

How asymmetry in animals starts

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This review aims to present a speculation about mechanisms that shape the brains of humans and other animals into an asymmetrical organization. To this end, I will proceed in two steps: first, I want to recapitulate evidence from various experiments that show that some but not all asymmetries of the avian brain result from a prehatch light stimulation asymmetry. This should make it clear that avian embryos have a genetic predisposition to turn their head to the right. This results in a higher level of prehatch light stimulation of their right eye. The concomitant left–right difference in sensory input alters the brain circuits of the animal for the entire lifespan in a lateralized way. In the second part of the paper I will present evidence that some of the asymmetries of the human brain take a similar ontogenetic path as those observed in birds. This review provides the evidence that critical ontogenetic processes discovered in animal models could also be involved in the ontogeny of human cerebral asymmetries.

Introduction

It has been known for about 140 years that our brain is asymmetrically organized.¹ In this span of time, countless lateralized sensory, cognitive, emotional, or motor functions as well as several dozen neural systems which display anatomical left–right differences have been revealed.² Despite these discoveries, which seem to reflect a true scientific success story, our understanding of one of the most fundamental issues in lateralization research has made little progress: we still have little information on the ontogenetic variables that shape the primordial brain into its asymmetrical architecture.

A part of the limitations of our knowledge is due to the fact that the great majority of asymmetry studies are performed in humans. A deeper experimental analysis of the ontogenetic scenario, which ultimately leads to adult lateralized behaviour, is therefore limited. Although comparative studies on left–right-differences in non-human animals started shortly after Broca's initial discovery,^{3,4}

this tradition ceased and was slowly replaced by the erroneous assumption that lateralization is a uniquely human attribute, associated with language and higher cognitive abilities.⁵ However, a wealth of recent studies show that brain lateralization is indeed widespread among all vertebrate classes.⁶ Neural systems for vocalization,⁷ visual categorization,⁸ spatial cognition,⁹ social recognition,¹⁰ handedness/footedness¹¹ and many others are organized in the same lateralized way in dozens of studied species from fish to primates, including humans.¹² This cross-species invariance in the organization of various lateralized systems is a strong argument for a common ancestry of many asymmetrically organized systems. Thus, a useful strategy to further our understanding on the ontogeny of asymmetry is first to analyse in detail the critical conditions in an animal model then and to look for similar circumstances in other species. Following this line of thought, I will first present a short overview on the ontogenetic conditions that result in the establishment of visual asymmetry in birds, before speculating on comparable ontogenetic conditions in other species, including humans.

The beginning of asymmetry in birds

Life in the egg

How the brain becomes lateralized is poorly understood, but much is known about the molecular cues that specify the left–right axis of the body, fashioning the asymmetric morphology and positioning of the visceral organs as in the case of the heart, which invariantly loops to the right side.¹³ These processes are also accompanied by a slight torsion of the embryo with the forehead pointing to the right.¹⁴ This is just what is needed to induce visual lateralization in birds. The rightward spinal torsion seems to be true for all amniotes,¹⁵ including human embryos, which also display a preference for a right-turn of their head.¹⁶

For a bird embryo, degrees of freedom to move rapidly get smaller during pre-hatch development until it is finally trapped in a fixed position where the head is bent forward and rotated so that it rests with the left eye on the chest.¹⁷ At this stage, the beak points to the right, such that the right eye is close to the translucent shell. Pigeon parents display a rather regular breeding behaviour and leave their clutch about every 43 minutes and come back after approximately 55 seconds.¹⁸ Every time the adult incubating the eggs stands up, light traverses the eggshell and stimulates the developing visual system of the pigeon embryo. Since birds regularly turn their eggs, each portion of the egg's surface has about the same probability of being directed to the light source. Due to the position of the embryo, the light stimulation is not equal. On the average, the right eye will be activated by light to a larger extent than the left. As outlined below, this stimulation asymmetry induces left–right differences of the visual system.

