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# Hemispheric Asymmetry in the Visual System of Birds

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The quest for the biological foundations of functional cerebral asymmetries has dominated lateralization research since the days of Broca (1865). Meanwhile, several anatomical asymmetries correlating with certain lateralized functions have been described in man. However, our knowledge of the ontogenetic variables that shape these structural asymmetries is still limited to an important extent (Previc, 1991). Likewise, we have few clues to how these asymmetries are translated into the lateralized functioning of a whole brain. Animal models can provide a powerful tool to permit detailed insights into the neuronal processes governing lateralized function. Avian visual lateralization is a particularly useful model because it not only allows experimental investigation of the interplay of neurobiological substrate and behavioral functions, but also provides an opportunity to study the ontogenetic events leading to asymmetries. Therefore the main emphasis of the following account is threefold. First, the behavioral framework of visual lateralization will be recapitulated in various species of birds. Then, the neuronal substrate of visual asymmetry will be outlined. Finally, the ontogentic scenario that ultimately results in a lateralized functional architecture will be described. The picture emerging from this overview will show that visual asymmetries in birds develop due to a tight interplay of genetic and epigenetic factors that finally, during a short critical period, mold ascending visual pathways into a lateralized status. Once the neuronal substrate is wired in this lateralized fashion, perceptual, cognitive, and motor systems start to function asymmetrically for the rest of the individual's lifetime.

## Tasks Favoring the Left Hemisphere

Birds are the most visually dependent class of vertebrates, and the statement of Rochon-Duvigneaud (1943) that a pigeon is nothing but two eyes with wings is probably valid for most avian species. Man, a highly visual primate, sees the world with the information transmitted by about 1 million fibers within each optic nerve. This is only 40% of the number of retinal axons counted in a single optic nerve of pigeons and chicks (Binggeli & Paule, 1969; Rager & Rager, 1978). The acuity of many birds of prey surpasses that of other living beings (Fox et al., 1976), and even the unspecialized pigeon excels relative to humans in its ability to discriminate luminances (Hodos et al., 1985) and to discern subtle color differences (Emmerton & Delius, 1980). However, the most important advantage of the avian model for asymmetry research is not its visual specialization, but the ease with which each hemisphere can be tested virtually separately. The optic nerves in birds decussate nearly completely, and only less than 0.1% of the fibers proceed to the ipsilateral side (Weidner et al., 1985). Since only limited numbers of axons recross via mesencephalic and thalamic commissures, the avian visual system is remarkably crossed.

This anatomical condition enables the use of eyecaps to study the performance of the animals with sight restricted to one eye, and thus mainly the contralateral hemisphere. With this procedure, visual lateralization can be demonstrated using a wide range of techniques. Using the right eye, adult pigeons are superior in discriminating two-dimensional artificial patterns (Güntürkün, 1985) and three-dimensional natural objects (Güntürkün & Kesch, 1987). These results are very similar to experiments with zebra finches (Alonso, 1998) and with chicks tested with the pebble-floor task. Here, young chicks peck food grains from a background of small pebbles that are stuck to the floor. The animals usually learn to discriminate food from pebbles within 60 pecks. Under either left- or right-eye learning conditions, their performance is higher with the right eye/left hemisphere (Hambley & Rogers, 1979; Mench & Andrew, 1986). In pigeons this greater visual processing capacity of the right eye system in pattern discrimination also leads to a higher degree of illusion of this side when being confronted with geometrical optic illusions (Güntürkün, 1997b).

All experiments summarized up to now employed a positive and a negative stimulus that had to be distinguished. A new aspect of avian visual lateralization emerges if more than two stimuli are used to induce a memory load. In a visual memory task pigeons learned under binocular conditions to discriminate between 100 negative (S−) and 625 positive (S+) artificial patterns. The stimuli had been randomly assigned to these two categories (figure 1.1). After reaching criterion, the birds were tested alternately with their left or right eye seeing. The pigeons were able to remember most of the 725 patterns with their right eye, but were barely above chance level with their left (Fersen & Güntürkün, 1990). This experiment suggests that visual engrams learned during training were stored, at least in part, unilaterally in the dominant left hemisphere, although both eyes had equal access to the patterns during acquisition.

Indeed, the existence of such unilateral memory stores with limited access by the other hemisphere could be shown in another complex task in which pigeons had to distinguish symmetric from asymmetric patterns. In this study they faced two vertically arranged pecking keys on which the same patterns were displayed. If these two identical patterns were symmetric, the animals had to peck the lower key; if they were asymmetric, the upper key was correct. Pigeons needed about five months to learn this conjunction of stimulus class and location. Up to that point they did not wear eyecaps. Then they were to proceed with the left or the right eye open, alternately. This new condition revealed that most animals had learned the task with their right eye/left hemisphere. The other side was completely naive, and in some birds needed an additional five months to catch up with the "knowing" hemisphere (Güntürkün, 1997a). This experiment is a very dramatic demonstration of unilaterality of engrams.

Such unilateral storage is not restricted to pigeons but has also been demonstrated, albeit for shorter time spans, with chicks (Gaston & Gaston, 1984), macaques (Doty et al., 1973), and even humans (Risse & Gazzaniga, 1978). Thus, it is likely that the avian left hemisphere stores large amounts of acquired pattern information to which the right hemisphere has only limited access.

It is probably this asymmetry in memorizing visual stimuli that results in a significant right eye advantage when homing from a distant release site over known territory to the loft (Ulrich et al., 1999). Homing makes great demands on spatial orientation. To find a left hemisphere

