

Visual Asymmetries in Japanese Quail (*Coturnix japonica*) Retain a Lifelong Potential for Plasticity

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Adult Japanese quail display left-eye/right-hemisphere dominance in visually guided sexual tracking. In 2 experiments, the authors set out to answer if this functional cerebral asymmetry is modifiable by posthatch monocular deprivation. In Experiment 1, the left or the right eye of 2-day old quail were closed for 70 days. Quail were run in a left- or a right-turning runway to obtain access to a conspecific of the opposite sex. The performance of both left and right eye systems was equal. In Experiment 2, the deprived eyes of the quail were opened and the previously open eyes were closed. They were tested with the same runways. Overall, running speed was very low, but the quail showed a left-eye/right-hemisphere superiority. Altogether, these experiments evince 3 insights into cerebral asymmetries in quail. First, posthatch asymmetries of visual input can alter lateralized behavior to an important extent. Second, cerebral asymmetries could involve an interhemispheric inhibition that can be modified by epigenetic factors. Third, even long-term visual deprivation does not abolish a previously established cerebral asymmetry.

Keywords: visually guided sexual behavior, hemispheric asymmetry, plasticity, Japanese quail

Over the past 3 decades, various behavioral and neural asymmetries have been discovered in a variety of species (Rogers & Andrew, 2002; Vallortigara & Rogers, 2005; Vallortigara, Rogers, & Bisazza, 1999). Among them, birds are probably the most intensely studied group of animals (pigeons: Fersen & Güntürkün, 1990; Güntürkün, 1997a; Güntürkün & Kesch, 1987; Güntürkün & Kischkel, 1992; chicks: Deng & Rogers, 2002b; Dharmaretnam & Rogers, 2005; Mench & Andrew, 1986; Rogers, Andrew, & Johnston, 2007; Vallortigara & Andrew, (1994); quail: Gülbetekin, Güntürkün, Dural, & Çetinkaya, 2007; Valenti, Sovrano, Zucca, & Vallortigara, 2003; Zucca & Sovrano, 2008; zebra finches: Alonso, 1998; Herrmann & Bischof, 1986b; parids: Clayton & Krebs, 1993; corvids: Clayton & Krebs, 1994). The fact that birds lack a corpus callosum and display a virtually complete decussation of optic fibers at the optic chiasm makes them an exceptional animal model because direct visual input can easily be restricted to one hemisphere without invasive procedures (Güntürkün, 1997a).

A further major advantage of the bird model is the fact that the ontogenetic emergence of several asymmetrically organized visual functions can be experimentally controlled. Avian embryos as-

sume an asymmetrical position before hatch that brings the right eye close to the translucent shell, whereas the left eye is occluded by the body and the yolk sac (Kuo, 1932). Because brooding parents regularly turn their eggs and often leave their nests for short time periods, the embryo's right eye has a high probability to be stimulated by light before hatching (Buschmann, Manns, & Güntürkün, 2006). Experiments in chicken and pigeons show that this prehatch visual stimulation asymmetry activates the onset of a left hemispheric dominance in visual feature discrimination tasks (Rogers, 1982; Skiba, Diekamp, & Güntürkün, 2002). It is even possible to reverse the direction of this behavioral and anatomical 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, 1990).

Chicken are precocial birds, and their neural development has to be fast to be functional from hatch onward. Visual asymmetry in chickens does not seem to be modifiable by reversed eye exposure after hatch, indicating an offset of a time window for asymmetrical plasticity until hatch (Rogers, 1995). Because pigeons are altricial birds, 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 behavioral and anatomical asymmetries (Manns & Güntürkün, 1999). The same procedure has virtually no effect when applied from the 11th to the 20th day posthatch (Manns, 1998). Thus, light stimulation asymmetry during a critical ontogenetic time span seems to be the trigger for avian visual feature discrimination asymmetry. The critical time window seems to end with hatch in precocial birds and by 10 days posthatch in altricial birds. This general conclusion, however, was never tested

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in a third avian species and with a more prolonged time table. To do this is the first aim of the present study.

