Gyrification and sulci are for protecting brain from threat of head impact

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Gyrification is often presumed to be about brain functions. However, gyrification hinders brain functions that are advantageous to brain. For example, when a head impact occurs, the head will be forced to accelerate. Acceleration can cause damage to brain [17]. Fortunately, sulci can mitigate the damage.

II. SULCI AND ACCELERATION

When a head impact occurs, the head will be forced to accelerate. Acceleration can cause damage to brain [17]. Fortunately, sulci can mitigate the damage.

Sulci are filled with cerebrospinal fluid (CSF), whose density is 1.00 [18]. For brain tissue, the density is 1.05 [19]. Different matters of different densities react differently when an acceleration is applied, giving rise to the effect that manifests in centrifugation and sedimentation. The effect is both advantageous and disadvantageous.

On the one hand, the density difference can cause an unusual effect that manifests in centrifugation and sedimentation. Fortunately, sulci can mitigate the damage.

I. INTRODUCTION

Most animals, especially large mammals, have a gyrencephalic brain characterized by cortical folds: grooves known as sulci penetrate brain tissue, creating folds known as gyri. It is intriguing to find out the reason for gyrification. Large mammals also tend to have high intelligence. Thus, the widely accepted presumption is that gyrification is for increasing intelligence [1]. However, the presumption is not grounded on solid evidence.

It is attempting to think that increasing cortical surface area would increase the number of neurons. For this thinking to be validated, however, the cortical thickness must be either constant or increased, which has not been observed. For example, ungulates have highly gyrencephalic brains, but thin cortex [2].

One model assumes that cortex is made of radial units [3], and increasing the cortical surface would increase the number of radial units. Even if radial units exist, however, they can be extended in the radial direction [4, 5], just like the cortical thickness can be increased in the radial direction. Besides, three-dimensional circuitry is more efficient than two-dimensional circuitry, even if the latter can be folded to let some distant parts be in touch.

The presumed link between gyrification and intelligence is questionable itself. After all, primates are more intelligent but have a less gyrencephalic brain than ungulates [2].

One hypothesis assumes that the presence of cortical folding is a result of the cranial constraint (although the hypothesis has been refuted by experiments [6]). Indeed, no matter serving what purpose, cortical folding needs to be addressed from the perspective of mechanism [7, 8], such as how it develops [9] and what the forces behind [10–12].

Yet, how cortical folding takes place and what purpose it serves are two separate questions, especially when there is a wide variety of gyrification patterns. Grey seal [13] and manatee [14] have similar-sized brains but different gyrification patterns. Different species have different priorities.

Life has a choice over gyrification pattern to serve a purpose. If that purpose is not about intelligence, it must be about safety. Brain needs protection. The most common danger is head impact, which can cause traumatic brain injury (TBI) [15]. One simulation (finite element simulation) suggests that gyrification can act as a damping system to reduce mechanical damage [16]. This kind of protection may be the reason why gyrification should exist in the first place.

We propose in this study that the purpose of gyrification is to create sulci whose presence can protect brain from head impact. We also suggest that sulci hinder neural connections. Having sulci is both advantageous and disadvantageous. Different species have different priorities, resulting in different cortical folding patterns.
FIG. 1. Schematic of sulcus protecting gyrus against acceleration. (a) A piece of brain tissue. It is a part of a single gyrus surrounded by CSF on two sides. (b) Acceleration. When a head impact occurs, a force, via other parts of the brain, acts upon the brain piece, resulting in an acceleration $a$. (c) A different scenario. A sulcus is introduced; a second gyrus splits off from the first gyrus. The sulcus is filled with CSF. (d) Protection. The remaining first gyrus has the same acceleration as before, but the second gyrus has a smaller acceleration, $a' < a$, due to CSF being squeezed out from the sulcus.

FIG. 2. Schematic of sulci protecting the brain against acoustic wave. A head impact generates an acoustic wave pulse traveling through the brain. The brain has sulci filled with CSF. The boundary between brain tissue and CSF causes the wave pulse to reflect and refract, reducing the wave energy. The wave becomes less harmful every time it passes an interface.

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2. When the pulse hits the boundary of a gyrus, it generates a reflected pressure wave, a transmitted pressure wave, a transmitted shear wave (transverse wave, S wave), and some surface waves (e.g., Rayleigh wave and Love wave) that propagate along the boundary.

3. The transmitted pressure wave and the transmitted shear wave travel through the gyrus. The former travels faster than the latter, and therefore, they separate. When they hit the boundary on the other side of the gyrus, each gives rise to a reflected pressure wave, a reflected shear wave, a transmitted pressure wave, and some surface waves.