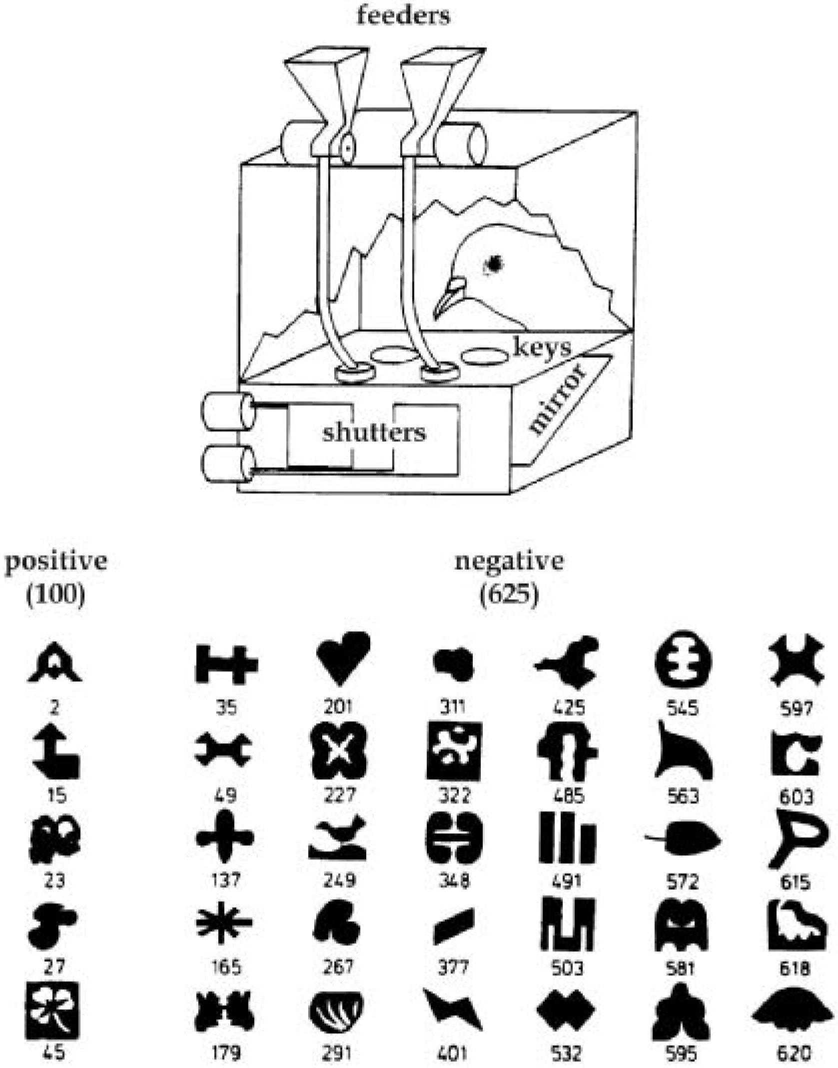

**Figure 1.1** Setup and some of the stimuli used in the study of Fersen and Güntürkün (1990). Two out of 725 stimuli (100 positive [S+], 625 negative [S−]) were backprojected onto the vertical pecking keys with S+ and S− randomly changing between left and right. (Adapted from Fersen & Güntürkün, 1990.)

advantage during homing is therefore astonishing, considering the large body of data showing a right hemisphere dominance for visuospatial tasks. However, spatial orientation is a multicomponent feature in which several cognitive processes with diverse cerebral asymmetries interact (Hellige, 1995). It is therefore conceivable that the pigeons used a cognitive strategy that is more left-hemisphere based. As discussed by Ulrich et al. (1999), it is likely that the birds utilized visual memory-based snapshot tracking to pursue visual features along their prelearned route. Due to their left-hemisphere dominance for memorizing and discriminating visual features, the homing task was therefore probably performed by a succession of visual feature discriminations. If pigeons are tested in a maze where they cannot utilize this strategy, the left hemisphere advantage vanishes (Prior & Güntürkün, 2001).

Visual lateralization also affects cognitive processes of the animals. Diekamp et al. (1999) tested pigeons under monocular conditions in successive color reversals. The animals learned to favor green (S+) over red (S−) until reaching learning criterion. Then the conditions were changed; red was now rewarded (S+) and green was not (S−). As soon as the pigeons successfully learned the reversal, conditions were altered again, and so on. One group of animals performed 30 reversals under right-eye-seeing, and the other group under left-eye-seeing, conditions. After a couple of reversals both groups showed a "learning-to-learn" effect such that each reversal was achieved with fewer trials. Reversal learning can be described best on a mathematical basis by an exponential function of the type $y = a + \exp^{(b-cx)}$ with $a$ representing the asymptote (i.e., the error rate around which the performance oscillates after several reversals), $b$ determining the starting value of the function for the first reversal, and $c$ representing the steepness of the curve (i.e., the rate of error reduction over successive reversals). For both $a$ and $c$, Diekamp et al. (1999) could reveal a right eye superiority. Thus, using the right eye/left hemisphere, the animals were faster in understanding the basic principle of this experiment ($c$) and exhibited a higher level of performance after reaching asymptote ($a$). Visual lateralization in birds, therefore, not only consists of asymmetries in simple pattern recognition and memorization processes, but also affects "cognitive" systems that extract general properties of the visual world.

The behavioral asymmetry summarized in these studies is very likely not due to simple psychophysical differences between the eyes (but see Hart et al., 2000, in starlings), but involves differences in "higher" functions that affect hemisphere-specific performances in cognitively demanding tasks. This conclusion is supported by studies showing no left-right differences in purely psychophysical tasks: There are no asymmetries in acuity (Güntürkün & Hahmann, 1994), in depth resolution (Martinoya et al., 1988), or in wavelength discrimination (Remy & Emmerton, 1991). That visual lateralization is generated by central mechanisms is additionally shown by experiments revealing asymmetrical effects of unilateral lesions or pharmaceutical insults of the left or the right hemisphere (Howard et al., 1980; Güntürkün & Hoferichter, 1985; Güntürkün & Hahmann, 1999; Deng & Rogers, 1998a).

**Interim Summary** When distinct features of visual objects have to be identified, memorized, and/or categorized, a right eye/left hemisphere dominance arises in all avian species studied up to now (Andrew, 1991). This right eye superiority is valid for the majority of individuals of a population (65–79%, Güntürkün, 1997b; Güntürkün et al., 2000), indicating a clear population asymmetry.

### Tasks Favoring the Right Hemisphere

None of the avian hemispheres completely dominates visual analysis, but cerebral asymmetries are organized in complementary specializations for different kinds of stimuli within the visual scenery. If birds have to encode spatial configurations, a left eye/right hemisphere superiority can be demonstrated (but see the discussion above for homing data from Ulrich et al., 1999). This was clearly shown by Rashid and Andrew (1989). They trained chicks to find food buried under sawdust in an arena. When the chicks were tested monocularly without food, birds under monocular left conditions searched from posthatch day 9 onward in the two areas specified by cues, while chicks in the monocular right condition searched randomly over the complete arena.

The lateralized role of different spatial and nonspatial cues 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 that they can retrieve many days later with astounding accuracy (Shettleworth, 1990). 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 (Clayton & Krebs, 1994) four feeders were used that were distinguishable by their specific location and by markings that made them visually unique. Under monocular conditions birds were given parts of a nut in one out of four feeders 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 reentered and were allowed to retrieve the rest of the nut with the same eyecap condition. With the left eye, marsh tits looked for the seed at the correct spatial location, while they relied on object-specific cues when using the right eye. Thus, the right hemisphere used spatial cues, while the left half of the brain utilized object cues to locate the nut.

Vallortigara and colleagues were able to design a variety of ingenious tasks that demonstrate a similar pattern of results in chicks. In one of these experiments (Vallortigara, 2000; Tommasi & Vallortigara, 2001), chicks were trained to find food under sawdust by scratching ground in the center of a square arena. The position of the food was indicated by its geometric position (arena center) and by a conspicuous landmark, which also was placed centrally (figure 1.2). After learning attainment, the landmark was displaced to a novel position so as to generate conflicting local (the landmark) and global (the center of the arena) information. Chicks viewing with their left eye (right hemisphere) still searched in the center, completely ignoring the new location of the landmark. Right-eye chicks (left hemisphere) did exactly the opposite, searching close to the landmark and ignoring the global spatial information provided by the environment. Binocular-seeing chicks were mainly relying on right hemisphere mechanisms and scratched in the arena's center. Thus, different species of birds utilize left hemisphere mechanisms if relying on object cues and right hemisphere functions if using spatial cues. Chicks also scrutinize the stimuli mainly with their right eye when object-specific cues are to be used, but look mainly with their left eye when spatial cues have to utilized (Vallortigara et al., 1996).

