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RESEARCH ARTICLE

Dual coding of visual asymmetries in the pigeon brain: the interaction of bottom-up and top-down systems

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Abstract The pigeon's visual system is an excellent model to investigate the ontogenetic and the neuronal foundations of cerebral asymmetries. Before hatching, lateralized visual stimulation induces structural asymmetries within the tectofugal pathway during a critical time window. Interhemispheric control mechanisms emerge presumably after hatching and stabilize these induced asymmetries. Once established, visual asymmetry in pigeons displays a left hemispheric dominance for complex learning and discrimination tasks and unravels how the interplay between bottom-up and top-down mechanisms generate a lateralized, hemispheric-specific visual analysis. The ascending visual (tectofugal) pathway displays cell size asymmetries and directs more bilateral visual information towards the left hemisphere. This bottom-up system is controlled by telencephalic top-down projections, which affect intra- and/or interhemispheric inhibitory systems in a presumably lateralized manner. Such a flexible organization allows the control of information transfer depending on the visual input and hence adapt the dominant processing mode to environmental requirements.

Keywords Asymmetry formation · Avian · Interhemispheric inhibition · Lateralization · Tectofugal · Visual Wulst

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Introduction

Cerebral asymmetries are characterized by a functional superiority of one hemisphere for certain perceptual, cognitive or motor processes. For many decades, humans were thought to be unique in having an asymmetrically organized brain. The increasing number of reports describing various asymmetries in animals supplants this long-held view and characterizes cerebral asymmetry as a ubiquitous phenomenon that possibly is not the exception, but the rule (Halpern et al. 2005; Vallortigara et al. 1999; Vallortigara and Rogers 2005). Left–right differences in neuronal structure and processing can be found in all vertebrate classes (Rogers and Andrew 2002) and also in octopuses (Byrne et al. 2006), fruit flies (Pascual et al. 2004), bees (Letzkus et al. 2006; Rogers and Vallortigara 2008) and even in nematodes (Suzuki et al. 2008). This widespread appearance in animals of quite different complexity and phylogenetic background entails a strong interest in the evolutionary advantages and neuronal foundations of neuronal lateralization. Nevertheless, our understanding about how and why left-sided neuronal circuits operate differently from right ones is still limited.

Human research still discusses to what extent differences of intrahemispheric neuronal circuits (e.g. Galaburda et al. 1990; Grabowska and Nowicka 1996; Rosen et al. 1992) or interhemispheric cross talk via the corpus callosum (e.g. Bloom and Hynd 2005; Chiarello and Maxfield 1996) are crucial for the generation and maintenance of lateralized functions. We will present evidence that both intra- as well as interhemispheric aspects are relevant for the emergence of visual asymmetries in the avian brain. A further aspect where research on animal lateralization can provide valuable information is the field of development of brain asymmetries. While some genetic factors could be identified as a starting point of lateralized brain development (Annett 1985; Sun et al. 2005), the critical role of environmental influences is still a matter of debate (Provins 1997; Manns 2006).

Using the pigeons' visual system as a model, we will review new insights into the ontogenetic and neuronal mechanisms of lateralized information processing. In the avian visual pathways, anatomical and behavioural asymmetries develop in response to asymmetrical light stimulation and hence exemplify the crucial role of experience. In pigeons, a lateralized development results in an adult neuronal organization that is characterized by lateralized interactions of bottom-up and top-down systems. A functional lateralization of the ascending processing stream is based on structural left–right differences. This system is modulated by top-down influences, which generate lateralized control onto visuomotor behaviour by a dynamic integration of left and right hemispheric processing (Fig. 1).

Hemispheric-specific analysis of the visual environment

Cognitive, pharmacological as well as physiological experiments show that the left and the right hemisphere of the avian brain process to some extent different aspects of visual stimuli. The optic nerves cross almost completely in birds (Weidner et al. 1985). Therefore, hemispheric specializations can easily be tested in birds by temporarily covering one eye with an eye cap and thereby directing the flow of information primarily to the contralateral brain side (Güntürkün 2002a).

