alliance. One dolphin individual can be a member of multiple alliances as well as go through many alliance partners. Another complexity in dolphin group alliances is the fact that most involve triadic interactions or a trio of individuals. Triadic interactions may further complicate relationships since any two members within the triad try to compete for the third member. Therefore, the bottlenose dolphin society is very complex since there are many social relationships within each super-alliance embedded in a larger society.

3.2 Synchrony

To affirm and maintain these complex alliances and relationships, dolphins utilize a variety of "intelligent behaviors" such as synchrony as a form of communication. Synchrony is the phenomenon when two or sometimes three dolphins execute a synchronized movement such as surfacing alongside each other, which they do less than a meter apart. According to Connor (2007), frame–by frame video analysis shows that males broke the surface of the water within 80-120 milliseconds of each other during synchrony. Dolphin synchrony behavior can involve multiple individuals synchronizing their swimming moves and postures, as well as their vocalizations. Because there are various levels of relationships in the dolphin society and lots of uncertainty with alliance relationships, synchrony is advantageous because it gives a strong alliance signal. For example, a male dolphin can test who his allies are by using synchrony as well as observing synchrony in other allied dolphins. When Connor (2007) observed males in stable first-order alliances and second-order alliances, he found that synchrony was more common between first-order alliance partners when two first-order alliances were together. Behaviors of synchrony are commonly intertwined with alliance relationships, as male dolphins often use it during competition as well as coordinate with other males to get access to female dolphins.

Not only does synchrony serve as a clear alliance signal between members of a stable alliance, but it can also serve to reduce tension when members of alliances do it with members of different alliances. Specifically, synchrony can be used to create a more friendly atmosphere between different dolphin alliances. Connor (2007) also observed how inter-alliance synchrony was more common in a "competitive context", perhaps to reduce animosity such as when the males were engaged in excited socialization in the form of "clashing, mounting, and splashing with a female consort". While one can argue that synchrony is merely a motor and visual skill, synchrony is ultimately still an intelligent behavior since it relies heavily on social context and not just on the strength of an association. Synchrony not only gives knowledge for alliance relationships between dolphin individuals, but it is also dependent on social circumstances and context. Thus, for bottlenose dolphins, synchrony is an intelligent behavior that communicates a clear alliance signal and is contextualized by social cues, and it likely involves more complex neural activation processes than that of just the neocortex, which Dunbar's Social Brain Hypothesis postulates.

3.3 Vocalizations and Signature Whistles

Like synchrony, vocalizations can also affirm and maintain alliance status. Dolphins can generate a wide range of whistles, clicks, and pulses to communicate with each other. Furthermore, they even have a "signature whistle" that conveys identity. Thus, similar to humans, bottlenose dolphins may have the ability to address each other by name and for dolphins to communicate with other dolphins in their absence. Furthermore, allied males have similar whistle-sharing, which points to the idea that whistle-sharing can communicate information about alliance status. When two bottlenose dolphins produce the same whistle type, this reflects their affiliative social relationships.

To understand how and why bottlenose dolphins utilize these vocalizations and signature whistles, Janik & Slater (1998) investigated whether signature whistles were only used in contexts that required maintenance of group cohesion. Individual bottlenose dolphins were recorded while they were both in a group setting in the same pool and when they were separate from the group. The authors found that when it was alone, each dolphin primarily produced one stereotyped signature whistle (Fig. 4.) Likewise, the remaining group in the other pool also mainly used their signature whistles if only one other dolphin was in a separate pool. Each dolphin primarily produced one stereotyped signature whistle when it was separated from the group. However, when all the dolphins were in the same pool, they usually used non-signature whistles. Signature whistle copying was rare and did not initiate reunions or specific vocal responses. Thus, there is strong evidence for context-dependent signature whistle imitation when bottlenose dolphins address each other "by the name", and that signature whistles are used to maintain group cohesion.

