

Review

A Matter of Degree: Strength of Brain Asymmetry and Behaviour

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Abstract: Research on a growing number of vertebrate species has shown that the left and right sides of the brain process information in different ways and that lateralized brain function is expressed in both specific and broad aspects of behaviour. This paper reviews the available evidence relating *strength* of lateralization to behavioural/cognitive performance. It begins by considering the relationship between limb preference and behaviour in humans and primates from the perspectives of direction and strength of lateralization. In birds, eye preference is used as a reflection of brain asymmetry and the strength of this asymmetry is associated with behaviour important for survival (e.g., visual discrimination of food from non-food and performance of two tasks in parallel). The same applies to studies on aquatic species, mainly fish but also tadpoles, in which strength of lateralization has been assessed as eye preferences or turning biases. Overall, the empirical evidence across vertebrate species points to the conclusion that stronger lateralization is advantageous in a wide range of contexts. Brief discussion of interhemispheric communication follows together with discussion of experiments that examined the effects of sectioning pathways connecting the left and right sides of the brain, or of preventing the development of these left-right connections. The conclusion reached is that degree of functional lateralization affects behaviour in quite similar ways across vertebrate species. Although the direction of lateralization is also important, in many situations strength of lateralization matters more. Finally, possible interactions between asymmetry in different sensory modalities is considered.

Keywords: functional asymmetry; strength of lateralization; direction of lateralization; advantages; disadvantages; vertebrate species; limb preference; eye bias

1. Introduction

A number of papers have reviewed the evidence for functional asymmetry of the brain, citing research showing that it is present in a growing list of vertebrate species [1–4], as well as more recent research demonstrating its presence in invertebrate species (summarized in [5]). The ubiquity of functional asymmetry suggests that it confers selective advantages [6], and some evidence in support of this deduction has been found by comparing the performance, within a species, of individuals with strongly versus weakly lateralized brains. By summarizing the research on different species, this paper attempts to arrive at a conclusion about the benefits versus deficits of strong versus weak lateralization.

The first obstacle encountered in an attempt to bring the research together is that different measures of the strength of laterality have been used [7]. Strength of paw or hand preference has been used as the axiom of strength of laterality in humans and other primates, although other techniques are now being used. In birds, strong versus weak or no laterality of visual responses has been generated by incubating eggs in the light or in darkness during the final days before hatching [4,8], and a similar method has been used to manipulate strength of lateralization in fish [9].

Although it is recognized that using different measures of the strength of lateralization could lead to different results, at this juncture it is worth taking a broad perspective to see how these disparate measures of laterality may be related to cognitive performance. The hypothesis considered is that cognitive ability is enhanced by having a strongly lateralized brain. That is, general cognitive performance may be enhanced by having a brain that is largely, if not entirely, subdivided to process information differently on the left and right sides (i.e., with distinctly separate computational processes being carried out in the left and right hemispheres [10,11]).

As summarised previously [3,4], in a range of vertebrate species the left hemisphere is specialized to categorize stimuli (e.g., food from inedible objects, general characteristics shared by all conspecifics versus those of other species), to focus attention and attend to specific targets and cues, to control established/learnt patterns of behaviour under relaxed conditions and to sustain responding by inhibiting fleeing and inhibiting attention to extraneous stimuli. The right hemisphere has broad attention, used to monitor the surrounds for the presence of predators and attend to other distracting stimuli, and also to detect novel stimuli. The right hemisphere also attends to social cues and, as part of that, recognizes faces of conspecifics, controls aggressive and sexual behaviour, as well as fear responses, and assesses multiple properties of stimuli. As an example of the right hemisphere's control of social responding, pigeons display more rapid social reactions to members of the flock on their left side, processed by the right hemisphere [12]. Also, as shown in a wide range of vertebrate species, infants are positioned more commonly on their mother's left side [13], thus being monitored by her right hemisphere. The right hemisphere also comes into play when the animal is under stress, and in these circumstances it has a dominant role in controlling responses [4].