Besides spatial tasks, visually guided social recognition also seems to be a domain of the right hemisphere. If chicks have to choose in a runway between a cagemate and an unfamiliar chick, male animals decide for the stranger, while females take the cagemate (Vallortigara & Andrew, 1994). Under monocular conditions these sex-dependent choice patterns persist when using the left eye, whereas the animals behave at random when using the right (Vallortigara, 1992). This has also been shown with the social pecking test, which takes advantage of

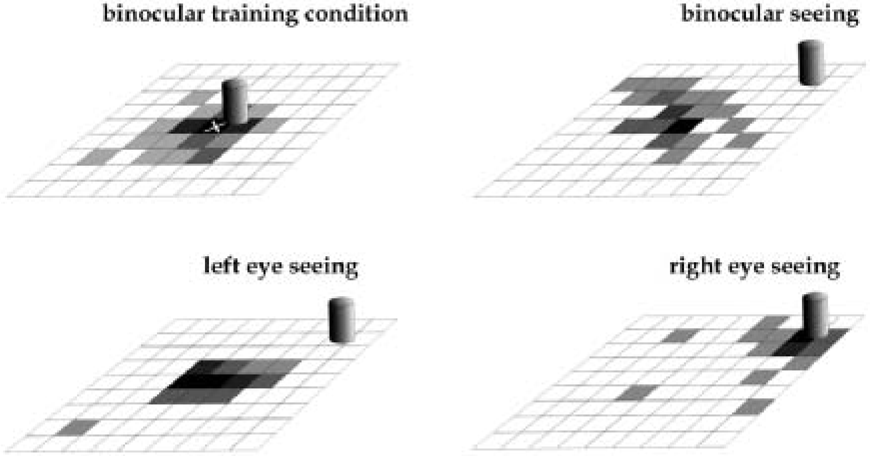

**Figure 1.2** Search behavior of chicks trained to find food in the center of a square arena next to a conspicuous object. The upper left picture depicts areas of searching intensity under binocular conditions after initial training. The darker the areas, the more often the chicks searched under sawdust. The other three pictures show the results after displacement of the landmark to a novel position, inducing a conflict between geometry-based and object-based spatial codings. After landmark displacement, chicks were tested under binocular, left-eye, and right-eye seeing conditions. Right and left hemispheres seem to code for geometry- and object-specific cues, respectively. (Adapted from Vallortigara, 2000.)

the marked xenophobia exhibited by young socially reared chicks toward unfamiliar conspecifics, which become the target of aggressive pecking bouts. If young chicks wearing eyecaps are confronted with both a familar and an unfamiliar bird, they mainly peck the stranger when viewing with the left eye, while their aggressive encounters against the other two animals are random under monocular right conditions (Vallortigara, 1992). These data indicate that right hemisphere processes are of prime importance for social recognition. Up to now this has been demonstrated only in preference tests where it is up to the animal to behave in a certain way. Whether the results of these preference tests will reveal the same data pattern as in forced discrimination studies is presently an open question.

**Interim Summary** When birds have to locate food in a complex environment, they rely on object-specific cues when seeing with the right eye and on geometric information when seeing with the left. In preference tests it can be shown that visually guided social recognition also seems to be a right hemisphere domain. However, it is at present unclear how the pattern of right hemisphere dominances for social recognition and the previously reviewed data on a left hemisphere superiority in visual feature categorization can be matched, since a social companion first has to be recognized as a visual object, which is a typical left hemisphere task. It is conceivable that social cues are rich in emotional (Vallortigara & Andrew, 1994) or movement information, and thus may be treated differently from static visual cues (Dittrich & Lea, 1993).

## ANATOMICAL SUBSTRATES FOR VISUAL LATERALIZATION

In birds, retinal information to the forebrain is processed by two parallel pathways: the tectofugal system and the thalamofugal system, suggested to be equivalent to the extrageniculo-cortical and the geniculo-cortical visual pathways of mammals, respectively (Shimizu & Karten, 1993). The avian tectofugal pathway is composed of optic nerve fibers projecting to the contralateral optic tectum, from which fibers lead bilaterally to the thalamic n. rotundus (Rt) and n. triangularis (T), which themselves project to the ipsilateral ectostriatum (E) of the forebrain (figure 1.3). The thalamofugal pathway projects from the retina via the contralateral n. geniculatus lateralis, pars dorsalis (GLd) bilaterally to the visual Wulst in the telencephalon (see figure 1.5) (Güntürkün, 2000). The tectofugal and thalamofugal pathways have been shown to constitute structural asymmetries related to lateralized visual behavior in pigeons and chicks, respectively.

### The Tectofugal Pathway

In the asymmetry experiments with pigeons, the stimuli fell into the frontal binocular visual field of the animals. Since this portion of the visual field is mainly represented within the tectofugal pathway in pigeons (Hellmann & Güntürkün, 1999; Güntürkün & Hahmann, 1999), it is conceivable that it is mainly the tectofugal system which generates visual lateralization in this species (figure 1.3).

About 90% of all retinal ganglion cells project to the tectum in pigeons (Remy & Güntürkün, 1991). The optic tectum is a highly complex neural entity in which even simple histological techniques visualize