Birds display asymmetries in various visually guided tasks that encompass imprinting (Vallortigara, Regolin, & Pagni, 1999), object discrimination (Güntürkün & Kesch, 1987), categorization (Yamazaki, Aust, Huber, Hausmann, & Güntürkün, 2007), spatial orientation (Vallortigara, Pagni, & Sovrano, 2004), homing (Ulrich et al., 1999; Wiltchko, Traudt, Güntürkün, Prior, & Wiltchko, 2002), and long-term visual memory (Fersen, & Güntürkün, 1990). Generally, the right hemisphere of birds is specialized for detecting variance, recognizing novelty, and utilizing relational spatial cues, whereas the left hemisphere is specialized for detecting invariance, interpreting input, using learned mental templates, and focusing attention (Vallortigara et al., 2008). However, hemispheric specialization for visually guided sexual behavior in birds has only rarely been studied. In an early study, Rogers, Zappia, and Bullock (1985) showed that intramuscular administration of testosterone started precocious copulatory behavior in young male chickens but only if a proper sexual stimulus was presented to the left eye. Also, the right hemisphere dominance of sexual behavior in male chickens was evidenced by Bullock and Rogers's (1986) study, in which monosodium glutamate blocked left hemisphere activity, resulting in elevated copulatory behaviors in male chickens. In a similar vein, Ventolini et al. (2005) supported the previous findings by showing a laterality in sexual behavior of black-winged stilt (*Himantopus himantopus*): The shaking behavior, a component of courtship displays, and copulatory attempts by males were more likely to occur when females were seen through the left monocular visual field.

Gülbetekin et al. (2007) also demonstrated an apparent association between the right hemisphere and visually guided sexual behavior in Japanese quail. They trained male quail to run across either a left- or a right-turning runway to obtain sexual access to female quail. For the quail to be motivated to perform the task, they first have to learn that they get access to copulation with a conspecific of the opposite sex at the end of the runway. Then, when reaching the last corridor during training and test, the birds approach the opposite-sex partner. As soon as they get close, a wire mesh door is opened, and the quail start to copulate. Because the quail do not run down the corridors without having subsequent access to a sexual partner, we call our procedure a visually guided sexual task. In the Gülbetekin et al. (2007) study, the quail tested with their right eye in use showed significantly higher latencies to complete the task than the birds tested binocularly and with their left eye. Thus, various studies support right hemisphere dominance for sexually motivated behavior in birds.

The aim of the present study was to determine whether the asymmetry of visually guided sexual behavior can be modified by an ontogenetic manipulation of the lateralized visual input. Japanese quail (*Coturnix coturnix japonica*) are an excellent model for such an experiment because they learn a task rapidly if reinforced with copulation. Additionally, quail are precocial birds that are closely related to chickens. Indeed, Valenti et al. (2003) showed that an asymmetry in pebble versus grain discrimination is only transitory in quail, identical to chicks. Thus, we would expect that, in quail, the period of plasticity of their asymmetry ends very early. As discussed later, this is not the case. Quite contrary, our results reveal that even adult Japanese quail preserve a potential to modify asymmetries of visually guided sexual behavior.

Experiment 1

The aim of Experiment 1 was to investigate whether a change in the eye/hemisphere advantage occurs when the quail are monocularly deprived during the first 75 days of their life. We assumed that all critical ontogenetic events were terminated at that age because the quail had already reached sexual maturity. For testing this, one eye of 2-day-old quail was patched until they reached adulthood, and they were then tested in a runway task.

Method

Quail. Forty 2-day-old quail served as subjects in the experiment. Chicks were randomly assigned either to the right eye/left hemisphere (RE/LH; thus the right eye is in use) or the left eye/right hemisphere (LE/RH, thus the left eye is in use) group. Because sexing in quail is difficult right after hatch, this was performed when 35 days old. Twelve male and 8 female quail were used for the experiments. A total of 4 males had to be excluded because of death or sexual inactivity. At the end, 10 males and 8 females in each group were included in the experiment. The experimental sessions started when they were 70 days old. In addition to the quail used as subjects, 4 female and 4 male adult quail were used as stimuli.

The quail had been incubated at 38 °C in continuous light and hatched in the laboratory. They were descendents of a stock obtained from the Poultry Science Department of the Akdeniz University of Turkey. Quail were maintained in two groups for the first 2 weeks after hatching and then were reared individually in metal cages (25 × 23 × 20 cm) without any restriction of food and water. The brooder and colony rooms were maintained on a 16:8 light–dark schedule with lights on at 6:00 a.m.

Apparatus. Two identical runways, one of which turns left, the other turns right, with a start and a goal chambers at each end were used (see Figure 1). The runways were constructed in such a way that the goal chamber was not visible from the start chamber. Therefore, the test quail could not see the goal quail until reaching the last turn of the runway. The end chambers were separated from the runway by sliding doors. The walls of the runway were made of 18-mm-thick plywood and were painted white. The sliding door at the start chamber was wooden, but the door at the goal chamber was wire mesh. The floor and the ceiling of the apparatus were made of wire mesh. A video camera installed above the runway was used to record experimental sessions. The video recordings were used to measure the time that quail took to get to the goal chamber from the start chamber.