Early light stimulation asymmetry triggers left-right differences of behaviour

Dark incubation of chick and pigeon eggs prevents the establishment of visual lateralization in grain–grit discriminations,^{19,20} and a mere 2 hr of light exposure with 400 lux within the last days before hatch suffice in dark incubated chicken eggs to establish visual lateralization.¹⁹ It is even possible to reverse the direction of the behavioural asymmetry by withdrawing the head of the chicken embryo from the egg before hatch, occluding the right eye and exposing the left eye to light.²¹ Since pigeons are altricial animals, the developmental plasticity of their visual pathways is prolonged and extends far into post-hatching time.²² Covering the right eye of newly hatched pigeons for ten days reverses the behavioural visual lateralization of these animals as tested up to three years later.²³ Thus, light stimulation asymmetry during a critical ontogenetic time span seems to be the trigger for visual discrimination asymmetry in pigeons and chickens.

However, other asymmetries in birds are either unaffected by embryonic light exposure or are modulated by embryonic light without being triggered by it. For example, uni-hemispheric sleep patterns,²⁴ lateralized mechanisms of social recognition²⁵ or the asymmetrically organized imprinting system²⁶ seem to display genetically pre-wired left–right differences whose asymmetries are displayed also in dark-incubated birds. Although these systems can be modulated in a lateralized way by a pre-hatch light stimulation asymmetry, they do not need embryonic light input to develop their left–right differences. This is very important since obviously some neural systems are genetically predisposed to be asymmetric. Therefore, their adult phenotype does not depend on lateralized ontogenetic experiences, although they can be modulated by it. Other neural pathways, like those required for object discrimination, seem not to display inborn asymmetries but develop left–right differences by a lateralized sensory input during a critical ontogenetic period.

Early light stimulation asymmetry triggers anatomical left–right differences

Lateralized embryonic light input also gives developing visual pathways an asymmetrical architecture. Visual information ascending to the avian forebrain is processed by two parallel pathways, the thalamo-fugal and the tecto-fugal systems, suggested to be equivalent to the geniculocortical and the extrageniculocortical visual pathways of mammals, respectively.²⁷ The thalamo-fugal pathway starts with a projection of retinal ganglion cells to the contralateral nucl. geniculatus laterale, pars dorsalis (GLd), from where axons go bilaterally to a

forebrain structure called 'Wulst'.²⁸ The tecto-fugal system is composed of optic nerve fibres projecting to the contralateral optic tectum, from which fibres project bilaterally to the rotundal nuclei on each side of the thalamus. Each nucl. rotundus (Rt) by itself projects to the ipsilateral entopallium of the forebrain.²⁹ The thalamo-fugal and the tecto-fugal pathways have been shown to constitute structural asymmetries related to lateralized visual behaviour in chickens³⁰ and pigeons,⁸ respectively.

In chickens, unilateral injections of retrograde tracers into the Wulst labels cells in the GLd of both sides. The ratio of contralaterally to ipsilaterally labelled GLd neurons is higher after right than after left sided Wulst injections in 2-day-old chicks.³¹ As shown by Rogers and Deng³² this lateralized ratio difference is due to a higher number of fibres from the left thalamus going to the contralateral right forebrain than to the left. The asymmetry of the crossed thalamo-telencephalic projection is pronounced in young males but disappears at about three weeks of age; this is consistent with the behavioural data on lateralized performance in the pebble-floor task.³³ Dark incubation prevents the establishment of thalamo-fugal asymmetry³⁴ and alters the composition of ascending projections from the GLd.³⁵ Reversing the direction of pre-hatch stimulation by occluding the embryo's right eye and exposing the left to light before hatch reverses thalamo-fugal asymmetry.³¹ Thus, the anatomical asymmetry of the ascending thalamo-fugal system in chickens is linked to pre-hatch light asymmetry.

