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S21-1 Structure-function relations of lateralized visual behavior in the pigeon

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Abstract Visual asymmetry in birds is induced by an embryonic right-eye light stimulation that establishes a left hemispheric superiority in object discrimination. It is possible that the prehatch asymmetry of light stimulation only alters visual circuits in the light-stimulated hemisphere, making that side dominant for some visual tasks. However several experiments clearly show that transient lateralized stimulation changes left- and right-hemispheric functions. One examines visuoperceptual discrimination accuracy as well as visuomotor speed in dark- and light-incubated pigeon embryos. Whereas birds hatched from eggs incubated in the dark are not asymmetrically organized at all, those from eggs incubated in light displayed increased visuoperceptual discrimination accuracy in the left hemisphere, and a decrease of visuomotor speed in the right. Thus, both measures result in superiority in the right eye (left hemisphere) but by different mechanisms. A similar result is obtained in the second study, by analyzing the effect of light- and dark-incubation on tectal GABA- and Parvalbumin- neurons. Both GABA- and Parvalbumin- cells comprise non-overlapping interneuronal populations which modulate intratectal processes. This study reveals that both cell types develop asymmetrical soma sizes after embryonic light stimulation while dark incubation prevents the establishment of left-right differences. However, light engendered a significant size decrease in GABA-cells in the right tectal hemisphere while inducing a significant shrinkage of Parvalbumin-cells in the left. Since these neurons probably participate in different neuronal circuits, visual asymmetry seems to be established by differentially altering divergent intratectal circuits on the left and right sides of the brain.

Key words Left and right vision, Visuoperceptual discrimination, Visuomotor speed, Tectofugal neurons, Retinal pathway

1 Introduction

The following review brings together information towards substantiating a hypothesis first formulated by Jerre Levy in 1972 (Levy et al., 1972). According to her view, neither of the hemispheres in the brain dominates a sensory, cognitive or motor process, but makes different and complementary contributions to its achievement. The notion that left and right brains of humans and other animals divide tasks into complementary subprocesses to be executed in parallel has, since then, gained widespread acceptance. This is especially because the hypothesis provides a ready explanation for why asymmetries may have evolved: because complementarity inevitably involves a reduction of redundancy and therefore an increase of processing capacity, lateralized brains will have a selection advantage.

Indeed, human neuropsychological literature shows that language, face and spatial orientation systems are organized such that each hemisphere makes its own and unique contribution (Davidson and Hugdahl, 1995). The same notion has also been put forward convincingly in literature dealing with asymmetry in animals (Rogers and Andrews, 2002). What is lacking, however, is a detailed neurobiological analysis of how this complementarity is created neuronally, and how it is reflected in lateralized behavior. To this end, I review here a series of experiments with pigeons that show how a short lateralized stimulation during a critical developmental period can induce asymmetrical but complementary processes in the two hemispheres which result in divergently tuned aspects of visually guided behavior.

2 The avian visual system

Birds are the most visually dependent class of vertebrates; and the phrase of Rochon-Duvigneaud (1943) that a pigeon is nothing other than two eyes with wings is valid for most avian species. We humans see the world with about one million ganglion cells within each of our retinae. This is only 40% of the number of retinal ganglion cell axons counted in a single optic nerve of pigeons and chickens (Binggeli and Paule, 1969; Rager and Rager, 1978). The optic nerves in birds decussate nearly completely, and less than 0.1% of the fibres proceed to the ipsilateral side (Weidner et al., 1985). Because only limited numbers of axons recross via mesencephalic and thalamic commissures, the avian visual system is remarkably crossed.