Procedure. To monocularly deprive the hemispheres of 2-day-old quail chicks, we used eye caps by following the procedure developed by Prior, Wiltchko, Stapput, Güntürkün, and Wiltchko (2004). Each eye cap was mounted on a velcro ring glued around either the left (RE/LH condition) or the right eye of the quail (LE/RH condition). The eye caps were controlled for damages and dismounts on a daily basis to ensure continuous monocular deprivation. The quail were left undisturbed in their colony cages until they became adults. When they became sexually mature, they were kept in individual cages.

Before the start of the experiment, the quail were equalized for their sexual experience. To do so, each quail was provided a 5-min copulatory opportunity with one of its opposite-sex conspecifics in their colony cages, once a day and for 5 consecutive days.

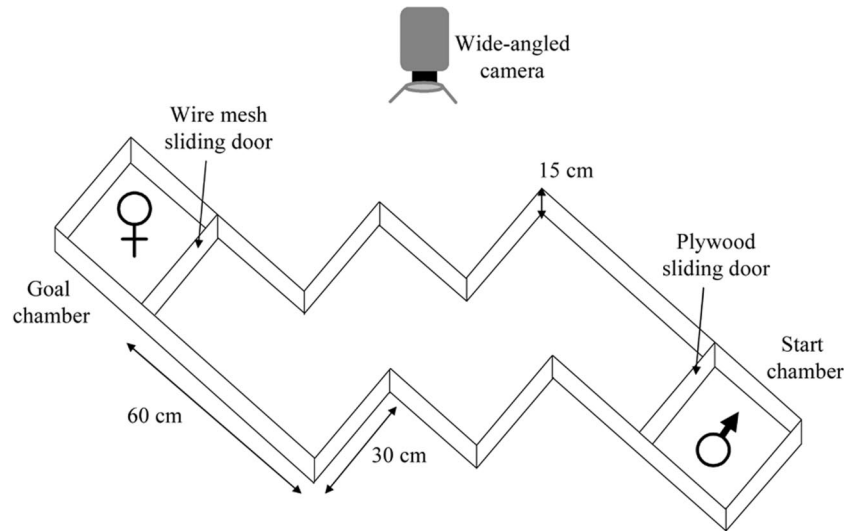


Figure 1. A schematic drawing of the left-turning runway.

When the quail became 65 days old, they were given five habituation trials in the different compartments of the runway, in a randomized fashion. Each trial took 5 min a day and lasted for 5 consecutive days. The sliding doors were open, and the end chambers were empty in the habituation trials.

At the end of the habituation period, equal numbers of female and male quail in each group were randomly assigned to either left-turning or right-turning runway conditions. The experiment consisted of one test trial on each day for 6 days. Each test day consisted of morning and afternoon sessions. The sessions were counterbalanced for each quail across the trials.

In each trial, a stimulus quail was placed in the goal chamber, and an opposite-sex subject quail was placed in the start chamber and allowed 30 s for settling. Then the sliding door was opened to let the quail walk in the runway. When the goal chamber was visible to the subject quail, the door was raised and the quail was provided a 3-min copulatory opportunity. After copulation, the quail were housed individually in the colony cages to ensure that their sexual motivation remained elevated until the next day. Test trials were videotaped for later quantification. The visually guided runway performance was measured as the time that a quail took to reach the goal chamber. The analyses of runway performances were based on the sixth trial of the experiment. Training performances for six trials are shown in Figure 2.

Results

We conducted a 2×2 analysis of variance (ANOVA) to determine the effects of eye in use (LE/RH and RE/LH conditions) and sex of the quail on runway performance. Data analyses were conducted with eye in use and sex of the quail as between-subject factors. The ANOVA results indicated that main effects of eye in use, $F(1, 32) = 0.68$, $p = .41$; sex of the quail, $F(1, 32) = 0.16$, $p = .69$; and interaction of eye in use and sex of the quail $F(1, 32) = 0.89$, $p = .35$, were not significant (see Figure 3).

Experiment 2

Experiment 1 revealed that both eyes/hemispheres performed equally when the chicks were monocularly deprived for more than 2 months and were thus forced to see unilaterally. In Experiment 2, we set out to test the performance of the nondeprived eye/hemisphere in the same task.

Method

Quail. The quail used in Experiment 1 also served as subjects in Experiment 2. The eye caps now changed sides so that quail in the RE/LH condition of Experiment 1 were assigned to the LE/RH condition in Experiment 2 and vice versa. The same male and female quail served as stimuli.