Studies comparing performances with sight restricted to one eye have demonstrated that the left hemisphere is specialized for detailed object analysis and attends to local features of visual stimuli. This becomes especially visible in studies with pigeons like that of Yamazaki et al. (2007) where visual stimuli were fragmented in smaller and smaller pieces. The left hemisphere is then clearly superior in identifying critical details in these tiny fragments. The generally better discrimination abilities of the left eye become also apparent in visual discrimination of grain versus grit (chicken: Rogers et al. 2006; pigeon: Güntürkün and Kesch 1987; quail: Valenti et al. 2003; zebra finch: Alonso 1998), two-dimensional artificial patterns (Güntürkün 1985), geometrical optic illusions (Güntürkün 1997b), colour reversal learning (Diekamp et al. 1999), memorization of hundreds of complex patterns (von Fersen and Güntürkün 1990) or categorization of the object category "human" (Yamazaki et al. 2007).

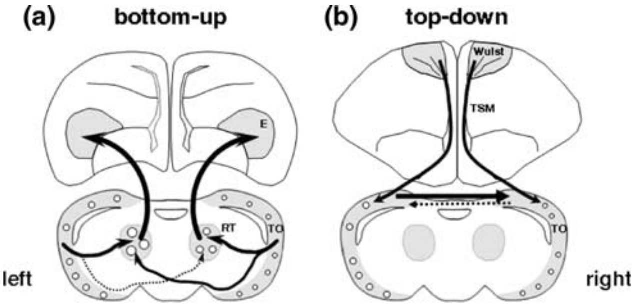

Fig. 1 Lateralized visual processing in the pigeon brain arises by the interaction of bottom-up and top-down systems: **a** Bottom-up asymmetries are implemented in the tectofugal pathway (TO→RT→E) with larger cells and stronger bilateral input in the left hemispheric system. **b** Tectofugal processing is modulated by top-down projections arising from the Wulst and terminating within the ipsilateral tectum. Moreover, both tectal hemispheres are connected by asymmetrically organized tectotectal commissures. *E* entopallium, *RT* nucleus rotundus, *TO* optic tectum, *TSM* tractus septomesencephalicus

In contrast, the right hemisphere extracts relational configurations of visual stimuli and possibly analyses global aspects of the visual scenery (chicken: Chiesa et al. 2006; Tommasi and Vallortigara 2001, 2004; marsh tit: Clayton and Krebs 1994; pigeon: Kahn and Bingman 2004). This is presumably related to a right hemispheric superiority in some aspects of spatial cognition (chicken and pigeon: Diekamp et al. 2005; Regolin 2006). Moreover, the right hemisphere is in charge of species-typical or instinct-based reactions like novelty detection (chicken: Andrew et al. 2004), social discrimination and attack (chicken: Vallortigara and Andrew 1994; quail: Zucca and Sovrano 2008), fear and escape responses (chicken: Dharmaretnam and Rogers 2005; magpie: Koboroff et al. 2008) and sexual behaviour (chicken: Bullock and Rogers 1992; quail: Gülbetekin et al. 2007).

These functional specializations suggest that each hemisphere processes visual stimuli in a different way. Anatomical, physiological and behavioural studies especially in the pigeon's brain support this dissociation and provide a starting point to unravel the neuronal organization underlying lateralized visual analysis (Güntürkün 2002a, 2002b).

Left–right differences in bottom-up processing

Like other amniotes, birds process visual information within two ascending pathways, the tecto- and the thalamofugal system (Güntürkün 2000). These systems display structural asymmetries, which differ between avian species and developmental stages.

The thalamofugal pathway corresponds to the mammalian geniculostriatal system and transfers retinal information via the contralateral geniculate complex (Gld) bilaterally onto the telencephalic visual Wulst (Güntürkün 2000). In the chicken, this pattern displays a transient asymmetry in the number of ascending fibres (Koshiba et al. 2003). Comparable asymmetries are neither present in young nor in adult pigeons (Freund et al. (in prep.); Table 1).

Table 1 Differences in the structural organization of visual asymmetries between chicken and pigeon

Asymmetry	Chicken	Pigeon
Thalamofugal		
Cell size	?	–[c]
Projection	+[a] (stronger bilateral output from the left thalamus)	–[c]
Tectofugal		
Cell size	?	+[d–g]
Projection	–[a]	+[h] (stronger bilateral input onto the left thalamus)
Development	Transient[b]	Permanent[c–h]

[a] Rogers and Deng (1999)

[b] Deng and Rogers (2002)

[c] Freund et al. (in prep.)