In pigeons, morphometric studies revealed asymmetries of cell size within the optic tectum^{36,37} and the nucl. Rotundus³⁸ that disappeared after dark incubation²⁰ or were reversed after post-hatch occlusion of the right eye for ten days.^{23,38} Thus, the pigeon's tecto-fugal system displays significant morphological asymmetries that are tightly related to left-right differences of visual stimulation during the development of the tecto-fugal system. In addition, there is strong evidence in pigeons that the connectivity of the visual system is organized in a lateralized fashion³⁹ and that the transcommissural interhemispheric interaction is left-right different.⁴⁰ Taken together, both in chickens and pigeons, ascending visual pathways are asymmetrically organized and in both species these neurobiological left-right differences result from a skewed visual asymmetry during ontogeny. The fact that these two species display asymmetries in different pathways (thalamo-fugal in chickens, tecto-fugal in pigeons) shows that this scenario is not special to one neural system. Instead, the asymmetrical ontogenetic light stimulation seems to have the potential to induce a lateralized architecture in many systems. It is possible that the different developmental speeds of the thalamo-fugal and tecto-fugal pathways co-varies with the difference in the ontogeny of the precocial chicken and the altricial pigeon, producing either a thalamo- or a tectofugal asymmetry.⁸

Embryonic light asymmetry alters both hemispheres

Up to now, this could be read as telling the simple story of a developmental advantage that is gained by the left hemisphere's visual system as a result of a pre-hatch right eye light stimulation. If the story were so simple, we should observe a dominance of the left hemisphere for all aspects of visual object analyses as long as embryos develop in the light. However, what we observe in birds is not a simple dominance, but a cerebral asymmetry with complementary cognitive patterns. This is best illustrated in the domain of visual spatial orientation.

The complementary roles of left and right hemispheric mechanisms can be beautifully studied in food storing birds during cache localization. Marsh tits store food in large numbers of caches scattered over the home range, which they can retrieve many days later with astounding accuracy.⁴¹ It is possible to study lateralization of food storing and cache retrieval under controlled conditions using a room with artificial trees, perches, and small holes for caching. In one of these studies,⁴² four feeders were used that were distinguishable by their specific location and by markings, which made them visually unique. Birds were given parts of a nut in one out of four feeders under monocular conditions and were then removed for 5 min. During this interval, the location of the correct feeder was swapped with an empty one so that spatial and object cues could be dissociated. Then the animals were re-entered and allowed to retrieve the rest of the nut with the same eye cap condition. With the left eye, marsh tits looked for the seed at the correct spatial location, while they relied on object specific cues using the right eye. Thus, the right hemisphere seems to use spatial cues, while the left half of the brain utilizes object cues to locate the nut.

Several lines of studies could reveal more details of this distinction and showed that the left hemisphere is specialized to orient according to landmarks by using absolute distances of objects to the goal.⁴³ The right hemisphere, on the other side, is able to utilize the relation of the position of major objects to each other to locate the goal.^{44,45} Both strategies work and probably both hemispheres complement each other during normal search events.⁴⁶ But depending on certain circumstances, one strategy can be more useful than the other. In this case we have to assume that a single hemisphere can temporarily be solely in charge for generating spatial orientation. It is clear that the avian visual system is organized with complementary cognitive strategies of both hemispheres.

There is some evidence that embryonic light stimulation activates this complementarity. Skiba *et al.*²⁰ compared the lateralized performance of light- and dark-incubated pigeons in two different tasks. One task placed heavy demands on the ability of the birds to perceptually distinguish between objects, while the visuo-motor speed was of secondary importance. The other task was the reverse, here the animals had to be very fast, but perceptual distinctions were not so

important. In both tasks the animals were better when using their right eye (left hemisphere). Looking at the detailed results of the light- and dark-incubated birds revealed an interesting pattern. The perceptual asymmetry was due to a performance *increase* of the left hemisphere. The visuo-motor asymmetry resulted from a performance *decrease* of the right hemisphere. Thus, the same treatment (light incubation) had altered two neural systems in different ways in the two hemispheres.²⁰ Anatomical studies reveal similar results. Manns and Güntürkün showed that light incubation induces morphological asymmetries in some midbrain cell types.³⁷ However, different cellular systems were differently affected on the left and on the right side, resulting in complementary asymmetry patterns.