Left-analytic encoding versus right-global encoding has been demonstrated clearly in chicks using tests similar to those designed for testing humans [14]. These subdivisions of function have been determined by testing a range of non-human species, primarily but not exclusively domestic chicks [15], pigeons [16], zebra fish [17], sheep [18] and dogs [19]. Observation of some species in the wild has confirmed that these asymmetries are seen not only in laboratory settings but also in natural habitats; for example, in Australian magpies responding to a predator [20] and in cetaceans feeding with a right side bias [21].

Similar or the same left-right specialisations are present in humans. A body of research has shown ([1], for example) that the majority of humans use the left hemisphere when they perform established or routine patterns of behaviour and, when using this hemisphere, their attention is focused. By contrast, the right hemisphere of humans has a broad attention used in detecting and responding to unexpected stimuli and responding to affective stimuli [22]. The right hemisphere of humans is also used to recognize faces, especially their emotional expressions [23], and to process other aspects of social information. Not surprising therefore, the right hemisphere is specialized for expressing anger and hostility and for processing of speech with emotional prosody [24] and it also has a role in depression (see later).

The question addressed in this paper is: does cognitive performance depend on the *degree* of lateralization of all or any of these respective hemispheric specializations present in vertebrate species?

2. Limb Preference and Performance

Not surprisingly, since each limb is controlled by its contralateral hemisphere [25], a good deal of research on humans has investigated associations between hand preference and cognitive performance. In general, left-handed subjects excel in tasks requiring cognitive functioning and behaviour associated with the right hemisphere, such as visuospatial ability [26,27] and arithmetic ability [28], whereas right-handed subjects excel on tasks associated with the left hemisphere, such as verbal tasks [29]. It is noted, however, that the association between handedness and cerebral asymmetry is not strong and, as Badzakova-Trajkov et al. [30] found, there is no correlation between handedness and spatial attention, measured in a line-bisection task and as memory of faces.

A study by Denny [31] conducted on a very large population of people from various European countries found that left-handers were significantly more likely to have depressive symptoms than were right handers. Non-right handers, meaning either ambidextrous or left-handed (also referred to as mixed handedness), are more prone than right-handers to suffer from a range of conditions, including schizophrenia [32,33], psychosis [34] and post-traumatic stress disorder [35]. Also, as found in a large sample of 11-year-old children [36], ambidextrous handedness is associated with poorer verbal, nonverbal, reading and mathematical skills compared to either left- or right-handers. This finding has been supported by the results of follow-up studies conducted on children of various ages and adolescents [37,38].

Many studies have compared right-handed with non-right-handed subjects and not weak handedness with strong handedness; this may not be the best way to categorise subjects. A study by Tsuang et al. [39] classified subjects into three categories (left-, right- and mixed handedness) and reported that schizotypy is associated with mixed handedness only, thus making the point that classification into right- versus non-right handed groups is not sufficient to reveal significant relationships. One study found heightened anxiety in strongly left- and right-handed people compared to mixed-handers [40]. Another study reported higher incidence of health problems, including heart disease, thyroid disorders, allergies and epilepsy, in individuals with inconsistent handedness, or ambidexterity [41]. Along these lines, research linking handedness to the development of dyslexia is now progressing and dyslexia-candidate genes have been discovered to play a role in the biological mechanisms that establish left-right asymmetry of the body and influence handedness [42]. Nevertheless, as Ocklenburg et al. [43] point out, the ontogenetic relationship of handedness to lateralization of language (and, by extrapolation, dyslexia) is multifactorial and complex.

Some studies have calculated hand preference using several tasks for scoring the hand used and then categorized subjects into consistent versus inconsistent left- or right-preferring. For example, using this method Hardie et al. [44] found that social anxiety was highest in the inconsistent left-hand preferring group. This result exemplifies the need for precise measurement of hand preference as a finer approach in future studies.

Using another measure of laterality, Johnson et al. [45] have reported that weak lateralization of auditory perception is more common in humans with dyslexia. Neuroimaging studies can also reveal lateral asymmetries, as for example hypoactivity in the left extrastriate cortex in dyslexic subjects compared to controls [46]. These are just some examples from the quite extensive body of research on functional lateralization and behaviour in humans. Handedness has commonly been used as the proxy measure of lateralization but more recent studies have used more direct measures of cerebral asymmetry [47,48].