In birds, two parallel retinal pathways process information to the forebrain: the tectofugal and the thalamofugal system, which are suggested to be equivalent to the respective extrageniculo-cortical and the geniculo-cortical visual pathways in mammals (Güntürkün, 2000). Within the thalamofugal pathway, visual input comes from within the contralateral nucleus geniculatus lateralis, pars dorsalis (GLd), which itself projects predominately ipsilaterally to the telencephalic visual Wulst (Miceli et al., 1990). In pigeons, approximately 90% of the retinal ganglion cells project topographically on to the contralateral tectum opticum (TO), the first center of the tectofugal pathway. Tectal output is instituted by neurons of the deep tectal layer 13 that project bilaterally on to the nucleus rotundus (Rt), which is connected to the ipsilateral ectostriatum of the forebrain (Hellmann and Güntürkün, 2001).

3 The asymmetry of vision

The avian visual system is asymmetrically organized. Studies in various avian species reveal a superiority of the right eye in experiments which require the birds to distinguish visual objects (Mench and Andrew, 1986; Güntürkün and Kischkel, 1992; Vallortigara et al., 1996), to memorize hundreds of abstract patterns (Fersen and Güntürkün, 1990), or to infer a higher-order rule from serial visual color reversals (Diekamp et al., 1999). Due to the virtually complete crossover at the optic chiasm, these asymmetries could arise from a left hemispheric dominance in the processing of visual objects. Studies in chickens and food-storing birds also reveal a right hemispheric superiority in relational spatial processes (Mench and Andrew, 1986; Clayton and Krebs, 1994; Tommasi and Vallortigara, 2001). These and other experiments reveal that the left hemisphere is not dominant for vision as such, but that each side makes its own and unique contribution to visually guided behavior.

Left hemispheric superiority for object discrimination correlates closely with neuroanatomical asymmetries of the tectofugal pathway. In pigeons, structural asymmetries in the tectofugal pathway have been found in morphological differences between left and right tectofugal structures (Güntürkün, 1997; Manns and Güntürkün, 1999a,b), excessive bilateral afferents on the left side of the tectofugal pathway (Güntürkün et al., 1998), and a prominent left-right difference in transcommissural interactions over midbrain commissures (Keysers et al., 2000).

Visual lateralization is triggered by exposure of the embryo in the egg to light shortly before hatching. Avian embryos adopt an asymmetrical posture with the head turned to the right such that the right eye receives proportionately more light through the translucent shell, leaving the left eye covered by the body. Such asymmetrical stimulation by light modulates synaptic patterns of the ascending pathways in a brief period shortly before to shortly after hatching. If birds are incubated and hatched in the dark, lateralization does not develop (Rogers, 1982; Güntürkün, 1993). The direction of lateralization can even be reversed experimentally by shutting off light to the right eye shortly before hatching in chickens (Rogers, 1990) or thereafter in pigeons (Manns and Güntürkün, 1999b). Together with behavioral asymmetries, anatomical left-right differences can also be reversed or altered according to experimental manipulation of light stimulation. These experimental interventions have to be performed before hatching in chickens and shortly after in pigeons (Rogers, 1996; Manns and Güntürkün, 1999a,b).

At the first glance, it would seem that only light stimulation early in ontogeny induces changes in the left hemisphere to give it an advantage in object discrimination. However, it is also possible that both hemispheres are altered, albeit in different ways. Skiba et al. (2002) investigated this possibility by testing dark- and light- incubated pigeons in two visual experiments which both yield a right eye advantage but probably tap different kinds of visual processes. One tested grain-grit discrimination, in which the birds had to peck grain from a trough mixed with grain and grain-resembling grit for 30 seconds. Because the number of grains eaten depends on left and right monocular conditions, not the number of pecks, visual asymmetry is tested by accuracy in discrimination, not visuomotor speed.

This is different from the other successive pattern discrimination test using lean variable ratio schedules like VR (visual receptor) 32. Here, the birds had to distinguish the correct pattern right at the beginning of the trial; success then should be reinforced by speed of pecking. Consequently, right eye superiority should be reflected in the number of pecks, while the two monocular conditions generally should not differ with respect to discrimination scores (Güntürkün and Kischkel, 1992). Pattern discrimination here should thus reflect mainly asymmetry in visuomotor speed.