4. The two transmitted pressure waves travel through CSF toward the next gyrus.

III. SULCI AND ACOUSTIC WAVES

Acoustic waves can be harmful too; they cause brain tissue to oscillate, causing brain damage. When the intensity of a wave exceeds the limit of the strength of brain tissue, brain tissue may rupture. When a head impact occurs, an acoustic wave pulse is generated from the skull, traveling through the brain. The pulse passes a series of gyri separated by sulci (or fissures). CSF has different acoustic properties than brain tissue or the covering membrane. Therefore, the pulse is partly reflected every time it hits the boundary. On the one hand, the reflected wave may interfere with the incoming wave, resulting in a more damaging wave at some locations. On the other hand, the reflection reduces the energy of the incoming wave so that the transmitted wave is less harmful. All considered, the reflection should be beneficial.

The brain tissue is covered by a thin membrane called pia mater. Let us focus on the boundary between CSF and pia mater and omit the boundary between pia mater and the brain tissue. Similarly, we omit other boundaries and details. The brain tissue is protected against acoustic waves. Again, sulci can protect the brain against acoustic waves.
The acoustic wave coming from CSF is a pressure wave because CSF is liquid. When the wave hits the boundary between CSF and pia mater, it generates a reflected pressure wave, a transmitted pressure wave, a transmitted shear wave, and some surface waves propagating along the boundary. When the two transmitted waves hit the boundary on the other side of the gyrus, each splits again. Similar processes also occur on other boundaries.

The pulse loses some energy every time it hits an interface and becomes less harmful. Without sulci, the pulse would travel farther because the ability of brain tissue to absorb the wave energy is limited. The greater the distance a pulse travels, the more likely it causes damage.

Fig. 2 shows only one acoustic wave path from the head impact. In fact, the generated wave travels in every direction. In addition, the impact generates surface waves (e.g., Lamb wave) that propagate along the skull, and the surface waves generate pressure waves travelling inward.

Altogether, we propose the following:

1. Sulci can protect the brain from head impact; animals living under severe threat of head impact need a high level of gyrification.

2. Sulci should be distributed perpendicular to every direction so that the brain is protected in every direction. Yet, some directions may face more significant threats than others, resulting in different sulci distributions in different directions.

Sulci are especially beneficial to those animals that fight using head ramming, such as ibex and orca. Their brains are highly gyrencephalic.

IV. GYRIFICATION INDEX

Gyrification is often quantified by the gyrification index (GI) \[ \text{GI} = \frac{S_c}{S_e} \] where \( S_c \) is the total outer cortical surface, and \( S_e \) is the superficially exposed part of the outer surface. Sometimes, people use different notations or even slightly different definitions.

For a given brain size across species of large brains, the more severe the threat of head impact, the denser the distribution of sulci and, therefore, the higher the gyrification index [Fig. 4]. Head impact threat is associated with animals’ lifestyles. Animals in the same order or family often share similar lifestyles and, therefore, similar gyrification patterns. Ungulates tend to have a more gyrencephalic brain compared to primates or carnivores [2]. This is because ungulates tend to fight using head ramming, whereas primates and carnivores tend to fight using limbs and teeth. Similarly, cetaceans have a more gyrencephalic brain than sirenians [36]. Unlike sirenians who live quietly in shallow water, cetaceans live in deep water where head ramming is a common way to hunt or be hunted. To be exact, gyrification patterns should be species-specific. Species Orcinus Orca uses head ramming on a daily basis and hence needs a more gyrencephalic brain than other cetacean species [37].

Different species often have different brain sizes [38]. Fig. 5 depicts a small brain and a big brain; the size of the small brain is comparable to a single gyrus of the big brain. Different brains share the same brain tissue. A wave pulse traveling through the small brain is also reflected on the boundary between CSF and brain tissue. In addition, the wave is also reflected on the skull, losing some energy there. If we omit the beneficial energy losing aspect of skull reflection, the pulse transiting the whole small brain is analogous to a similar pulse transiting a single gyrus of the big brain. The two pulses lose their energies at the same rate, travelling the same distance and causing possible damage with the same prob-

![FIG. 3. Schematic of an acoustic wave passing through a gyrus. The acoustic wave coming from CSF is a pressure wave because CSF is liquid. When the wave hits the boundary between CSF and pia mater, it generates a reflected pressure wave, a transmitted pressure wave, a transmitted shear wave, and some surface waves propagating along the boundary. When the two transmitted waves hit the boundary on the other side of the gyrus, each splits again. Similar processes also occur on other boundaries.](image)

![FIG. 4. Schematic of gyrification index (GI) of gyrencephalic brain. GI is largely proportional to brain size and threat level of head impact. Gyral size is dictated by the level of threat of head impact, regardless of brain size. Severe threat of head impact demands narrow gyral size, resulting in high GI. When the level of threat of head impact is given, the gyral size is determined; then, a bigger brain will have more gyri, giving rise to a higher GI.](image)
ability. In other words, the two brains are protected on the same level. We may further deduce that gyral size determines the level of brain protection, regardless of the brain size. (The gyral size can be defined as the average distance between two adjacent sulci along a random straight line [Fig. 2].)