In nonhuman primates, as in humans, strength of hand preference has been used as a proxy measure of strength of brain lateralization. An early report of association between strength of hand preference and performance in chimpanzees was made by McGrew and Marchant [49] and it concerned termite fishing. This behaviour involves tool use: the chimpanzee holds a stick in one hand and inserts it into the termite nest. The termites attack, and they remain clinging to the probe as the chimpanzee withdraws it, thus allowing the chimpanzee to consume them, usually after rubbing them off the stick by running it over their other hand or arm. Chimpanzees with a stronger preference to insert the probe repeatedly using the same hand were more successful in gaining termites to consume than were those with weaker hand preferences. Some chimpanzees preferred to use their right hand and some their left hand but direction of hand preference did not determine success in termite fishing. It was the strength of hand preference that counted.

Even though this review is focused on vertebrate species, it is worth mentioning a study of motor performance in desert locusts showing that locusts with strong limb preferences make fewer errors when they cross a gap than do locusts with weak limb preference [50]. To my knowledge, this is the only study, so far, investigating strength of lateralization and performance in invertebrates.

Strength of hand preference is associated with ability to attend to two tasks simultaneously, as shown in common marmosets [51]. The marmosets had to forage for food and at the same time respond to a model predator. First their hand preferences were determined by scoring the hand used to pick up pieces of food and take them to their mouth, scored 100 times over several days. They were also trained to search for mealworms, a favourite food, presented in blue bowls at different locations within a room furnished with branches at various angles and heights and to avoid green bowls, placed next to the blue bowls and not containing mealworms. Hence, they were trained to use a win-shift strategy. On testing they were released into the room to search for mealworms and, once they had commenced searching, one of three model predators was presented. One predator was a taxidermic specimen of a kestrel moved overhead using a fishing line and a system of pulleys. Another was a model snake pulled across the floor. The third was a wooden carving of two frogs, resembling rearing snakes, also moved across the floor, and chosen because previous research had shown that the marmosets mobbed this stimulus consistently [52]. The stronger the hand preference the shorter was the latency to detect/react to the predator and the negative correlation between latency and strength of hand preference was significant for the test using the kestrel and the test using the frog carving. Marmosets utter phee calls when aroused and tsik calls when they mob a predator, and the number of these calls correlated positively with strength of hand preference. In summary, marmosets with stronger hand preferences, regardless of whether their preference was for the left or right hand, detected the predator sooner and reacted to it more strongly. Since in control trials, in which the predator was presented but the marmosets were not required to search for food, no significant relationship was found between hand preference and latency to detect the predator or number of calls, it can be concluded that strength of laterality has an effect only when the two tasks have to be undertaken simultaneously. Given that marmosets with weaker laterality are less able to perform the two tasks simultaneously, one can predict that they would be more vulnerable to predation in the natural environment.

The above results did not depend on whether the left or right hand was preferred by the marmosets. However, a number of other studies on primates have found behavioural differences between left- and right-hand preferring animals. Left-handed marmosets are generally more fearful than right-handed marmosets: they are less likely to touch novel objects [53], less likely to sample novel foods and react more strongly to calls made by a natural predator [54], and they are more likely to have a negative cognitive bias [55]. Left-handed marmosets are less responsive to social group influences than are right-handed ones [56]. Similar left- versus right-hand differences in behaviour have also been reported for chimpanzees [57] and rhesus macaques [58] and at least one study of humans has shown that left-handed subjects are more cautious in a novel problem-solving task than are right-handed ones [59].

A number of studies have examined relationships between paw preference and general performance [60–64]. One measure of paw preference in dogs involves scoring repeated trials in which the dog holds steady a Kong with one paw while it licks inside it to obtain a favourite food. A study using this measure found that dogs with no significant preference to use one paw over the other expressed more fear on hearing the sounds of thunderstorms than did dogs with either a left- or right-paw preference [60]. Other studies have found that dogs without a significant paw preference are more excitable when exposed to novel stimuli or environments [61] and are less aggressive to strangers [62]. Dogs without a significant paw preference also show shorter latency to obtain food from a novel puzzle-box than do either left- or right-pawed dogs [63]. In contrast, Siniscalchi et al. [64] found no association between paw preference and the reactivity of dogs to hearing thunderstorms although the dogs used their right hemisphere to respond to the sounds.