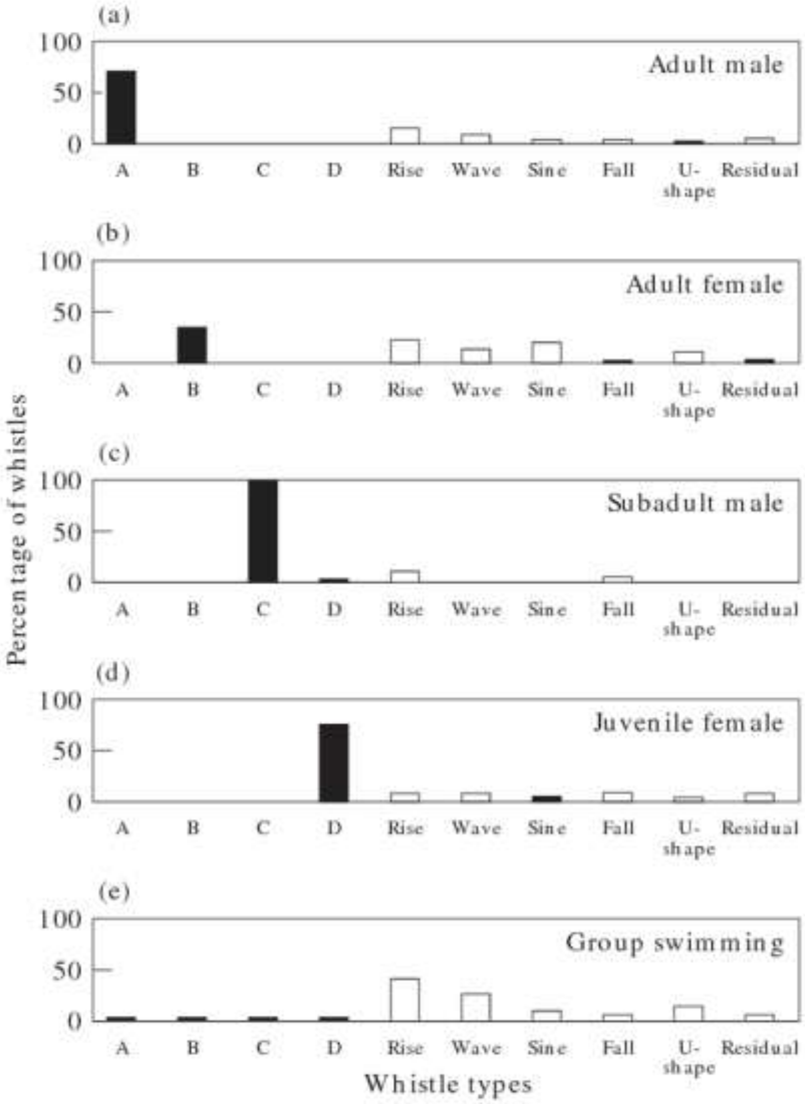

Figure 4. *Whistle type usage in different contexts: (a) adult male in a separate pool; (b) adult female in a separate pool; (c) subadult male in a separate pool; (d) juvenile female in a separate pool; (e) all animals together in one pool.*

3.4 Pectoral Fin Contact

In addition to affirming alliances via signature whistling, dolphins are also able to communicate their affection with each other when their vocalizations are paired with pectoral fin contact. Bottlenose dolphins have pectoral fins, which are used for steering and movement; they are located on each side (Fig. 5.) When dolphins use their pectoral fins to touch those of other dolphins, this method can enhance the communicated message of preference or disinterest between a pair of dolphins. Evans-Wilent & Dudzinski (2013) researched types of vocalizations (whistles and click trains) with pectoral fin contact in bottlenose dolphins. The authors noted that the vocalizations significantly differed by the vocalizer's role as the initiator or receiver and by sex. They found that both males and the receivers of pectoral fin contact clicked and used overlap vocalizations more often. The type of vocalization was based on the relationship between two dolphins. Whistles were used more to initiate pectoral fin contact or to show partner preference, while click trains were mainly vocalized to reflect disinterest in pectoral fin contact or to signal the end of contact.

As such, the vocalizations changed based on the social context between the two dolphins, whether the dolphins wanted to affirm or disaffirm interest in each other. Thus, vocalization with pectoral fin contact reflects a high cognitive capacity and an understanding of social cues between bottlenose dolphins. Ultimately, with their wide repertoire of vocalization sounds, signature-whistling, and paired pectoral fin contact, the complexity of dolphin social relationships in Shark Bay is matched by complexity in social communication.