[d] Güntürkün (1997a)

[e] Skiba et al. (2002)

[f] Manns and Güntürkün (1999b)

[g] Manns and Güntürkün (2003)

[h] Güntürkün et al. (1998)

The tectofugal system corresponds to the mammalian extrageniculocortical pathway and projects via the contralateral mesencephalic optic tectum and the diencephalic nucleus rotundus to the telencephalic entopallium (Bischof and Watanabe 1997; Güntürkün 2000; new nomenclature according to Reiner et al. 2004). Different from the thalamofugal system, this pathway is characterized by anatomical left–right differences in the pigeon (Güntürkün 2002a, 2002b; Fig. 1a; Table 1), but not in the chicken (Rogers and Deng 1999). Within the optic tectum, a majority of cells including GABAergic neurons display larger cell bodies in the left tectum (Güntürkün 1997a; Manns and Güntürkün 2003; Skiba et al. 2002).

In parallel, the tectorotundal projection is asymmetrically organized with respect to its connectivity. While the majority of tectal efferents ascend ipsilaterally onto the rotundus, a subpopulation projects into the contralateral side with more fibres crossing from the right tectum to the left rotundus than vice versa (Güntürkün et al. 1993, 1998; Fig. 2a). The stronger bilateral innervation of the left rotundus correlates with the enlarged rotundal neuron somata on this side (Manns and Güntürkün 1999b). In line with the stronger bilateral input, electrophysiological studies could demonstrate a higher number of neurons in the left than in the right rotundus, which respond to contra- as well as ipsilateral visual input (Folta et al. 2004; Fig. 2b).

Thus, anatomical and physiological data suggest that the left rotundus integrates input from both eyes to a higher degree than the right rotundus and likely enables a more complete representation of the visual scenery at the forebrain level. This was already shown by Güntürkün and Hahmann (1999), who placed unilateral lesions into the rotundus and compared acuity reductions with each eye. They demonstrated that damages to the left rotundus led to a significant decrease in ipsi- as well as contralateral visual acuity, whereas right-sided lesions alone did not affect the performance. Valencia-Alfonso et al. (2008) could demonstrate this kind of asymmetry of representation with more elaborate behavioural techniques. They trained pigeons in monocular colour discrimination with a rewarded and a non-rewarded colour displayed on two pecking keys. The colours were presented to one eye while the other one was temporally covered. Each eye and, hence, the respective contralateral hemispheres learnt to discriminate a different

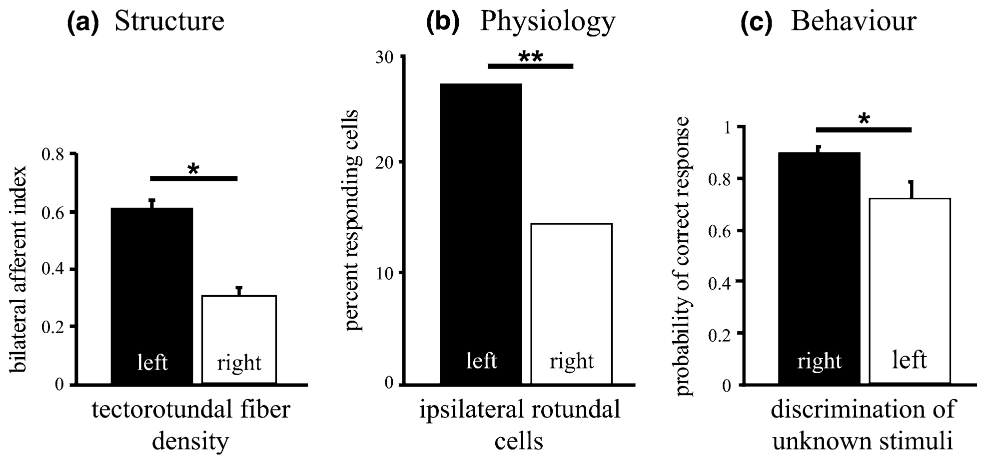

Fig. 2 Enhanced bilateral processing in the left hemisphere is due to: **a** structural *left–right* differences as indicated by a stronger bilateral tectal input onto the *left* rotundus (Güntürkün et al. 1998); **b** electrophysiological asymmetries as indicated by a higher percentage of ipsilaterally responding cells in the *left* rotundus (Folta et al. 2004; Valencia-Alfonso et al. 2008); **c** behaviour as indicated by a better knowledge of information learnt with the ipsilateral eye by the *right eye/left hemisphere* (Valencia-Alfonso et al.2008)