The results of the Skiba et al. (2002) experiments showed that all birds incubated under light revealed a pronounced right eye / left hemisphere dominance in both behavioral testing paradigms. A closer inspection of the results, however, revealed that, in the grit-grain task, the marked right eye dominance in light incubated birds resulted from a selective enhancement of left hemispheric performance. In contrast, right eye superiority in the pattern discrimination test followed from a decrease in right hemisphere performance. Because the grain-grit and successive discrimination tasks teased apart perceptual and visuomotor processes, respectively, these functions are obviously altered differently in both hemispheres. Taken together, incubation under light seems to induce a visual left hemispheric superiority in object discriminations by modulating two different processes: a) an increase in left hemisphere capacity for visuoperceptual processes, and b) a decrease in right hemispheric capacity for visuomotor speed.

4 Complementary morphological changes in both hemispheres

The results of Skiba et al. (2002) imply that the effects of embryonic light stimulation are not restricted to simple unihemispheric enhancement of visual processing, but involve mechanisms selectively supporting some neural circuits in one hemisphere and inhibiting other circuits in the other. Indeed, several recent experiments show that asymmetrical light stimulation results in cellular alterations in both hemispheres. Manns and Güntürkün (submitted) studied soma sizes of tectal GABA- and Parvalbumin- neurons (PV) in adult pigeons which had been light- and dark-incubated during embryogenesis. Both GABA- and PV- cells comprise mostly non-overlapping tectal interneurons which modulate intratectal processes. For example, GABAergic neurons in layer 5 tune the glutamatergic visual input to projection neurons of layer 13 and thus directly influence the tectofugal system (Tömböl, 1998; Tömböl and Németh, 1999).

Manns and Güntürkün (submitted) found that both cellular populations develop asymmetrical soma sizes after embryonic light stimulation whereas dark incubation prevents the establishment of left-right differences. Thus, without asymmetrical light stimulation during embryogenesis, no morphological left-right-differences develop. Light stimulation, however, induced a significant decrease in the size of GABA-cells in the right tectum and a significant shrinkage of PV-cells in the left tectal hemisphere. Since these neurons probably participate in different neuronal circuits, visual asymmetry seems to be established by differential altering of different intratectal circuits. To my knowledge, this is the first demonstration of complementary and lateralized alterations of morphological factors. It strongly underscores the notion that visual asymmetry in birds does not imply a simple enhancement of left hemisphere efficiency but results from differential adjustments of left- and right- hemisphere circuits.

These complementary and hemisphere-specific adjustments of cellular populations and behavioral constituents are probably parts of a general system in which left- and right- brain mechanisms diverge along a small set of principal variables. Studies in humans suggest that the difference between a left-hemispheric “feature”-based and a right-hemispheric “gestalt”-based mode could be among the main driving forces inducing behavioral asymmetries. Studies using discriminations of visual geometrical and object cue-based spatial locations may reveal a similar dichotomy in birds (Tommasi and Vallortigara, 2001). If so, the complementary behavioral and morphological asymmetries outlined above could be constituents of this dichotomy.

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References

Binggeli RL, Paule WJ, 1969. The pigeon retina: Quantitative aspects of the optic nerve and ganglion cell layer. J. Comp. Neurol. 137: 1–18.

Clayton NS, Krebs JR, 1994. Memory for spatial and object-specific cues in food-storing and non-storing birds. J. Comp. Physiol. A. 174: 371–379.

Davidson RJ, Hugdahl K, 1995. Brain Asymmetry. Cambridge: Massachusetts Institute of Technology.

Diekamp B, Prior H, Güntürkün O, 1999. Lateralization of serial color reversal learning in pigeons (*Columba livia*). Animal Cogn. 2: 187–196.

Fersen L von, Güntürkün O, 1990. Visual memory lateralization in pigeons. Neuropsychologia 28: 1–7.

Güntürkün O, 1993. The ontogeny of visual lateralization in pigeons. German J. Psychol. 17: 276–287.

Güntürkün O, 1997. Morphological asymmetries of the tectum opticum in the pigeon. Exp. Brain Res. 116: 561–566.