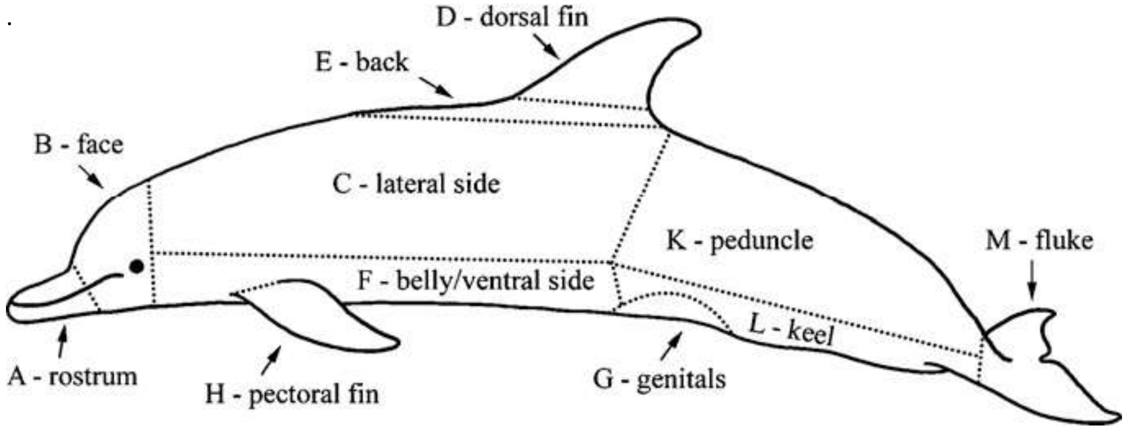

Figure 5. *Body parts of a bottlenose dolphin*

IV. ANALYSIS OF JERISON AND DUNBAR'S HYPOTHESES

Both synchrony and vocalization are examples of dolphin intelligence since both behaviors rely on social context. Furthermore, synchrony and whistling involve advanced sensory processing abilities in the motor, visual, or auditory area and thus high cerebellar usage. The large cerebellum lobule size, which correlates with auditory and other sensory processions as stated earlier in this paper, is directly correlated with these intelligent behaviors.

These intelligent behaviors due to a large number of social relationships can explain the large expansion of the cerebellum instead of simply stating Jerison's hypothesis that a large relative brain size (EQ) directly points to intelligence. We know that Dunbar is correct when he says that intelligence is correlated to large brain sizes, not because large brains mean high intelligence, but because intelligent behaviors require more use and therefore expansion of higher cognitive processing areas.

On the other hand, there are other aspects of Dunbar's Social Hypothesis that are both consistent and inconsistent with scientific research. Evidence that the complexity of a fission-fusion society led to socially cued behaviors in bottlenose dolphins is consistent with Dunbar's Social Hypothesis. However, there are aspects of the dolphin neocortex such as its small size that led us to ultimately reject the Social Brain Hypothesis.

V. CONCLUSION

In conclusion, there are accuracies as well as deficiencies in both Jerison's Encephalization Quotient (EQ) Hypothesis and Dunbar's Social Hypothesis, as analyzed in the abovementioned section. As discussed, Dunbar's Social Brain Hypothesis does not directly translate to what is observed in both the neocortex and social behaviors of bottlenose dolphins. Thus, there is a wide potential to conduct further experiments in exploring Dunbar's Social Hypothesis and dolphin intelligence. For example, we can examine the neocortex and behaviors of a less complex dolphin society and compare it to the fission-fusion society of bottlenose dolphins. We can also derive a test to compare intelligence between bottlenose dolphins and other animal species. This may prove to be challenging since land and water animals face different challenges and it may be difficult to come up with a universal intelligence test.

Furthermore, there are remaining questions about the internal neurological and physiological differences in both the dolphin neocortex and brain and further research can be conducted to see what specific parts of the brain are associated with intelligence and not just with motor and sensory skills. Ultimately, there is a lot of potential to uncover a better understanding of not only dolphin intelligence, but also a standard measure of intelligence in all animals. Dolphins are known for their high level of intelligence, social complexity, and adaptability. By measuring their intelligence, we can gain a better understanding of the cognitive abilities of non-human animals and how they compare to humans.

Additionally, there are many different applications for understanding dolphin cognitive intelligence. For instance, dolphins are facing a variety of threats, including habitat loss, pollution, and human disturbance. By studying their intelligence, we can better understand how they perceive and respond to these threats and develop more effective conservation strategies to protect them. Measuring dolphin intelligence can also help us better understand their mental and emotional states, which is important for ensuring their welfare in captivity and the wild. For example, if we know that dolphins have a high level of cognitive complexity and social intelligence, we can ensure that their captive environments provide appropriate social and cognitive stimulation. Lastly, a lot of technological advancements can be made by understanding dolphin cognitive abilities. Studying dolphin intelligence can also inspire the development of new technologies, such as underwater robots, that mimic the abilities of these intelligent animals.

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