pair of colours. Accordingly, each hemisphere had only direct experience with one pair of colours. As a consequence, there was a pair of “known” (learnt with the contralateral eye of a hemisphere) and “unknown” (learnt with the ipsilateral eye) colours for each hemisphere. After reaching the learning criterion, each eye/hemisphere was separately tested with a mixture of known and unknown colour pairs. While no difference in discriminating known colour pairs could be detected between the left and right eyes, the right eye (left hemisphere) demonstrated a better performance in discriminating the unknown stimulus pair (Fig. 2c). Thus, the left hemisphere had more access to information from the ipsilateral eye (contralateral half brain) than the right hemisphere. This is a strong argument for the left hemisphere having a more bilateral representation of the visual input compared to the right hemisphere.

In sum, the ascending tectofugal pathway displays a neuronal organization that creates an asymmetrical representation of the visual scene at the forebrain level. However, tectofugal processing is also modulated by top-down influences arising in the forebrain and descending towards the brainstem level. As will be outlined below, the impact of this top-down system is also lateralized, but is differently organized from the ascending one.

Asymmetries in top-down control of visual processing

Telencephalic top-down efferents arise from several major descending pathways of which the tractus septomesencephalicus (TSM) is known to be asymmetrically organized (Fig. 1b). The neurons, which constitute the TSM, are mainly located within the visual Wulst (Leresche et al. 1983; Miceli et al. 1987). This connection allows the Wulst to control tectofugal processing depending on actual cognitive demands. The visual Wulst is not only a primary visual telencephalic target, but it is also involved in higher cognitive functions, playing a role in learning and attentional processes (Shimizu and Hodos 1989; Powers 1989; Maekawa et al. 2006; Bingman et al. 2008; Watanabe 2003). Physiological studies could demonstrate that the top-down control generated in the Wulst is lateralized and primarily derives from the left forebrain (Folta et al. 2004; Valencia-Alfonso et al. 2008, in prep.). At the rotundal level, electrophysiological recordings revealed that a subpopulation of rotundal units is modulated by top-down influences, which can be detected by very late response components of these cells. These late responses originate exclusively from the left Wulst (Folta et al. 2004).

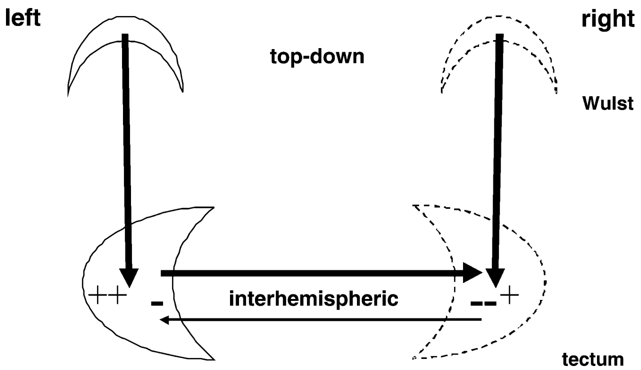

Fig. 3 Asymmetrical top-down control of the Wulst presumably emerges by the interaction of descending fibres with intra- and interhemispheric tectofugal circuits. The inhibitory commissural systems modulate the balance of the left and the right hemispheric processing and exerts a higher input onto the right tectal hemisphere

The behavioural significance of top-down regulation arising mainly from the left Wulst was tested in a second experiment of the aforementioned monocular discrimination task of Valencia-Alfonso et al. (2008). After training each eye/hemisphere to discriminate a different pair of colours, pigeons were tested for known and unknown stimuli while the left and/or right visual Wulst was blocked with tetrodotoxin (TTX). Temporal silencing of the Wulst decreased the discrimination performance for the known as well as for the unknown stimulus pair. But a significant effect could only be observed when the left Wulst was blocked. Left-sided Wulst blockade affected not only performance with the contralateral right, but also with the ipsilateral left eye. This provides evidence for a facilitating effect of the left Wulst for the memory read-out of both hemispheres and substantiates the higher impact of the left forebrain in controlling information transfer in both brain halves (Valencia-Alfonso et al. 2008).