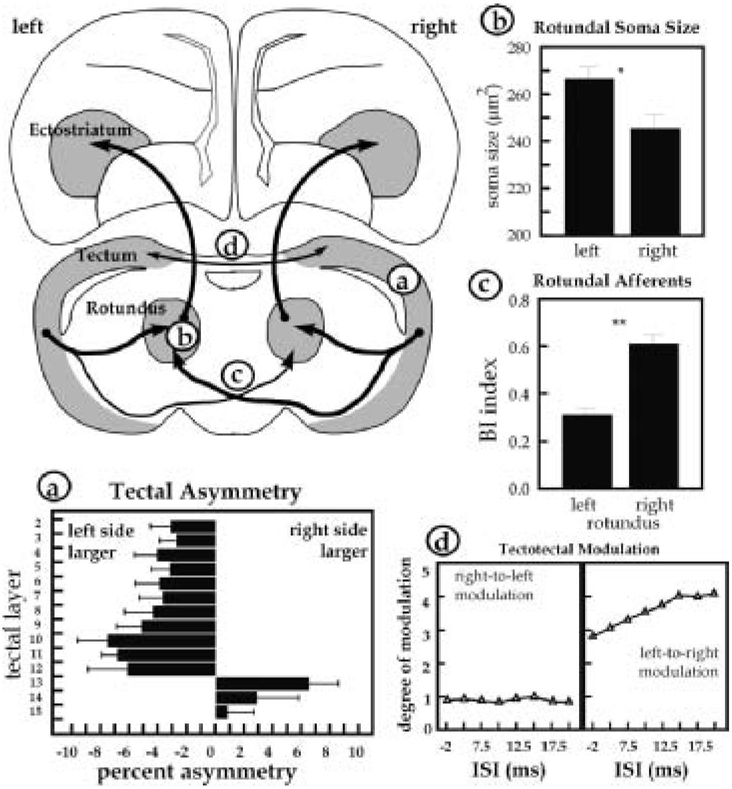

**Figure 1.3** Schematic view of the tectofugal visual pathway as seen in frontal sections. Letters within the figure indicate areas or connections for which asymmetries were described. (*a*) Morphological asymmetries of neuronal somata in different tectal layers. Layer 1 is not shown because it consists of fibers. Left or right skews of histograms depict larger somata on the left or right tectal side for this layer, respectively. Note consistent left skews in layers 2–12, which are mostly visual. (Based on Güntürkün, 1997c.) (*b*) Average soma size of rotundal neurons on the left or the right side. (Based on Manns & Güntürkün, 1999b.) (*c*) Bilaterality of rotundal afferents from the ipsilateral and the contralateral tectum. An index of 0 decribes absolute symmetry, while 1 constitutes a system that is characterized by ipsilateral afferents only. The significant difference in the bilaterality index points to a larger proportion of contralateral tectal afferents in the left rotundus. (Based on Güntürkün et al., 1998.) (*d*) Asymmetries of tectotectal modulation. Electrical stimulation of the right tectum was unable to substantially modulate the amplitude of a visual evoked potential recorded within the left tectum (right-to-left modulation), regardless of different interstimulus intervals (ISI). However, electrical stimulation of the visually dominant left tectum resulted in much higher modulations of visually evoked potentials within the right tectum (left-to-right modulation). (Based on Keysers et al., 2000.)

15 laminae (Ramón y Cajal, 1911). In pigeons, a morphometric study of tectal perikarya sizes revealed morphological asymmetries with the superficially located retinorecipient cells being larger on the left side, contralateral to the dominant eye (Güntürkün, 1997c). This is also the case for the n. rotundus, the next tectofugal entity (Manns & Güntürkün, 1999b). Thus, the pigeon's tectofugal system displays significant morphological asymmetries that might be related to the behavioral lateralization of the animals.

Tectal lamina 13 neurons project bilaterally onto the n. rotundus (Hellmann & Güntürkün, 1999). The bilaterality of this projection should lead to representations of both the ipsi- and the contralateral eye in the tectofugal system of each hemisphere. Indeed, Engelage and Bischof (1993) were able to show that binocular input is represented in the ectostriatum. In pigeons, Güntürkün et al. (1998) demonstrated with anterograde and retrograde tracers that the ratio of ipsi- to contralateral tectorotundal projections is asymmetrically composed. While the number of ipsilateral tectorotundal projections is about equal, the number of neurons projecting contralaterally from the right tectum to the left rotundus is about twice the number in the opposite direction (Güntürkün et al., 1998). As a result, the n. rotundus on the left side receives, beside a massive ipsilateral tectal input, a large number of afferents from the contralateral tectum. Consequently, the visual input of the n. rotundus that projects to the left hemisphere is bilaterally organized to a significantly higher degree than its counterpart in the right halfbrain. Functionally, this anatomical condition could enable the left rotundus to integrate and process visual inputs from both eyes, and thus from both sides of the bird's visual world. Indeed, a study has shown that left rotundal processes are significantly related to acuity performance with the right and the left eye, whereas right rotundus participates only in binocular acuity (Güntürkün & Hahmann, 1999).

These data on the tectofugal system suggest that visual asymmetry is anatomically wired, and thus probably "static" and unmodifiable over the lifetime. However, several lines of evidence suggest this assumption is incomplete. If the tectal and the posterior commissures, which connect the tecta of both hemispheres, are transsected, visual lateralization reverses to a left eye dominance; this laterality reversal is proportional to the number of transsected fibers (Güntürkün & Böhringer, 1987) (figure 1.4). If hemispheric asymmetry is reversed by tectal commissurotomy, it is likely that this asymmetry was maintained pre-

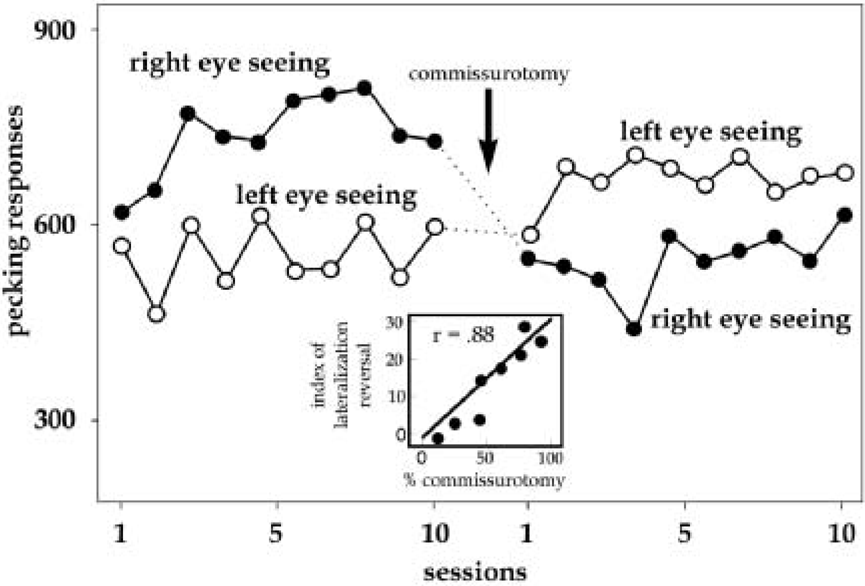

**Figure 1.4** Lateralization reversal after tectal commissurotomy in pigeons. Pigeons performed a pattern discrimination with right eye or left eye seeing. Preoperatively, significantly more pecks on the correct pattern were made with the right eye seeing; this lateralization changed after commissurotomy. The inset shows that the degree of asymmetry change, as expressed with an index, was significantly related to the extent of the commissurotomy. (Based on Güntürkün & Böhringer, 1987.)

viously, at least partly, by asymmetrical interactions between the tecta (see also Parsons & Rogers, 1993) that are known to be primarily inhibitory (Robert & Cuénod, 1969; Hardy et al., 1984). Keysers et al. (2000) tested this hypothesis by recording field potentials from left or right intratectal electrodes in response to a stroboscope flash to the contralateral eye and an electrical stimulation of the contralateral tectum. They found that the left tectum was able to modulate the flash-evoked potential of the right tectum to a larger extent than vice versa. This lateralized interhemispheric cross talk thus could constitute an important "dynamic" component of asymmetric visual processing (figure 1.3).

This result makes it likely that the emergence of visual asymmetry in pigeons is related to a dual coding of left-right differences. Thus, visual lateralization cannot be explained entirely by the anatomical differences between left and right components of the tectofugal pathway. Obviously a second, more dynamic component exists that is able to modulate neural processes of the optic tecta in an asymmetrical manner. Altering this second dynamic component, as in the commissurotomy experiment of Güntürkün and Böhringer (1987), results in an important alteration of visual asymmetry.

**Interim Summary** The pigeon's tectofugal pathway displays numerous morphological asymmetries that are probably related to the visual lateralization at the behavioral level. On the left side of the brain, which dominates object recognition mechanisms, soma sizes of most visual cells are larger. In addition, the left n. rotundus integrates input from both eyes to a greater extent than the right rotundus. In addition to these structural left-right differences, the tecta inhibit each other differently, with the left tectum modulating visual processes of the contralateral side to a greater degree than vice versa. Thus, visual asymmetry within the tectofugal pathway is dually coded by structural and by dynamic properties.