In conclusion, and despite some reported differences in behaviour between subjects with significant left- and right-forelimb preferences, the above studies show that subjects without a preference, or with a relatively weak preference, to use one hand/paw consistently are more fearful and excitable, less able to perform two tasks simultaneously, less responsive to novel stimuli and less responsive to social group influences.

A recent report on wild elk [65] supports some aspects of this conclusion: viz., elk with weaker forelimb preferences were more reactive to predator-like chases by humans than were those with stronger forelimb preferences (cf. similar findings in dogs). Other results obtained in this study (e.g., elk with stronger limb preferences were more likely to migrate) have not yet been matched by similar studies of group behavior in other species.

3. Strength of Lateralization and Performance in Birds

A strong body of experimental data demonstrates the presence of lateralization of visual processing and behaviour in the avian brain (summarized in [66]). Although the focus of this research has been on lateralization in domestic chicks and pigeons, laterality has been reported for visual behaviour in other avian species (e.g., zebra finches [67]; Australian magpies [20]; parrots [68]) and for production and processing of song (e.g., canaries [69]; and see paper by Kaplan in this special issue).

Lateralization of control of visual behaviour in the avian brain was first reported in 1979 [70], but it was not until some twenty years later that the potential function of the strength of lateralization, which varies between individuals, was examined. The first paper was published by Güntürkün et al. [71] and it reported a significant correlation between strength of lateralization in pigeons and success in discriminating grain from inedible grit. Pigeons were tested in three conditions: left-eye covered, right eye covered and both eyes uncovered. A laterality index for each bird was determined by the comparison of left- versus right-eye performance, the absolute value of which gave the strength of asymmetry. This value was then correlated against binocular performance and it revealed that the stronger the asymmetry, the more successful was the binocular performance (better at avoiding pecking at grit). Since most birds performed better on this task when they used the right eye (and left hemisphere) [72], as found previously to be the case in chicks [70] (also summarized in [66]), on this task the right eye is dominant. The authors suggested that asymmetry of the visual system enhances computational speed of object recognition by confining to one hemisphere the particular processing necessary to categorize grain as separate from grit (actually in the left hemisphere) and preventing conflicting information from the other hemisphere.

Experiments using domestic chicks have tested this hypothesis by manipulating conditions during development in order to produce groups of chicks that are lateralized for a range of visual functions and groups not lateralized for these same functions. The two types of chicks were generated by either exposing the developing embryos to light in the final days before hatching or by keeping them in darkness until after hatching (summarized in [66]). As a consequence of embryos being oriented in the egg so that the right eye is next to the shell and the left eye is next to the body and thus occluded, light exposure during this critical period stimulates only the right eye and causes asymmetrical development of the visual pathways [73]. In the absence of light exposure no such asymmetry develops and this difference persists throughout the first few weeks of life. Hence, it is possible to test the advantages of having (or not having) brain asymmetry for visual processing by comparing light-versus dark-incubated chicks, usually during the first and second week of post-hatching life. Clear differences in performance have been found.

Rogers et al. [74] tested the hypothesis that lateralization would enhance performance when two tasks had to be performed simultaneously, one relying on processing by the left hemisphere and the other on processing by the right hemisphere. One task was to search for grains of food scattered on a floor to which pebbles had been adhered: chicks learn to avoid pecking at pebbles using their right eye and left hemisphere [75]. The other task was to detect, and respond to, a model predator (a silhouette of a hawk) moved over the top of the cage, a function of the left eye and right hemisphere [76]. The light-exposed (lateralized) chicks performed well on both tasks, whereas the non-lateralized, dark-incubated chicks performed poorly on both tasks and their performance deteriorated as the task continued. Not only were they unable to avoid pecking at the pebbles, but also they were slow to detect the model predator and, once they had detected it, they became less and less able to peck at grains of food and avoid pebbles. They became very disturbed. This result was confirmed by Dharmaretnam

and Rogers [77], who additionally found that the dark-incubated chicks made more distress calls during the dual task than did the light-exposed chicks. This was also confirmed more recently by Archer and Mench [78], who found that the effect extends to at least six weeks post-hatching. Since monitoring for predators while searching for food is a common demand in the natural environment, the results of these experiments demonstrate a survival-relevant function of having a lateralized brain.