The threat level of head impact dictates the theoretical gyral size. When the gyral size is smaller than the brain, the brain is gyrencephalic; when the theoretical gyral size is bigger than the brain, the brain is lissencephalic. Thus, small brains tend to be lissencephalic. (In addition, small brains often belong to small-sized animals which do not fight using head ramming and do not suffer as much when they fall on their heads.)

For a gyrencephalic brain of a given gyral size, if we take gyri as building blocks, the surface area of all the blocks is a linear function of the volume of all the blocks, from which we may deduce that the cortical surface is proportional to the cortical volume,

$$S_c \propto V,$$

where $V$ represents cortical volume. Given that $S_c \propto V^{2/3}$, we get

$$GI \propto V^{1/3},$$

which means that gyrification index is proportional to brain size [Fig. 4] [2].

The bases of gyri are connected, and the connections reduce the surface area. Although Eq. (2) captures the main characteristic, the exact relationship should be

$$S_c \propto V^\beta,$$

where $\beta$ slightly deviates from 1. Observations show that $\beta \approx 0.9$ [41–43]. This is a reflection of the complexity of the connections between gyri; the connections become exponentially complex as the brain size increases. (For lissencephalic brains, on the other hand, $\beta \approx 2/3$ [43].)

V. DISADVANTAGE OF HAVING SULCI

Having sulci must have some drawbacks; otherwise, all species would have a high level of gyrification to gain maximum protection. We propose that the main drawback is that sulci decrease the efficiency of neural connections, as depicted in Fig. 6(a). Neurons separated in different gyri have to connect to each other by taking a detour; some connections that are otherwise possible have to be given up.

When a species is not in desperate need of protection, e.g., humans, they can choose a moderate gyrification so that neural connections would not be hindered as much. When a species is free of the threat of head impact, sulci should be eliminated, as illustrated in Fig. 6(b). (This gives rise to shortcuts for existing neural connections, saving room for establishing more neural connections.) One example is manatees [44]. Manatees have a lissencephalic brain, while their close relatives, elephants [45], have a gyrencephalic brain. Manatees and elephants evolved from the same ancestor, which is supposed to have a gyrencephalic brain. After the divergence, manatees moved to live in shallow water and gained an aquatic lifestyle. Manatees are quiet animals, passing the day by sleeping and grazing [46]. When feeling threatened, they flight instead of fight. Their brain sulci disappeared during evolution [47], leaving only some residue. As a result, the cortical thickness can be increased. The cortical thickness for manatees is 4mm [14]. For humans, the average thickness is 3.4 mm; for most other animals, the thickness is less than 2mm [48].

North American beavers also have a big lissencephalic brain [49]. This is because they live a safe lifestyle too. They care about their safety so much that they build dams to create ponds. (When they have to fight,
they use teeth instead of head ramming.) Their counterparts, capybaras [38] and otters [50], however, have gyrencephalic brains. Capybaras live on land most of the time and often face dangers. Otters live in open waters and are combative.

VI. CONCLUSION

Two determinants contribute to the wide variety of cortical folding patterns—brain safety and brain functions. Cortical folding protects the brain against head impact but, at the same time, hinders neural connections. While the demand for the efficiency of neural connection is universal across species, the need for brain protection varies. Some species live a quiet life; others fight. Different fighting styles pose different levels of threat of brain injury and therefore demand different levels of brain protection. Sulci provide protection; the level of protection is inversely proportional to gyral size.

Severe threat of head impact gives rise to small gyral size; examples include orca, bottlenose dolphin [51, 52] and mouffon [5]. Intermediate level of threat gives rise to intermediate gyral size; examples include capybara, humpback whale [53], elephant [54], chimpanzee and human [5]. Low threat gives rise to large gyral size, e.g., bowhead whale [59], which lives in the Arctic and subtropical waters where they can use sea ice to escape from the only predator orca [56]. When the brain size is smaller than the theoretical gyral size dictated by the level of threat of head impact, the brain becomes lissencephalic; examples include beaver and mouse [57]. When the brain size is comparable to the theoretical gyral size, the brain has few shallow sulci (or sulci residue) and is stuck between being lissencephalic and being gyrencephalic; examples include guinea pig [58], common marmoset [59, 60], manatee and dugong [61].

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