### The Thalamofugal Pathway

At first glance the general organization of the thalamofugal pathway seems to be similar in pigeons and chicks. However, in contrast to pigeons (Hodos et al., 1984), thalamofugal lesions affect frontal viewing in chicks importantly (Deng & Rogers, 1997). This suggests that, unlike pigeons, the frontal field is represented within the thalamofugal system in chicks. But this is not the only difference between chicks and pigeons. As will be outlined below, the organization of tecto- and thalamofugal pathways also seems to be different with respect to asymmetry in chicks and pigeons.

With unilateral injections of retrograde tracers into the Wulst label cells in the GLd of both sides (figure 1.5), the ratio of contralaterally to ipsilaterally labeled GLd neurons is higher after right-sided than after left-sided Wulst injections in 2-day-old chicks (Rogers & Sink, 1988). As shown by Rogers and Deng (1998), this lateralized ratio difference is due to a higher number of fibers from the left thalamus to the contralateral right forebrain than vice versa. The asymmetry of the crossed thalamotelencephalic projection is pronounced in young males but disappears at about three weeks of age, consistent with the behavioral

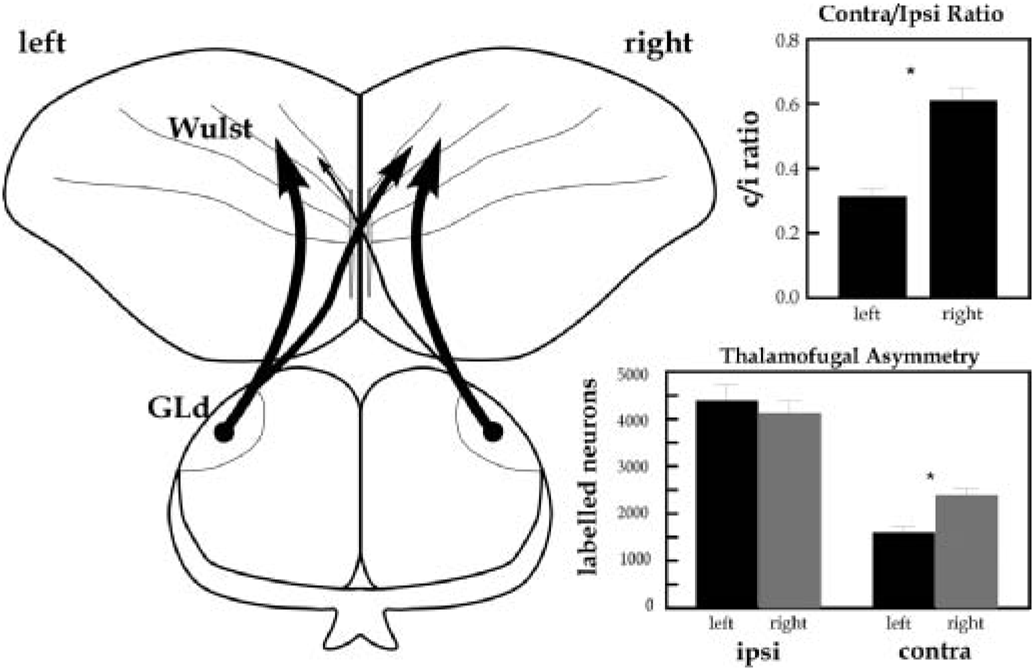

**Figure 1.5** Schematic view of the chick's thalamofugal visual pathway in frontal sections. The crossed projections from the left nucleus geniculatus lateralis pars dorsalis (GLd) to the right Wulst are more numerous than vice versa. The upper right histogram shows that the ratio of contralateral to ipsilateral fibers (c/i ratio) is significantly higher in the right Wulst. The lower right histograms depict that this asymmetry is mainly due to the number of contralateral afferents to the Wulst. (Based on Rogers & Deng, 1999.)

data on lateralized performance in the pebble-floor task (Adret & Rogers, 1989; Rogers, 1996). The asymmetry of the contralateral thalamofugal projections of female chicks is lower, but present and in the same direction as in males (Rajendra & Rogers, 1993). This sex difference in the degree of this connectional asymmetry could be an explanation for the gender difference in lateralized performance, which is more pronounced in male chicks (Zappia & Rogers, 1987).

The sex difference in visual asymmetry of chicks indicates a role of steroids. Indeed, injections of 17$\beta$-estradiol ($E_2$) in unhatched male embryos increases the number of forebrain-projecting GLd neurons and thus abolishes thalamofugal asymmetry, probably due to a ceiling effect (Rogers & Rajendra, 1993). Thus, the reduced behavioral asymmetry in females (Zappia & Rogers, 1987) might be due to their higher levels of circulating estradiol during a sensitive period and the subsequent increase in the number of GLd relay cells, which overshadow the projectional asymmetry observed in males. Injection of testosterone also reduces structural asymmetry in the thalamofugal projection in females and even reverses the thalamofugal asymmetry of males (Schwarz & Rogers, 1992). The reversal in male chicks is accompanied by a reversal of eye dominance in visual discrimination (Zappia & Rogers, 1987). Thus, the development of visual lateralization in chicks is fundamentally influenced by circulating sex steroids.

**Interim Summary** The thalamofugal pathway of chicks was shown to be asymmetrically organized with respect to the contralaterally ascending thalamotelencephalic components. Changes in the degree of this asymmetry correlate with alterations of visual lateralization. This pattern is sex-dependent, with males having more pronounced left-right differences.

### Species Differences in Asymmetrical Organization of Visual Pathways

Since visual lateralization in pigeons and chicks is similar at the behavioral level, a comparable organization of their neural asymmetries would be expected. Studies, however, have shown this not to be the case. While the thalamofugal pathway of pigeons is “frontally blind” (Remy & Güntürkün, 1991), there is strong evidence in chicks that this pathway receives input from the frontal visual field (Wilson, 1980; Deng & Rogers, 1997). Therefore, at the level of the retinothalamic projections, the thalamofugal system already seems to be organized differently in these two species.

A further point of divergence is the asymmetrical projections within the thalamo- and the tectofugal systems. In pigeons, the number of projections from the right tectum to the left rotundus is larger than from the left tectum to the right rotundus (Güntürkün et al., 1998). This condition creates a higher degree of bilateral representation in the left tectofugal pathway, which is functionally dominant for object discriminations (Güntürkün & Hahmann, 1999). The case is different with chicks, in which no asymmetry can be found in the overall tectorotundal projections (Deng & Rogers, 1998b; Rogers & Deng, 1999). Thus, the organization of the tectofugal pathway differs markedly in chicks and pigeons.

The same applies to the thalamofugal pathway. While in chicks there is a significantly higher number of contralateral fibers from the left GLd to the right Wulst (Rogers & Deng, 1999), a comparable asymmetry is absent in pigeons (Hellmann et al., in preparation). These species differences in asymmetry are accompanied by differences in the detailed composition of ascending projections: In pigeons the crossed projection from the GLd onto the contralateral Wulst is constituted by a large number of bilaterally projecting neurons (Miceli et al., 1990). In chicks, however, ipsi- and contralaterally projecting GLD cells come from different neuronal populations (Deng & Rogers, 1998a). In addition, the asymmetry of the thalamofugal system is sex-different in chicks (Rogers & Rajendra, 1993), while in pigeons there is, at least at the behavioral level, no evidence for a sex dependency of visual asymmetry (Güntürkün & Kischkel, 1992).