Chiandetti et al. [79] compared the performance of chicks exposed to light in ovo during the last three days before hatching and chicks incubated in the dark on a task in which grains of food were given to them in small paper cones with either a striped pattern or a checked pattern. The cones were placed along the walls of a rectangular arena, those with one type of pattern to the chick's right side and those with the other pattern on its left side. First the chicks were trained to expect food only in the cones with one of the patterns. Then they were tested either monocularly or binocularly with the cones, now empty, on the opposite sides (position reversed) and the choice made by the chicks was determined to see whether they chose the cones that they expected to contain food using object-specific cues (pattern) or position-specific cues (place). The dark-incubated (not visually lateralized) chicks chose pattern and largely ignored place: they attended to object-specific cues only. The light-exposed (lateralized) chicks chose either pattern or place, meaning that they attended to both possible cues specifying the location of food. Since the left-hemisphere attends to object-specific cues and the right hemisphere to position [80,81], it appears that the light-exposed chicks were able to use both hemispheres, whereas the dark-incubated ones could use only their left hemisphere. In other words, having a lateralized brain permits use of both hemispheres and thereby allows the chick to take into account more of the cues specifying food.

Later Chiandetti and Vallortigara [82] extended this research to show that, whereas light-exposed chicks could discriminate the left from right side, dark incubated chicks could not do so. The former could discriminate between a bowl of food placed in the corner of a cage with a blue wall on the right side from one placed with the blue wall on the left side. Dark-incubated chicks treated both bowls as the same.

In a study of eight species of Australian parrots, Magat and Brown [68] found that strength of laterality was associated with performance on a task requiring discrimination of pebbles from seed and another task requiring the bird to obtain a food reward suspended from its perch on the end of a string. On the pebble-seed discrimination task, individuals with stronger lateralization (measured as eye preference) scored better than individuals with weak lateralization, and performance of those with strong left-eye preference did not differ from those with strong right-eye preference. However, this relationship did not hold for lateralization measured as foot preference, which was contrary to the prediction made from a later paper by the same researchers showing, in 11 out of 16 species of parrot, that eye and foot preferences were correlated [83]. On the string-pulling task, strength of foot, but not eye, preference was associated with performance and, again, direction of foot preference had no significant association with performance. Overall, this study supports the previous research with chicks and pigeons in that performance is better in more strongly lateralized individuals, although it raises an issue about what behaviour is chosen to measure lateralization.

In birds, therefore, the evidence is clear that strength of lateralization is significantly related to performance.

4. Strength of Lateralization and Performance in Aquatic Vertebrates

In studies of species without limbs, laterality can be measured using eye preferences. One method is to determine the eye preferred by the test animal to view its image in a mirror [84]. Using such a measure of laterality and linking this to a test for "boldness", measured in terms of time to emerge from a dark box into an unfamiliar illuminated environment, Brown and Bilbost [85] found that rainbowfish not displaying an eye preference in the mirror test emerged sooner (were more "bold") than fish with significant eye preferences. Since it is currently impossible to say what cognitive abilities underlie this test, one can only speculate that earlier emergence could depend on attention to fewer cues by the

non-lateralized fish and hence the expression of less fear. Other possible explanations for the result were discussed by Brown and Bilbost [85]. For the purpose of this review, it is a question of whether shorter emergence time is advantageous or not, and that would depend on the potential presence of predators. Indeed, it has been shown that strongly lateralized fish respond to predators more rapidly than do non-lateralized fish [86], and exposing fish to higher levels of predation increases the strength of lateralization, irrespective of whether it is to the left or right side [87].

In an experiment designed to replicate that of Rogers et al. [74] but using fish, Dadda and Bisazza [88] tested gathering of prey by weakly versus strongly lateralized fish in the presence of a predator. Similar to the result obtained by testing chicks, the strongly lateralized fish obtained the prey in a shorter time than did the weakly lateralized fish, and they did so by attending to the prey with one eye and the predator with the other eye. Sailfish show a similar advantage of being lateralized, as shown in a recent study [89]. Sailfish attack schools of sardines by slashing with their bill to the left or right side and they have individual side preferences. The study found that prey capture is more successful in fish with strong biases than in those that are weakly biased [89].