Güntürkün O, 2000. Sensory physiology: vision. In: Whittow GC ed. Sturkie’s Avian Physiology. Orlando: Academic Press, 1–19.

Güntürkün O, Hellmann B, Melsbach G, Prior H, 1998. Asymmetries of representation in the visual system of pigeons. NeuroReport 9: 4 127–4 130.

Güntürkün O, Kischkel K-F, 1992. Is visual lateralization sex-dependent in pigeons? Behav. Brain Res. 47: 83–87.

Hellmann B, Güntürkün O, 2001. The structural organization of parallel information processing within the tectofugal visual system of the pigeon. J. Comp. Neurol. 429: 94–112.

Keysers C, Diekamp B, Güntürkün O, 2000. Evidence for asymmetries in the phasic intertectal interactions in the pigeon (*Columba livia*) and their potential role in brain lateralisation. Brain Res. 852: 406–413.

Levy J, Trevarthen C, Sperry RW, 1972. Perception of bilateral chimeric figures following hemispheric deconnection. Brain 95: 61–78.

Manns M, Güntürkün O, 1999a. ‘Natural’ and artificial monocular deprivation effects on thalamic soma sizes in pigeons. NeuroReport 10: 3 223–3 228.

Manns M, Güntürkün O, 1999b. Monocular deprivation alters the direction of functional and morphological asymmetries in the pigeon’s visual system. Behav. Neurosci. 113: 1–10.

Mench JA, Andrew RJ, 1986. Lateralization of a food search task in the domestic chick. Behav. Neur. Biol. 46: 107–114.

Miceli D, Marchand L, Repérant J, Rio J-P, 1990. Projections of the dorsolateral anterior complex and adjacent thalamic nuclei upon the visual wulst in the pigeon. Brain Res. 518: 223–254.

Rager G, Rager U, 1978. Systems-matching by degeneration. I. A quantitative electron-microscopic study of the generation and degeneration of retinal ganglion cells in the chicken. Exp. Brain Res. 33: 65–78.

Rochon-Duvigneaud A, 1943. Les yeux et la vision des vertebrés. Paris: Masson.

Rogers LJ, 1982. Light experience and asymmetry of brain function in chickens. Nature 297:223–225.

Rogers LJ, 1990. Light input and the reversal of functional lateralization in the chicken brain. Behav. Brain Res. 38: 211–221.

Rogers L, 1996. Behavioral, structural and neurochemical asymmetries in the avian brain: A model system for studying visual development and processing. Neurosci. Biobehav. Rev. 20: 487–503.

Rogers LJ, Andrew R, 2002. Lateralization, Learning and Memory. Cambridge: Cambridge University Press.

Skiba M, Diekamp B, Güntürkün O, 2002. Embryonic light stimulation induces different asymmetries in visuoperceptual and visuomotor pathways of pigeons. Behav. Brain Res. 134: 149–156.

Tömböl T, 1998. Golgi and electron-microscopic golgi-GABA immunostaining atudy of the avian optic tectum. Acta Anat. 162: 209–225.

Tömböl T, Németh A, 1999. Direct connections between dendritic terminals of tectal ganglion cells and glutamate-positive terminals of presumed optic fibres in layers 4–5 of the optic tectum of *Gallus domesticus*. A light- and electron- microscopic study. Neurobiol. 7: 45–67.

Tommasi L, Vallortigara G, 2001. Encoding of geometric and landmark information in the left and right hemispheres of the avian brain. Behav. Neurosci. 115: 602–613.

Vallortigara G, Regolin L, Bortolomiol G, Tommasi L, 1996. Lateral asymmetries due to preferences in eye use during visual discrimination learning in chicks. Behav. Brain Res. 74: 135–143.

Weidner C, Reperant J, Miceli D, Haby M, Rio JP, 1985. An anatomical study of ipsilateral retinal projections in the quail using radioautographic, horseradish peroxidase, fluorescence and degeneration techniques. Brain Res. 340: 99–108.