The asymmetrical top-down effects of the Wulst are not simply created by left–right differences in fibre numbers (Manns et al. 2007). This is in contrast to the ascending tectofugal system, which transfers more information to the left hemisphere via an asymmetry in the number of crossing projections. As outlined below, it is likely that a lateralization of top-down influences arises by cellular interactions at the subtelencephalic level, whereby the descending impact on the balance of interhemispheric interactions provides the left hemisphere with a higher probability to inhibit the right than vice versa (Güntürkün and Hoferichter 1985; Valencia-Alfonso et al. 2008; Figs. 1b, 3). Such a dynamic organization may allow the system to adapt the dominant mode of processing according to contextual needs. This is exemplified in the next part of this review.

Inhibitory systems control the balance of left and right hemispheric processing

The descending projections from the TSM terminate within the optic tectum (Dubbeldam et al. 1997; Leresche et al.

1983; Miceli et al. 1987; Zeier and Karten 1971, 1973) from where the projections lead to all the major midbrain targets (Güntürkün 1987; Hellmann et al. 2004). Accordingly, lateralized top-down effects as observed in the rotundus possibly represent secondary consequences of processes at the tectal level. In general, the optic tectum is an essential relay station for visuomotor behaviour, which is characterized by a set of connections that comprise topographically ordered input from the eyes and an output that reaches premotor hindbrain regions. Ascending and descending projections display a complex pattern of ipsi- and contralaterally projecting fibres, providing substrate for interhemispheric interactions (Hellmann et al. 2004). This connectivity pattern ascribes the tectum a central role in integrating and directing lateralized visual information (Manns et al. 2007). Top-down projections could specifically interact with tectal inhibitory pathways to exert their lateralized impact onto the balance of left and right hemispheric processing. Indeed, tectal TSM termination fields overlap with several major intratectal inhibitory subsystems, of which several display asymmetries of morphology (Miceli et al. 1987; Hunt and Künzle 1976a, 1976b; Manns and Güntürkün 2003). In addition to this effect on the ipsilateral tectum, TSM fibres could also modulate inhibitory tecto-tectal interactions. The optic tecta are connected by inhibitory intertectal commissures (Hardy et al. 1984; Robert and Cuénod 1969). This system is asymmetrically organized with the left tectum inhibiting the right tectum to a larger extent than vice versa (Keysers et al. 2000). This suggests that when the left hemisphere is active, a strong inhibition towards the right hemisphere is exerted. The crucial role of this system for lateralized visuomotor control is shown by commissural transections, which result in a reversal of behavioural asymmetries (Güntürkün and Böhringer 1987).

Last but not least, tectal projections also constitute a tectorotundal side pathway by terminating in the bed nuclei of the tectothalamic tract, which in turn constitutes an ipsilateral GABAergic projection onto the rotundus (Mpodozis et al. 1996; Theiss et al. 2003; Tömböl et al. 1999). This system is assumed to control attentional shifts between the hemispheres and is involved in the regulation of ipsilateral as well as bilateral visual input (Voss and Bischof 2003). They thus assume a prominent position to mediate the observed asymmetrical effects of top-down control. Although physiological asymmetries still have to be analyzed, asymmetric cell sizes in the nucleus subpretectalis (SP) as one of the major nuclei of this system suggest a lateralized function of this system (Freund et al. 2008).

To summarize, it is likely that the asymmetric action of top-down projections does not arise from left–right differences of the descending system itself, but by its interaction with lateralized tectal systems. Accordingly, inactivation of the left Wulst could alter the dynamics of the intertectal inhibition more profoundly than right Wulst blockade. This telencephalic participation might provide the left hemisphere with a dominant executive control.

Visual lateralization is generated by asymmetrical visual input during ontogeny

The described anatomical left–right differences as well as several aspects of functional asymmetries in the avian visual system develop in response to asymmetrical light stimulation before hatching (Deng and Rogers 2002; Güntürkün 2002b; Manns 2006). The late stage embryo consistently adopts a turned posture in the same direction such that the left eye is occluded by its own body and the right eye is close to the egg shell. Since breeding birds regularly turn their eggs and therefore often leave their nests for short time periods, eggs are frequently exposed to light (Buschmann et al. 2006). As a consequence, light entering through the egg shell and air sac membranes stimulates the right eye, while the left eye is visually deprived. The resulting biased photic input induces asymmetrical differentiation processes in the left and right hemispheric visual circuits, which ultimately establish the final lateralization pattern (Fig. 4).