Along similar lines, Sovrano et al. [90] found that lateralized fish (assessed by turning preference) displayed superior performance compared to non-lateralized fish on a task requiring them to orient using either geometric or non-geometric spatial cues. Within the lateralized group the direction of lateralization had no effect. Once again, strength but not direction of lateralization has been found to be important.

Lateralized tadpoles (*Lithobates sylvaticus*), determined using a swimming test and scoring clockwise versus anticlockwise rotation, are better at learning to recognize a predator's odour than are non-lateralized ones [91]. In this study, however, there was also a difference within the lateralized group: those with clockwise rotation learnt to recognize the threat associated with a predator's odour, whereas those with anticlockwise rotation were less able to do so. In other words, laterality in one particular direction enhanced predator detection and, in this aspect, these results diverge from the ones discussed immediately above.

Empirical evidence obtained by testing aquatic species indicates that stronger lateralization of the brain has advantages over weaker lateralization but there is some contrary evidence also. Dadda et al. [92] have found that fish (*Girardinus falcatus*) with weaker lateralization (determined from preferred eye used to monitor a predator behind a barrier) perform better than those with stronger lateralization on a task requiring them to enter a tank via a middle door in an array of nine doors: fish with stronger lateralization made more mistakes by swimming through doors to the left or right of the middle door. In addition, when these fish had to choose to join one of two shoals, each seen with a different eye, weakly lateralized fish were more likely to choose the high quality (larger) shoal, whereas strongly lateralized fish choose the shoal seen with the eye dominant for social behaviour regardless of the quality of the shoal.

5. Interhemispheric Communication and Lateralization

Communication between the left and right sides of the brain is essential for a lateralized brain. In humans this is achieved primarily via the large corpus callosum and, in other mammalian species, by a less well-developed corpus callosum. In birds a small anterior commissure connects the hemispheres and the tectal and posterior commissures (TC and PC) connect each side of the midbrain. In addition, the avian brain has a decussation that crosses the midline of the brain to allow left-right sharing of information [93,94]. Known as the supraoptic decussation (SOD), it is comprised of neural projections from the thalamus on one side of the brain to the hyperpallial region of the hemisphere/forebrain on the other side. In the SOD of chicks, more projections cross from left to right than from right to left [93,95]. This structural asymmetry correlates with some functional asymmetries: sectioning the SOD of chicks aged two days post-hatching removes the lateralization of visual search performance normally present in the second week of life [96]. Sham operated control chicks tested monocularly on a search task requiring them to find grain scattered amongst pebbles (for details of

the task see [97]) learn to avoid pecking pebbles when tested with a patch over their left eye but they cannot learn if the patch is on their right eye. This asymmetry is weakened or absent in chicks with a sectioned SOD: in these chicks performance is poor when using either the left or the right eye [83]. Furthermore, chicks tested binocularly after sectioning of the SOD are unable to perform the task, compared to excellent learning in the sham-operated controls. This result demonstrates the importance of thalamofugal visual projections that cross the midline of the brain. In the intact brain, and when both eyes are able to see, these midline-crossing projections enable learning by limiting it to the right eye/left hemisphere system.

Birds have two sets of visual projections: one involving the thalamus and SOD, discussed above, and the other involving the optic tecta and projecting to the entopallial region of the forebrain hemispheres. The optic tecta on each side of the brain are linked by a tectal commissure (TC) and crossing the midline right alongside the TC is the PC. Sectioning the TC/PC commissural system of the chick brain, on day two post-hatching, leads to lateralization of one particular type of visual behaviour [98]. When, on day five or six after hatching, the chicks were tested monocularly by presenting them with a small red bead, which stimulates pecking, unoperated chicks and sham-operated chicks pecked at the bead and did so on average only once each time it was presented (for 15 s and on eight times to each eye): no lateralization was apparent. Chicks with their TC/PC sectioned behaved in the same manner when tested using their left eye but, when they were tested using their right eye, they pecked at the bead more and more each time it was presented: the group data showed that there was a linear increase in pecking to over four pecks in 15 s on the eighth presentation. They appeared to find the bead more attractive each time they saw it. Such dishabituation suggests that, in intact chicks, the TC/PC commissure must transmit information from one optic tectum to the other in order to suppress continued and increasing responding to novel and attractive stimuli, such as the red bead. It is likely that this relies on a firm categorical memory of the red bead, which intact chicks tested using the right eye access via the TC/PC. Denied access to this memory the chicks using their right eye and without a TC/PC may be forced to use an imperfect memory, which makes the bead more attractive each time it is seen.