These differences between chicks and pigeons could reflect a simple species effect in the anatomy of the ascending systems. However, it is also possible that they result from age differences, since the data have been collected from adult pigeons and young chicks. In fact, age is known to affect the thalamofugal projections, with GLd-Wulst asymmetries disappearing by the time the animals are three weeks old (Rogers & Sink, 1988). Therefore, the species effect might arise due to the differences between the developmental speed of chicks and pigeons. Chicks are precocial animals that are active directly after hatch. Consequently, both visual systems seem to be functional at hatch in chicks (Mey & Thanos, 1992). This is remarkably different in the altricial pigeon, where the embryonic visual pathways are far less functional. There is evidence that retinotectal projections become functional shortly before hatch (Manns & Güntürkün, 1997), but the animals hatch with their lids closed and are initially unable to perform complex visuomotor behaviors. Up to now any information on the maturation of the thalamofugal system is lacking in pigeons. Since prehatch light input is of decisive importance for the maturation of the ascending visual pathways (see below), it is conceivable that the species differences between chicks and pigeons are triggered by their different maturational speed.

**Interim Summary** Although seemingly similar, visual lateralization in chicks and pigeons is generated by different visual systems. In both animals the contralateral components of the ascending projections are asymmetrically organized, with the thalamofugal and the tectofugal systems being the critical pathways in chicks and pigeons, respectively. These differences in neuronal wiring might be due to the maturational speed being slower in pigeons than in chicks. This could generate species-specific differences of the ontogenetic conditions that affect the developing visual systems of chicks and pigeons.

## Asymmetries of Associative Forebrain Structures: Imprinting

The important role of left hemispheric forebrain structures becomes especially evident when using stimuli for which chicks have a predisposition, as in imprinting studies. When young chicks are exposed to a visually conspicuous object, they approach it, learn its characteristics, and form a social attachment to it. In natural conditions the object is usually the hen, but it need not to be; a wide range of objects will do, though some are more effective than others. Given a choice between a stimulus to which it was exposed and a different object, a chick will prefer the training stimulus and will actively avoid the other one.

Evidence from autoradiographic and lesion studies suggests that the intermediate part of the hyperstriatum ventrale (IMHV), an associative forebrain structure, is part of a memory system in which the representation of the imprinting stimulus is at least partly stored (Horn, 1991). The IMHV partly overlaps with the more ventrally located mediorostral neostriatum/hyperstriatum ventrale (MNH), which is especially involved in processing auditory imprinting stimuli (Bredenkötter & Braun, 2000). Neurons in the left and right IMHV are active during imprinting learning, as judged by the number of neurons expressing Fos-like immunoreactivity about 1 h after the end of training, and expression of this protein increases with the strength of learning (McCabe & Horn, 1994). At about 60 min after imprinting, however, the changes that can be detected in the right IMHV diverge from those in the left. The protein kinase C mediated phosphorylation of proteins that have the capacity to contribute to synaptic plasticity increases in left IMHV (Meberg et al., 1996). Consequently, strongly imprinted animals develop, on the average, 10% larger postsynaptic densities in the left IMHV than in the right, with the values of the right IMHV not being different from controls (Bradley et al., 1981). The amount of binding to NMDA receptors in the left, but not in the right, IMHV correlates significantly with the behavioral preference scores of the chicks for the imprinting stimulus (McCabe et al., 1982). Since morphological changes are a prerequisite for long-term synaptic plasticity, Solomonia et al. (1997, 1998) studied clathrin proteins and neural cell adhesion molecules (N-CAMs), which are both involved in synaptic remodeling. They found higher amounts of clathrin and N-CAM in the left IMHV 24 h after learning, with both clathrin and N-CAM amounts correlating with learning strength of imprinting.

Bilateral IMHV lesions impair imprinting but have no effect on visual associative learning in general (Johnson & Horn, 1986). These lesions also impair sexual imprinting, so that lesioned adult females no longer show clear preferences for males that are selected by control females (Bolhuis et al., 1989). The neurobiological differences between left and right IMHV suggests that the two hemispheres participate differently in the imprinting process. Indeed, studies in which the IMHV of the left and the right side were lesioned sequentially support this assumption. These experiments suggest that the left IMHV is important for the first acquisition and also can act as long-term store. The right IMHV acts as a buffer store, passing information out to further, probably distributed, long-term stores over a period of about 6 h (Horn & Johnson, 1989). Due to this sequence of processes, a chick that receives a left IMHV lesion 3 h after imprinting, followed 26 h later by lesioning of the right IMHV, can recall the memory on retest because in this case the engram could successfully be transferred to structures outside the IMHV (Cipolla-Neto et al., 1982).

Thus, both IMHVs contribute to imprinting (Johnston & Rogers, 1998), albeit with functional differences. These differences are reflected in the single unit properties of left and right IMHV neurons. About 30% of cells within this structure respond highly selectively to the familiar imprinting object, irrespective of left or right (Brown & Horn, 1994; Nicol et al., 1995). The difference between the hemispheres seems not to be related to the training stimulus but to the stimuli that were *not* used for imprinting training. While for the left IMHV, training results in an increase of cells responding to the training stimulus without affecting responses to the other stimuli (Brown & Horn, 1994), the same increase occurs in the right IMHV, but is associated with a decrease in sites responding to the alternative stimuli (Nicol et al., 1995). These alterations should result in an overall higher signal-to-noise ratio in the right IMHV. Taking these single unit data into account, Nicol et al. (1995) assume that the lack of ultrastructural and molecular changes observed in the right IMHV after imprinting is not due to an absence of changes, but to the presence of two contrary events, one increasing synaptic efficiency for the trained stimulus, and one decreasing efficiency for the untrained stimulus. Obviously the simpler changes in the left IMHV suffice for recognition in the context of imprinting tests of animals with right IMHV lesions. However, these chicks are unable to utilize the training stimulus as an S+ in subsequent visual discrimination tasks (Honey et al., 1995). Only chicks with an elaborate representation in different forebrain areas manage this transfer, and the differentiated alterations in right IMHV synaptic structure seem to be a prerequisite for the formation of a distributed memory store with widespread effects for the adult animal.

**Interim Summary** Young chicks very quickly form an attachment to a conspicuous object. This imprinting learning requires the forebrain IMHV to be intact. Left and right IMHV contribute differently to this learning process. While the left IMHV seems to be essential during initial learning, the right IMHV is essential to induce processes that subsequently stabilize and elaborate the imprinting engram.

### Asymmetries of Associative Forebrain Structures: One-Trial Avoidance Learning

Young chicks peck spontaneously at small, conspicuous objects, and thus learn to discriminate between unpleasant and tasty items. If they are confronted with a small, bright bead coated with the bitter-tasting substance methylanthranilate (MeA), their pecking behavior is followed by an intense disgust response. Subsequent tests with the same bead lead to avoidance. This highly discrete passive avoidance learning (PAL) is accompanied by a number of lateralized events in the forebrain.

