Brain Lateralization and Cognitive Capacity

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One way to increase cognitive capacity is to avoid duplication of functions on the left and right sides of the brain. There is a convincing body of evidence showing that such asymmetry, or lateralization, occurs in a wide range of both vertebrate and invertebrate species. Each hemisphere of the brain can attend to different types of stimuli or to different aspects of the same stimulus and each hemisphere analyses information using different neural processes. A brain can engage in more than one task at the same time, as in monitoring for predators (right hemisphere) while searching for food (left hemisphere). Increased cognitive capacity is achieved if individuals are lateralized in one direction or the other. The advantages and disadvantages of individual lateralization are discussed. Directional, or population-level, lateralization, which occurs when most individuals in a species have the same direction of lateralization, provides no additional increase in cognitive capacity compared to individual lateralization although directional lateralization is advantageous in social interactions. Strength of lateralization is considered, including the disadvantage of being very strongly lateralized. The role of brain commissures is also discussed with consideration of cognitive capacity.

Keywords: individual lateralization ; directional lateralization ; cognitive capacity ; parallel processing ; social behaviour ; visual attention ; vertebrates ; invertebrates ; commissures ; strength of lateralization

1. Introduction

The left and right sides of the brain are specialised to attend to different information, to process sensory inputs in different ways and to control different types of motor behaviour. This is referred to as hemispheric specialization or brain lateralization.

Lateralization has now been well-documented across species, ranging from the small brains of insects to early vertebrates, birds and mammals ^[1]. Regardless of the absolute size of the brain, its capacity and efficiency may be increased by not duplicating all functions on the left and right sides. Cognitive capacity can be increased in this way without the biologically more costly process of increasing brain size.

The left hemisphere directs attention to specific categories of stimuli, often learned categories, and controls feeding responses $[\underline{1}][\underline{2}]$. The right hemisphere has broad attention to a wider variety of stimuli and especially to novel stimuli and to predators, as shown in several species $[\underline{3}]$. As first shown in domestic chicks, attack and copulatory behaviour are controlled by the right hemisphere.

Prior to the discovery of laterality in chicks and songbirds, in the 1970s, it had been thought that laterality was unique to the human brain. In chicks, it was discovered by inhibiting protein synthesis in the left or right forebrain hemisphere at critical stages of development and then investigating the longer-term effects on behaviour ^[4]. In songbirds it was discovered by lesioning specific regions of the left or right hemisphere and assessing the effects on song production ^[5].

Later, lateralization was revealed simply by testing animals monocularly ^[6] and this has become a standard method to investigate lateralized behaviour. In species with eyes positioned on the sides of their head, and thus with little overlap of the visual fields, visual information goes from each eye mainly to the contralateral side of the brain. The eye-system of the open (seeing) eye has predominant control of behaviour, and different behaviour is elicited when the left versus the right eye is seeing.

Within a species, the strength of lateralized responses can vary between individuals. Some individuals exhibit strong laterality, while others have weaker laterality or no laterality. However, weak or absent laterality expressed in motor behaviour (e.g., hand or limb preference) may not mean that the brain is itself less lateralized for cognitive processing. It is rather a matter of whether one hemisphere alone controls a particular behaviour, as is the case in strong laterality, or that the other hemisphere is involved to some degree.

Even when both hemispheres participate in the control of behaviour and interhemispheric control occurs, cognitive capacity is increased as long as each hemisphere performs different computations of available information. By contrast, if both hemispheres are processing information in the same way, and hence duplication is occurring, there is no enhancement of cognitive capacity. In short, more lateralization means greater cognitive capacity.

2.Advantage of having a lateralized brain

Brain lateralization should be beneficial when both hemispheres have to be used simultaneously to perform different functions. To test this hypothesis performance of chicks with lateralized visual function was compared to that of chicks without visual lateralization. The chicks were tested on a dual task requiring search for grains against a distracting background of pebbles and, at the same time, they were presented with a silhouette of a predator moving overhead. Chicks with lateralization of visual function performed both aspects of this task better than chicks lacking lateralization [7]. The lateralized chicks learnt to find grain scattered amongst pebbles, whereas the non-lateralized ones were unable to do so, and the lateralized chicks detected the predator sooner than the non-lateralized chicks. Once they had detected the predator, the non-lateralized chicks were more disturbed by it, as shown by distress calling and being less able to ignore it in order to continue pecking for food. The behaviour of chicks without visual lateralization indicated that they became increasingly confused, or disturbed, by the dual task since their ability to find food grains scattered among the pebbles deteriorated as the task continued ^[2]. Hence, the chicks' ability to function well in the dual task was compromised by an inability to separate the required functions into different hemispheres.

Similar results have been found in both fish and a primate species tested on dual

tasks. The fish had to feed on shrimps in the presence of an on-looking predatory fish, and those with stronger lateralization were faster at catching the shrimps than were the fish with no lateralization ^[8].

There are a number of other tests in which lateralized individuals perform better than non-lateralized ones (see [9]).

3. Tasks Performed Better When Lateralization Is Weak or Absent

Since not all individuals within a species have the same strength of brain lateralization, there may be some contexts in which being less lateralized is an advantage. When an animal must attend equally to both sides, it is a disadvantage to be lateralized, as shown in a fish species tested on a task requiring attention to both sides of their body, and hence, requiring the same use of both hemispheres ^[10].

In humans, stronger lateralization provides advantages in some but not all tasks $\frac{[11]}{1}$. This illustrates the important point that lateralization is largely specific for each different function. While it may be advantageous for some functions, it may confer no advantage or even a disadvantage for other functions. As Corballis $\frac{[12]}{1}$ has suggested, there may be a trade-off between symmetry and asymmetry of function, but where the balance point lies depends on the behaviour considered (for research on this issue in humans see $\frac{[13]}{1}$), the species, sex, stress levels and possibly other factors, as well as genetic. Within a population the strength of bias is maintained as an evolutionary stable strategy $\frac{[2]}{[24]}$.