Interhemispheric communication is more effective in strongly lateralized brains, as found by comparing pigeons hatched from eggs that had received exposure to light with pigeons hatched from eggs incubated in the dark [99]. In a task reliant on use of both hemispheres together, Manns and Römmling [99] tested pigeons that had been hatched from eggs either incubated in the dark or exposed to light. The task, known as transitive inference, required monocular training in which one eye was presented with red and blue keys, only the red being rewarded, and then blue versus green keys, only the blue being rewarded. This established a hierarchy of red preferred over blue and blue over green. A similar hierarchy was established when the bird could see using the other eye, except that, for this eye, two of the colours were different (green versus yellow, with green rewarded, and yellow versus pink, with yellow rewarded). Then in testing the birds were binocular and they were confronted with pairs of colours that they had not seen previously (e.g., blue versus yellow). Light exposed chicks could combine their training to choose, for example, blue over yellow, showing that they could integrate information stored in both hemispheres. Dark-incubated pigeons were unable to integrate the information from both hemispheres even though they were able to learn the combinations in the monocular condition just as well as could the light-incubated birds. Thus, binocular (normal) performance of tasks requiring integration of information on both sides of the brain, and depending on interhemispheric communication, is not possible in a non-lateralized (or weakly lateralized) brain. Since this research did not extend to investigation of what pathways might be involved in the transfer of information between hemispheres, it is not possible to say whether the communication is indirect via, for example, the TC/PC or, perhaps, occurs at the hemispheric level via the anterior commissure.

Although in its infancy, research on functional lateralization and interhemispheric communication at both the behavioural and neural levels promises to be a fruitful way of progressing our understanding of lateralized brain function.

6. Multiple Modality Laterality and Future Research

So far, lateralization has been discussed as a unitary phenomenon, involving processing of all information in the same way and to the same degree. However, it is possible that brains may be lateralized for processing, say, visual information, and not for processing auditory or olfactory information. We know, for example, that light exposure of chick embryos establishes lateralization for certain sorts of visual processing (discussed above) but this treatment has no effect on lateralization of olfactory processing [100] or on decision making about approach to familiar versus unfamiliar stimuli [101].

What does it mean to be strongly lateralized for some types of processing but weakly lateralized for others? Moreover, is there any concordance of lateralization of the brain and lateralization of the viscera? According to studies on zebra fish, some neural asymmetries are concordant with visceral asymmetry, since they are reversed together in *fsi* mutants, but not all behavioural asymmetries are concordant with visceral asymmetry and this appears to lead to the emergence of new patterns of behaviour [102].

Research examining the relationship of laterality across modalities and how they interact should provide a rich field of study and enhance knowledge of cognitive processing. So far we have very little information on the interaction between lateralization in different sensory modalities but fascinating evidence for the interaction between light exposure and birds' ability to orient using their magnetic compass has been discovered [103], and see the paper by Gehring and colleagues in this Special Issue, showing that monocular light stimulation influences the lateralization of processing magnetic compass information.

This raises another important aspect of lateralization: viz., that it is not fixed but can change in strength over an individual's lifespan. From research on chicks, we know that visual lateralization changes markedly over early, and critical, stages of development (see [4,104], p. 120) and that it can be modulated by steroid hormones [105–107] and environmental stimulation (e.g., light exposure, discussed above). A recent review by Hausmann [108] considers the influence of sex hormones on lateralization in humans and points out the difficulties in drawing conclusions from the research on humans. Future research on non-human species promises to shed light on all of these issues.

To conclude, the evidence indicates that brain lateralization is advantageous because it allows parallel processing in the two hemispheres and it suggest that greater efficiency is achieved by confining the neural circuits used in different types of processing to separate hemispheres, thereby reducing conflict and redundancy.

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