Avian visual asymmetry is induced by left–right differences of visual stimulation during a critical time window. Bilateral light exposure as well as incubation in complete darkness prevents the lateralized development of visual circuits (Deng and Rogers 2002; Skiba et al. 2002). Moreover, the normal lateralization pattern can be reversed by occluding the right eye and exposing the left eye to light (Deng and Rogers 2002; Manns and Güntürkün 1999a). This kind of plasticity ends with hatching in the precocious chicken, and visual asymmetry as a whole is mostly transient in this species (Deng and Rogers 2002). In the pigeon, however, it is possible to alter the visual asymmetries even after hatching (Manns and Güntürkün 1999a, 1999b; Manns et al. 2008a; Prior et al. 2004), as a consequence of the prolonged visual development of this altricial species (Manns and Güntürkün 1997; Manns et al. 2008b). Occlusion of the right eye for 10 days reverses visual asymmetries by inducing a functional dominance of the left eye in visual discrimination and by modulating tectofugal left–right differences. Conversely, left eye deprivation enhances the right eye dominance (Manns and Güntürkün 1999a, 1999b).

Pre- and posthatch plasticity of the adult lateralization pattern in pigeons delineates two developmental phases critically involved in the establishment of visual asymmetry: induction and stabilization. Asymmetries are *induced* during embryonic development by lateralized light input and are *stabilized* by tectal systems during posthatch development,

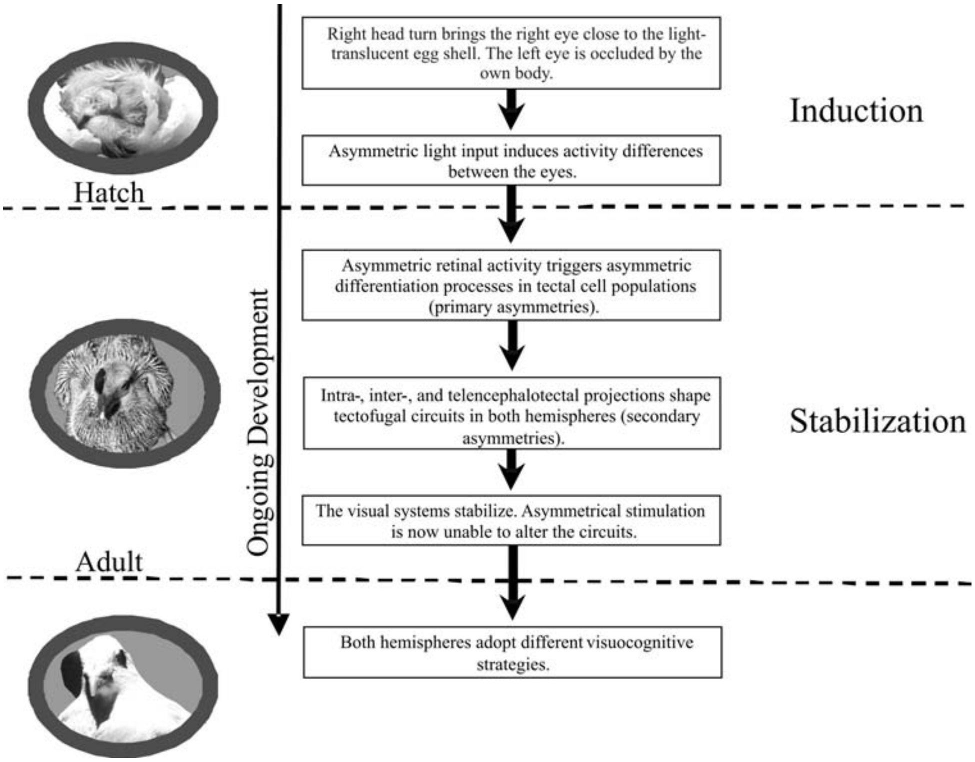

Fig. 4 Sequence of events that establish asymmetries in the pigeon's visual system

despite a usually symmetric light input. It is very likely that visual stimulation before or after hatching affects different neuronal processes in distinct neuronal systems. During embryonic development, asymmetrical photic stimulation primarily influences the differentiation of retinotectal connections, leading to hard-wired structural left–right differences in the tectofugal pathway. After hatching, asymmetric modulation of visual experience possibly mainly affects the differentiation of the non-retinorecipient components of the tectofugal systems, which mediate the stabilization of induced asymmetries (Fig. 4).