The development of avian visual asymmetry

Up to now we have shown that the genetic mechanisms that determine a slight torsion of the embryo to the right side within its egg mark the beginning of visual cerebral asymmetries in birds. The head turn brings the right eye close to the translucent eggshell while the left eye is covered by the body, resulting in asymmetrical stimulation of the two eyes with light. This lateralized light input comes just in time to mould the developing visual system into an anatomically asymmetric organization. Thus, the right-eye dominance for visual object analysis in birds results from a tight interplay between genetic and epigenetic factors. The anatomical and physiological asymmetries result in a lateralized functional architecture of the visual system. This asymmetry develops in about a week and maintains its function in pigeons for more than a decade, the whole lifespan of the animal. During this period the visual lateralization not only alters learning, memorizing, and recognition processes of objects in an asymmetrical fashion but also determines complex cognitive processes of the visual system.

The beginning of asymmetry in humans

Life before birth

Are there lessons from the avian brain that could shed some light on the ontogeny of human asymmetries, since some of the conditions in humans remarkably resemble those in birds? The body plan of vertebrates feature several consistent asymmetries in the placement, structure, and function of organs, such as the heart, intestine and brain. These similarities of overall asymmetries are related to similar pathways of asymmetrically expressed signalling factors that have been well-characterized in several model systems.⁴⁷ These processes result in a rightward looping of the heart and a slight torsion of the embryo with the forehead

pointing to the right.¹⁴ This condition seems to be true for all amniotes, including humans. Indeed, real-time ultrasound recordings from the foetal head relative to the body showed the existence of a rightward head bias.¹⁶ Additionally, beginning with the 10th week of gestation, human embryos move their right arm more than the left.⁴⁸ As shown by Hepper *et al.*, foetuses from 15 weeks of gestation to term have a strong lateralized bias of thumb sucking on the right side.⁴⁹

These early motor asymmetries are not driven by forebrain structures but have to be generated by brainstem and spinal mechanisms, because the corticospinal tract reaches cervical to thoracic segments much later in development, and even at term is only myelinated as far caudally as the cerebral peduncles.⁵⁰ The lateral sub-corticospinal pathway, which encompasses descending tracts crucial for distal limb and hand movements myelinates only at 28–34 weeks of gestational age.⁵¹ Together, these data show that human embryos are characterized by several lateralized motor patterns of the head and the arms that have to be guided by neural systems in the lower brainstem and spinal cord.

Asymmetries of newborns

The preference to turn the head rightward is visible directly after birth and results in a higher prevalence of right-sided mouth–hand contacts.^{11,52} It forms a neonate reflex called the asymmetrical tonic neck reflex (ATNR). The ATNR is defined as a body position where the head is turned and the arm and the leg on the same side are extended while the opposite limbs bend. By 6 months of age it is usually inhibited in the waking state. Right-sided head-turning is accompanied by a higher number of right-sided movement patterns of upper and lower limbs,⁵³ the grasp reflex with the right hand is already stronger after birth⁵⁴ and the right arm responds faster during tests of the Moro reflex.⁵⁵

These observations show that newborns display several motor asymmetries of the limbs and the head, but do not necessarily prove that these lateralized motor patterns are causally related, however several studies of the last two decades make it likely that head turning and handedness are indeed causally linked. Cioni and Pellegrinetti studied head turning preferences of newborns from right- or left-handed parents.⁵⁶ Babies from right-handed parents spend more time with the head turned to the right, those from the left-handed had no clear bias, so the handedness of parents seems to be genetically related to head turning in neonates. In addition, head turning and handedness of babies seems to be linked as first shown by Michel.⁵⁷ He showed that 65% of newborn infants preferred to lie with their heads turned to the right. This orientation preference was maintained for at least 2 months and predicted preferential hand use in reaching tasks at both 16 and 22 weeks. Michel and Harkins⁵⁸ observed ten newborn infants who preferred to lie with their heads turned rightward and ten who preferred to lie with their heads

turned leftward and analysed the hand-use preferences for reaching assessed at eight different ages during the period 12–74 weeks postpartum. Eighteen infants maintained stable hand-use preferences throughout this period and the direction of their neonatal head orientation preference predicted the hand they preferred to use. Thus, the dextral bias in handedness may be derived, in part, from the rightward bias in neonatal head-turn preference.