4. Balance between Being Lateralized or Not Lateralized

Overall, across and within species, lateralization is more common than non-lateralization. Using game theory analysis of a predator–prey model, Ghirlanda and Vallortigara ^[15] arrived at the conclusion that most but not all individuals in a group or population are lateralized. As predicted by game theory, and found in studies of animal populations, the proportion of lateralized individuals in a species ranges from 65 to 90% and such biases in populations are stable, meaning the natural selection restores the proportion of left versus right biased individuals whenever there are slight deviations from the species-typical equilibrium point ^[16]. Although there are examples of published data in which the group bias is greater than 90% (e.g., footedness in some species of cockatoo ^{[17][18]}), the sample size tested needs to be considered.

5. Population Versus Individual Lateralization

The increased cognitive capacity of brains that carry out different computational or neural processes on each side could be achieved regardless of the direction of the laterality. Despite this, most examples of lateralization discussed so far in this paper are directional, meaning that the direction of the laterality is the same in the majority of individuals in the group or species. In other words, lateralization is not only present at the individual level but also at the level of the population. There may be ontogenetic reasons for this situation. For example, in the final stages of incubation before hatching, the chick embryo is oriented within the egg so that its right eye is next to the shell and the left eye is occluded by the chick's body. This posture determines the direction of structural differences in developing visual pathways as a consequence of light stimulation of the right eye only ^[19]. Hence, light exposure at this critical stage of development leads to a population bias for asymmetry of visual behaviour ^[20].

Whatever the reason for individuals having the same direction of asymmetry, because it is widespread across species, the advantage that it confers must over-ride any potential disadvantages. Population lateralization to detect and respond more readily to predators on the left seems to be disadvantageous since predators are just as likely to approach on the right or the left, unless the predators themselves have population-level lateralization that predisposes them to approach prey from behind and capture them on the predator's right side. There are examples of such right-side bias in predatory response: the cane toad, for example, strikes at prey once the prey has moved into the toad's right visual field, whereas prey items are ignored when they are in the toad's left visual field ^[21].

If population-level lateralization, also called directional lateralization, does have certain disadvantages, these must be less important than the advantages which it bestows. It seems that the advantage of population-level lateralization must have something to do with social behaviour because it is in social interactions that it is manifested, as discussed next.

6. Social Cognition

The first evidence that directional lateralization is associated with social behaviour came from the study of social hierarchies in groups of chicks with lateralized brains for visual function compared to groups of chicks without this lateralization ^[22]. Quite rapidly, groups of chicks with population-level lateralization established stable social hierarchies, measured by scoring access to a limited food source, whereas those without laterality failed to form stable hierarchies.

Young chicks have a cognitive ability called transitive inference, by which a chick can infer the social rank of another chick by observing it rather than interacting directly with it ^[23]. Using transitive inference, the animal is able to predict its position in the social group and thereby avoid fights ^[24], and they can make such inferences only when they use their left eye. The ability to recognise familiar from unfamiliar conspecifics is a function of the left eye and right hemisphere, as also shown in chicks ^[25] and in fish ^[26]. These examples demonstrate that the right hemisphere is specialised for functions essential to social behaviour.

Specialisation of the right hemisphere to assess and respond in social situations is seen also in mammals. Sheep can recognise faces of other sheep using the right but not the left hemisphere ^[27] and they also respond to the emotional expression of faces using the right hemisphere ^[28]. Moreover, in a wide range of mammalian species, including bats, walruses, whales, dolphins, horses, kangaroos, sheep, deer and bison, maternal animals position their offspring on their left side ^[29], meaning that the maternal animal uses her right hemisphere to monitor her offspring. From these examples it is clear that directional bias is a widespread characteristic of social behaviour.

These and other studies show that population or directional lateralization evolves, or develops, in social interactions and it is, of course, evident in a wider range of behaviour in social species than it is in species that are largely solitary. During evolution, social interaction could have selected for alignment of laterality in most individuals. Could this lead to any increase in cognitive capacity? It has long been hypothesised that social interaction contributes to the evolution of increased brain size and cognitive capacity in primates ^[30]. It is not obvious, however, that aligning the direction of laterality in social animals provides any further increase in cognitive capacity than already gained by having individual lateralization. In fact, it seems that individual-level lateralization almost certainly evolved first and there was selection for it because it enhanced cognitive ability. Then, as sociality evolved, directional lateralization did so along with it, not because it further enhanced cognitive ability but because it conferred an advantage in social interactions.

7. Conclusions

Cognitive capacity is increased when each hemisphere can be used independently, at the same time. Strength of lateralization varies between individuals, as does cognitive capacity. This variation must depend on the task considered and a range of factors play a role, including developmental processes and the selective advantage/disadvantage of having a lateralized brain.

There is a need to investigate a broad range of lateralities within individuals to see what functions are associated in terms of lateralization and what functions are lateralized independently. Furthermore, cognitive capacity related to laterality in sensory modalities other than vision needs to be investigated, as well as potential interaction between laterality in the

different sensory modalities.

Whereas being lateralized confers cognitive advantage to individuals, aligning the direction of lateralization in the majority of individuals of a population, or species, seems unlikely to enhance cognitive capacity to any greater degree than does individual lateralization. Hence, selection for directional (population) lateralization is dependent on social interactions, and not enhancement of cognitive processing. While social behaviour might increase cognitive capacity of species via evolution of increased brain size, as hypothesised by Dunbar ^[30], it does not do so by brain lateralization *per se*.

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