The stabilization of lateralized neural circuits results in life-long visual asymmetries, which can be observed even in very old pigeons. This is exemplified by the following data set that derives from a grit grain discrimination task in senescent pigeons. A group of old birds ($n = 8$) with an average age of 9.38 years (range 7–14, SE = 0.73) was tested in a foraging task in which 30 pieces of grain had to be pecked from a trough filled with 30 g pebbles (about 1,000 pieces) within 30 s. The grains and pebbles were similar with respect to colour, size and shape. Each bird participated ten times, seeing with the left and the right eye (order of monocular conditions was balanced for the birds). The critical variable was the discrimination accuracy that is derived by the number of grains consumed divided by the number of pecks. This is a classic testing procedure first described in Güntürkün and Kesch (1987) and used in various studies since then. The control group consisted of 34 pigeons with an average age of 1.85 years (range 1–3, SE = 0.15). To calculate the extent of laterality, an asymmetry index (AI) was derived as $\mathrm{AI} = ((R - L)/(R + L)) \times 100$. R and L depict the average discrimination accuracies with the right and the left eye, respectively. The higher a positive AI, the more lateralized towards the right eye are the birds. The average AI was 3.3 (SE = 1.2) for the old and 1.9 (SE = 2.3) for the young birds ($t_{40} = 1.09$, ns). Thus, both groups displayed right eye superiority. Since visual laterality of very old pigeons was not significantly different from that of the young birds, cerebral asymmetries of object discriminations seem to exist for the entire lifetime of an individual.

The asymmetrical visual stimulation induces morphological tectofugal asymmetries by activity-dependent processes

The maturation of the retinotectal pathway is known to be regulated by photic stimulation, and changes in retinal activity quickly affect synaptogenetic processes (Cohen-Cory 2002; Ruthazer and Cline 2004). Accordingly, short periods of biased retinal activation are sufficient to induce asymmetrical differentiation processes in the optic tectum (Güntürkün 1997a, 1997b). Consequently, transient reduction of retinal activity by just a single ocular TTX-injection establishes a behavioural lateralization in adult pigeons with a functional dominance of the hemisphere, which is ipsilateral to the temporarily silenced eye (Prior et al. 2004).

Many light effects are mediated by neurotrophic factors and especially the brain-derived neurotrophic factor (BDNF) is a key player in activity-dependent development (Lindholm et al. 1994). Light adjusts the expression and/or release of neurotrophic factors and hence regulates trophic support of target cells (Cohen-Cory and Lom 2004; Vicario-Abejón et al. 2002). In turn, BDNF controls sprouting, branching and maintenance of axo-dendritic trees. Accordingly, this neurotrophin could be involved in the activity-dependent development of tectofugal asymmetry in pigeons. Indeed, BDNF and its high-affinity receptor TrkB are present in the developing retinotectal system (Theiss and Güntürkün 2001) and the tectal TrkB signalling cascade is asymmetrically activated in response to embryonic light stimulation (Manns et al. 2005). The small G protein p21Ras is one critical molecular switch for relaying neurotrophic actions into morphological changes (Heumann et al. 2000). Manns et al. (2005) revealed that p21Ras within the pigeon's optic tectum depends on photic stimulation and produces left–right differences during development via altering the morphology of chemically specified cellular intratectal populations (Manns and Güntürkün 2005).