In an interesting quasi-experiment, Konishi *et al.* were able to show that handedness is influenced by head turning preferences.⁵⁹ They observed 44 newborns, which were nursed in a supine position and 37 nursed in a prone position throughout their admission period. Persistent head-turning to the right was observed more often and continued longer in the infants lying supine. This difference was probably due to the fact that newborns can freely turn their heads while lying supine. In a prone position however, they lack neck muscle strength to turn their heads to a preferred side. At nine months, preference for the right hand was more marked in infants lying in supine, whereas infants lying in prone used their hands bilaterally, a tendency that persisted at 18 months. Thus, handedness had been modulated by head turning.

How could a head turning asymmetry influence handedness? One possibility is that a pre-existing slight preference to move the right arm is enhanced by an increased eye–hand contact on the right side. The same could be true for the right foot. Additionally, a bias to mainly utilize sensory input from the right eye (eyedness) could also be fostered by the same mechanism. Sensory and motor asymmetries in humans are slight and modifiable in the beginning but develop in a snowball-like fashion during ontogeny.⁶⁰ Asymmetries of head turning could thus give the developing nervous system an initial bias. Several right-sided dominances for the hand, the foot, the eye, and the ear could be initiated or at least modulated in this way.⁶¹ The mechanism would then be similar to the establishment of visual asymmetry in birds.

There is, however, a problem. A right-sided preference of hand-, foot-, ear- and eye-use takes years to fully establish,^{62,63} and thus remains undeveloped long after head-turning preferences of new-borns have disappeared.⁵² What, however, if head-turning preferences never cease but are simply more subtle to discover in adults?

Asymmetries in adults

There is good evidence that adults show the same head-turn preference to the right as seen in infants. I observed 124 couples at large international airports or other public places for evidence of a majority that might turn their head to the right during kissing.⁶⁴ Each couple was observed only once. Couples had to have lip-contact, had to stand facing each other and none of the two had to carry an

item on one side which could induce a side preference. The estimated age of the subjects varied from teenage to 60s. Sixty-five percent turned to the right and this 2:1 ratio was significantly different from chance. This bias suggests that a head bias persists in adulthood and could therefore modulate the establishment of various forms of sidedness over the entire lifetime. Additional evidence comes from the examinations of the occipito-cervical junction in 600 people⁶⁵ and 156 skulls.⁶⁶ These examinations showed that for 2/3 the right-sided occipital condyle was shifted against the atlas to a more medial position. Condyles are oval processes on either side of the foramen magnum and articulate with the first vertebra. The asymmetry may result from a stronger right-sided force of the rectus capitis posterior major and obliquus capitis muscles, which rotate the head to the right and extend it.⁶⁵ This condition emerges during the first decade so that a right-sided rotation preference lateralizes the cervicocranial junction.⁶⁷

These data show that we adults still go on having a preference for a right turn of our head. The right turn (rotation towards the right along the vertical axis) is different from a cranial right-tilt (leaning to the right towards the shoulder axis) for which there is less clear evidence.

Résumé

Bird embryos have several genetically prewired asymmetries. Some, like in the case of imprinting, acquire a lateralized neural function without left–right differences of embryonic visual stimulation, although they can be modulated by it. Others, like the tendency to turn the head to the right have no obvious impact on the visual system of the brain as long as the prehatch history of the young animal takes place in the dark. As soon as the egg is light-exposed, however, the head-turn to the right becomes a critical factor since it results in a more intense stimulation of the right eye and a concomitant development of asymmetries of visual neural processing.

The situation in humans could be similar. Human neonates already display several asymmetries of brain and behaviour.^{5,15,49,61} One of them is a tendency to turn the head to the right – a bias that is visible for the entire lifespan. This tendency for a right-turn could thus promote a constant bias towards the right space and thereby induce or enhance right-sided asymmetries of perception and action. The beginning of some of our asymmetries could thus be traced back to an early embryonic motor bias.

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