If chicks acquire PAL under binocular conditions with a bead of a certain color and are subsequently tested monocularly, they avoid all beads, irrespective of their color, with the left eye, but are selective for the color used during training with their right eye (Andrew, 1988). Thus, it is conceivable that the more specific memory trace has been laid down in the left hemisphere. This assumption is supported by 2-[$^{14}C$] deoxyglucose (2-DG) experiments which demonstrate that 2-DG injected shortly before training leads to higher radioactivity scores in the left IMHV and the left lobus parolfactorius (LPO) (Rose & Csillag, 1985). The early phase of memory consolidation involves a cascade of synaptic events that seem to hold the trace briefly and simultaneously initiate the gene activation processes required for long-term memory (Rose, 1995). In brief, these steps first require an increased glutamate receptor binding in the left, but not the right, IMHV (Stewart et al., 1992); a concomitant upregulation of NMDA (Steele et al., 1995); then a pre- and postsynaptic $Ca^{2+}$ flux (Salinska et al., 1999). The increased opening of $Ca^{2+}$ channels, combined with further molecular events, leads to an activation of the immediate early genes c-fos and c-jun (Anokhin & Rose, 1991), which probably initiate pre- and postsynaptic structure alterations.

These asymmetric morphological alterations are generally more pronounced in the left IMHV and have been analyzed at the ultrastructural level. Some of these lateralized changes show up within the first hour after PAL: the number of synapses per volume neuropil are significantly larger in the left but not in the right IMHV after training; similarly, posttraining vesicles per synapse are about 60% more numerous in the left IMHV (Stewart et al., 1984). Some other asymmetries exist before training, but are subsequently abolished or even reversed: The number of synaptic vesicles per volume neuropil are larger on the right in control animals, while this asymmetry is reversed after PAL (Stewart et al., 1984). These synaptic changes are accompanied by a reversal in the number of dendritic spines on large multipolar projection neurons. These were found to be more numerous in the right IMHV of unlearned animals, but subsequent to training there was an increase in number on the left such that this hemispheric asymmetry disappeared (Patel et al., 1988a, b).

Morphological changes after PAL are not restricted to the IMHV, but are also observed in the LPO and the paleostriatum augmentatum (PA), two structures that correspond to the dorsal corpus striatum of mammals. While the initial acquisition of memory involved largely transient changes in the spatial organization of synapses in the left IMHV, longer-term changes are more prominent in the LPO and involve a bilateral, albeit predominantly left-sided, increase in synaptic density and height (Stewart & Rusakov, 1995; Rose & Stewart, 1999).

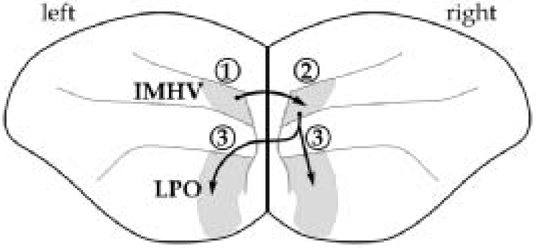

**Figure 1.6** Schematic frontal section through the forebrain of a chick showing the position of the intermediate medial hyperstriatum ventrale (IMHV) and the lobus parolfactorius (LPO). According to the "memory flow" model of Rose (1991), the engram for passive avoidance learning is first held in the left IMHV (1), then moves to the right IMHV (2), and then is further transmitted to the LPO of both hemispheres (3).

Lesion studies demonstrated asymmetric effects of unilateral IMHV and LPO lesions, and in addition support a model in which the memory trace after training is not fixed to a certain area but "flows" from one structure to the other (Rose, 1991; figure 1.6). The presence of an intact left IMHV seems to be a necessity for a long-term acquisition of PAL, and consequently pretraining lesions of this area make the animals amnesic shortly after the learning session. However, if the animals have learned the task and the left IMHV is lesioned 1 h after training, the chick is not amnesic (Patterson et al., 1990). The engram seems to have left the IMHV of the left hemisphere for yet another store, and it is likely that this second store is the right IMHV, followed, within about an hour, by the third store, which is LPO (Gilbert et al., 1991). It is yet to be determined what this "flow" actually is. Probably the engrams are not translocated from one store to another, but memory consolidation or mechanisms of retrieval require different forebrain areas to be activated successively.

**Interim Summary** After a single exposure, chicks learn to avoid pecking a bead with a bitter substance. IMHV, the forebrain structure that is of prime importance for imprinting, also seems to be essential for this kind of one-trial avoidance learning. The first and most prominent cellular changes after the first peck seem to occur in the left IMHV, but the right IMHV and, most important, both sides of the LPO (parts of the basal ganglia) are subsequently involved. Thus, the trace seems to "flow" from one area to the next in a lateralized fashion.

**Figure 1.7** A pigeon embryo during hatching. Note the position of the head, which is bent forward and points to the right. The right wingbud rests on the beak.

## THE DEVELOPMENT OF AVIAN VISUAL LATERALIZATION

Embryos of virtually all avian species keep the head turned so that the right eye is exposed to light shining through the translucent shell while the left eye is occluded by the body (Kuo, 1932) (figure 1.7). Since brooding parents regularly turn their eggs and often leave their nests for short time periods, the embryo's right eye has a high probability of being stimulated by light before hatching. Thus, it is conceivable that asymmetry of light stimulation is the key event leading to visual lateralization. Indeed, dark incubation of chick and pigeon eggs prevents the establishment of visual lateralization in grain-grit discriminations (Rogers, 1982; Güntürkün, 1993), and a mere 2 h of light exposure with 400 lux within the last days before hatch suffices to establish visual lateralization in dark-incubated chicken eggs (Rogers, 1982). It is even possible to reverse the direction of the behavioral and the thalamofugal asymmetry by withdrawing the head of the chicken embryo from the egg before hatch, occluding the right eye and exposing the left to light (Rogers & Sink, 1988; Rogers, 1990).

Since pigeons are altricial animals, the developmental plasticity of their visual pathways is prolonged and extends far into posthatching time (Manns & Güntürkün, 1997). Therefore, covering the right eye of newly hatched pigeons for 10 days reverses the anatomical asymmetry of tectal soma sizes and the behavioral visual lateralization of these animals as tested up to three years later (Manns & Güntürkün, 1999a). Thus, light stimulation asymmetry during a critical ontogenetic time span seems to be the trigger for visual asymmetry in pigeons, as it is in chicks.

In principle, these results are in accordance with findings from monocular deprivation studies in mammals. These experiments reported smaller soma sizes of neurons receiving afferents from the deprived eye (Sherman & Spear, 1982). This is similar to pigeons, where the right retinorecipient tectal neurons contralateral to the eye with the "natural monocular deprivation" are smaller.

However, different mechanisms must be involved. Morphological soma size effects of monocular deprivation in mammals are regarded as secondary consequences of synaptic competition at the cortical level between geniculate fibers representing the deprived eye and the nondeprived eye (Rauschecker, 1991). However, a detailed analysis in pigeons shows that "natural monocular deprivation" effects also occur in those neural structures in which a comparable competition is absent (Güntürkün, 2001). This suggests that visual deprivation effects in birds are mediated through activity-correlated, and eventually trophic, deprivation effects within one hemisphere, and that they possibly operate without direct synaptic competition between neurons representing the deprived eye and the nondeprived eye.