BDNF could translate asymmetrical visual input via two different mechanisms into left–right differences of morphology. First, asymmetrical intraretinal BDNF expression could shape the tectofugal system by anterograde trophic support. Second, retinal activity differences could secondarily regulate intratectal BDNF release in an asymmetrical manner. To decide between these two options, Manns et al. (2008a) injected BDNF into the right eye of dark-incubated pigeon embryos. Normally, these animals develop no visual lateralization. If intraretinal BDNF were responsible for igniting visual asymmetry, this extra portion of neurotrophins should mimic light stimulation asymmetry in light-incubated pigeon embryos and should result in a right eye dominance of these animals. But just the reverse was observed. Pigeons with BDNF injections into the right eye developed left eye superiority in visual discrimination tasks. Thus, it is more likely that light differently activates tectal neurons, which in turn produce left–right differences in tectal BDNF release. The unexpected finding that right eye BDNF injections result in left eye dominance shows that tectofugal asymmetry is not a matter of simple lateralized activity differences, but is due to asymmetrical intra- and intertectal differentiation processes. This is the topic of the next chapter.

Visual lateralization results from bilateral effects of asymmetric visual stimulation

The critical impact of intra- and intertectal mechanisms is supported by the observation that the consequences of asymmetric light stimulation are not confined to the stronger stimulated brain side. A detailed analysis of light- and dark-incubated animals reveals that visuomotor circuits are differentially adjusted in both hemispheres. Light induces an increase of visuoperceptual skills in the left hemisphere and a decrease of visuomotor speed in the right hemisphere (Skiba et al. 2002). The major effects of unilateral ocular manipulations can even be manifested within the primarily unaffected brain side. Transient silencing of retinal activity with TTX does not impair discrimination accuracy with the deprived eye, but enhances the performance of the non-affected eye. This means that monocular inhibition alters the activity balance between the left and the right eye system, eventually enhancing visuoperceptive skills in the activated hemisphere (Prior et al. 2004).

These bilateral effects after unilateral manipulations point to the critical impact of neuronal mechanisms controlling the balance between the left and the right hemispheric circuits. It is conceivable that especially inhibitory systems of the tectal complex are involved. Indeed, GABAergic tectal neurons are enlarged in the stronger stimulated left tectum (Manns and Güntürkün 2003). Additionally, the inhibitory tectotectal commissures provide an interhemispheric system, which controls the balance of activity between the left and the right. This system is functionally lateralized and inhibits the subdominant right tectum to a stronger degree than vice versa (Keysers et al. 2000). These intra- and intertectal inhibitory systems possibly constitute a feedback loop, which preserves asymmetric light effects into periods of symmetrical visual input (Manns and Güntürkün 1999a; Manns 2006).

Resume

Experimental evidences reviewed in this article highlight aspects of neuronal organization in the pigeon's visual system, which are critical for the generation and maintenance of a lateralized brain.

1. The pigeon's visual system displays hemisphere-specific differences that are mostly shared by all vertebrate classes. The left hemisphere excels in the discrimination of local features and is able to generate category-based decisions depending on the invariant properties of target stimuli. The right hemisphere, however, relies on stimulus configurations and possibly global cues of the stimuli and seems to form its decisions on a memory-based strategy.
2. This functional dichotomy is generated by a neuronal organization that is shaped by the interplay between bottom-up and down-down projection systems. They comprise: (a) bottom-up asymmetries, which are

implemented within the tectofugal pathway providing the left hemisphere with more bilateral information; (b) lateralized top-down input with a higher impact of the left forebrain in controlling information transfer in both brain halves.

3. Bottom-up and top-down systems converge onto subtelencephalic structures that give rise to inhibitory commissural projections. These projections in turn mediate lateralized cross talk between the hemispheres. Their action allows the integration of sensory input from the left and right sensory half fields to regulate a lateralized flow of information between the hemispheres.
4. This lateralized architecture of the visual system develops in response to asymmetrical visual input during embryonic development. But critical events during asymmetry formation happen also after hatching, during a time when light input is symmetrical. Thus, the establishment of a visual asymmetry proceeds in at least two steps: first, the ignition of asymmetry by minute left–right differences of stimulation; second, the establishment of morphological asymmetries that can take place without a biased input.
5. Visual asymmetries develop according to activity-dependent processes. This delineates a chain of events, which integrate asymmetry formation into ontogenetic plasticity. The establishment of visual asymmetries proceed with the same principles of synaptic plasticity that are well known from other sensory or motor systems.
6. Bihemispheric effects of asymmetrical visual stimulation require the action of commissural systems, which mediate the balance of left and right hemispheric circuits. It is likely that inhibitory mechanisms control these differentiation mechanisms. However, their cellular basis still has to be clarified.

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