In addition, only the unilateral absence of contoured visual patterns induces significant deprivation effects in the mammalian geniculocortical system. Asymmetries of luminance alone do not lead to alterations (Movshon & Van Sluyters, 1981). This supports the assumption that fiber competition is mediated by a Hebbian mechanism which requires correlated activity of pre- and postsynaptic cells for stabilization or retraction of synapses (Rauschecker, 1991). In chicks and pigeons, the situation must be different, since light has to shine through the eggshell and the closed lid of the embryo to induce cerebral asymmetries. Therefore, avian asymmetry triggered by "natural monocular deprivation" has to be induced by brightness and not by contoured visual pattern differences. Brightness differences are probably coded by mere activity differences between the eyes, and could induce asymmetries by activity-dependent cellular effects.

Prehatch light stimulation asymmetry seems to be the *conditio sine qua non* to induce visual lateralization of object discrimination. It is, however, not essential for other forms of visually guided behavior. Dark-incubated chicks have functional asymmetries in imprinting (Johnston & Rogers, 1998) and display biochemical left-right differences in IMHV (Johnston et al., 1995). These asymmetries can, however, be altered by a lateralized light input (Johnston et al., 1997; Johnston & Rogers, 1999). Therefore, for some asymmetries (visual discriminations) a lateralized light input is critical to induce neural left-right differences. In other lateralizations (imprinting), asymmetries are prewired but can be altered by a biased light input.

## ASYMMETRY PAYS

This overview has shown that visual lateralization in birds depends on an interaction of genetic factors that induce a torsion of the embryo's head to the right and the epigenetic factor light that subsequently induces higher levels of activity in the right eye system. As a consequence, neuronal systems are altered during a critical developmental period in a lateralized way such that multiple aspects of visually guided behavior of the animals are asymmetrically organized. Is all this *l'art pour l'art*, an epiphenomenon without costs but also without benefits for the animal? Or does visual lateralization pay? To seek an answer, Güntürkün et al. (2000) determined the individual asymmetry index of 108 pigeons by separately analyzing their left- and right-eye performances in grain-grit discrimination. Then the animals were tested on the same task binocularly, and their discrimination success was correlated with their asymmetry index. Animals with higher asymmetries were significantly more successful in discriminating grain from grit. This means that a rise in asymmetry resulted in a concomitant rise of food reward (figure 1.8). Thus, asymmetry pays.

## LESSONS FROM THE AVIAN BRAIN

Birds heavily rely on vision. If asymmetry pays, it is understandable that it is their visual system which is lateralized. Likewise, it is possible that asymmetries of language or manual skills improve human performance. According to the studies on avian lateralization, it might even be conceivable that these and other human asymmetries emerge during

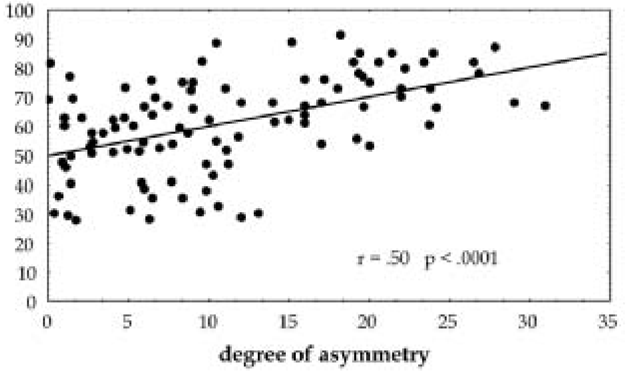

**Figure 1.8** Relationship between the degree of lateralization and binocular discrimination performance. Pearson's product moment correlation (scatter plot) reveals higher performance in more lateralized individuals. (Adapted from Güntürkün et al., 2000.)

ontogeny due to subtle left-right differences that in the beginning affect only subcortical mechanisms.

Indeed, as shown by Hepper et al. (1991), fetuses from 15 weeks of gestational age to term have a strong lateralized bias of thumb sucking on the right side. The corticospinal tract cannot mediate this asymmetry because it reaches cervical to thoracic segments much later and even at term is myelinated only as far caudally as the cerebral peduncles (Stanfield, 1992). Even in the adult the rubrospinal tract reaches only as far as the uppermost cervical segments, and the olivospinal pathway known from studies in rats seems not to exist in man (Nathan & Smith, 1982). The lateral subcorticospinal pathway, which encompasses a variety of descending tracts crucial for distal limb and hand movements, myelinates only at 28–34 weeks of gestational age (Sarnat, 1984). Thus, thumb sucking in the early fetus is mediated virtually only by spinal mechanisms without relay through cortical relays (Sarnat, 1989). In addition, asymmetrical gene expression mechanisms in early neuro-ontogeny result in a slight torsion of the embryo with the forehead turning to the right (Ramsdell & Yost, 1998).

This last point is probably common to all vertebrates, and could result in a higher probability of mouth-hand contacts on the right side. The rightward spinal torsion could also be the reason why most newborns still have a preference for a right turn of their head when in a supine position (Michel, 1981)—a preference that correlates with subsequent handedness (Michel & Harkins, 1986). Therefore, a lateralization of hand-mouth and hand-eye contacts in humans probably depends on spinal asymmetries. If they are manifested in early neuro-ontogeny, they may bias the processing mode of cortical structures that later connect to those motoneurons which innervate the hands and which are known to be significantly larger on the right side (Melsbach et al., 1996). Therefore, the initial bias for handedness might start subcortically, then be controlled much later by cortical structures. Thus, at least some human asymmetries might display a developmental pattern comparable with that outlined for birds.

## CONCLUSIONS

1. In birds, visual information is treated in a lateralized fashion. While object discrimination is left-hemisphere based, geometrical aspects of spatial encoding and social recognition are primarily processed in the right hemisphere.

2. This visual lateralization is also reflected in tasks, like imprinting and one-trial-avoidance learning, in which the animal very quickly forms a mental trace of the visual characteristics of a biologically relevant object.

3. The lateralized behavior corresponds to asymmetries in the morphology and connectivity of the ascending visual pathways. These anatomical asymmetries can vary between species. Thus, seemingly similar asymmetries of behavior can be generated by different lateralized neural systems.

4. At least in pigeons, visual lateralization seems to be dually coded; anatomically, by morphological and connectional differences of ascending visual pathways, and physiologically, by asymmetrical commissural interactions that result in a lateralized modulation of visual processing.

5. In the last days before hatching, avian embryos bend forward and keep their head turned to the right in such a way that the right eye is exposed to light which is shining through the translucent eggshell, while the left eye is occluded by the body. Ontogenetically, visual lateralization of object discriminations is triggered by the subsequently stronger light input to the right eye. This lateralized stimulation induces asymmetrical morphological effects within the developing visual system, and thereby establishes left-right differences at the behavioral level.

6. Birds with higher visual asymmetries are superior in visual discriminations. Thus, asymmetry increases efficiency of processing within the visual system.

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