Apparatus and procedure. The same apparatus was used. Twenty-four hours after the quail had had the sixth trial, their

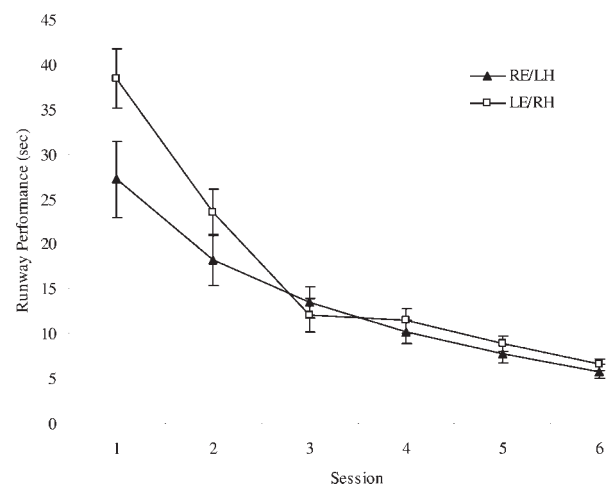


Figure 2. Runway performances (in seconds) of quail for all six trials.

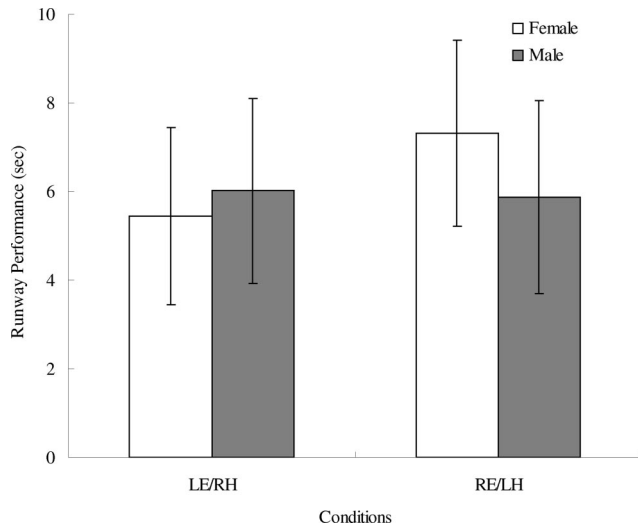


Figure 3. Mean runway performances (in seconds), with 95% confidence intervals, for the female and male quail in the left-eye/right-hemisphere (LE/RH) and right-eye/left-hemisphere (RE/LH) conditions in Experiment 1.

patched eyes were opened and their open eyes were patched with velcro rings and eye caps. Quail were then tested with the same procedure described for Experiment 1. Because these quail had been already trained in the same runway for Experiment 1, no additional training was applied. They were tested with their deprived eyes for only one session.

Results

We conducted data analyses using a 2×2 ANOVA, with eye in use (LE/RH and RE/LH conditions) and sex of the quail as between-subject factors. The results for the ANOVA indicated no significant main effect for sex of the quail, $F(1, 32) = 0.42, p = .52$; but did indicate a significant main effect for eye in use, $F(1, 32) = 4.11, p = .05$; partial $\eta^2 = .12$. The main effect for eye in use indicated that runway performance of the quail in the LE/RH condition were significantly faster than that of quail in the RE/LH condition. There was no significant interaction between eye in use and sex of the quail, $F(1, 32) = 2.76, p = .11$ (see Figure 4).

A t test for matched samples indicated a significant difference between the runway performances observed in Experiments 1 and 2, $t(35) = 8.16, p = .00$. The quail in the Experiment 1 performed much faster ($M = 6.14$) than those in Experiment 2 ($M = 59.56$).

The runway performances in Experiments 1 and 2 were not significantly correlated, $r = -.04, p = .80$. Accordingly, the performance in Experiment 1 explained only 0.2% of the variance of the performance in Experiment 2. Thus, the fast quail in Experiment 1 were not necessarily among the fast ones in Experiment 2.

General Discussion

The present study discovered three principles of cerebral asymmetries in the quail model. First, posthatch asymmetries of visual input are able to importantly modify lateralized behavior in a precocial quail. Second, at least for visually guided sexual behav-

ior, cerebral asymmetries seem to be exerted to some extent by an inhibitory crosstalk between the hemispheres. Third, asymmetries in the deprived hemispheres are not completely abolished, even after a very long period of monocular visual deprivation. Here we discuss these three points, one by one.

Posthatch Asymmetrical Light Input Alters Asymmetries in Quail

Chicken and pigeons are the two most intensively studied avian asymmetry models. Although showing a similar lateralized visual behavior in many respects, they differ fundamentally with respect to the critical visual pathways and their developmental modes. In chicken, it is the thalamofugal system, which is anatomically and functionally lateralized (Deng & Rogers, 2002a; Rogers, 1995). This pathway corresponds to the mammalian geniculocortical system and transfers retinal information through the nucleus geniculatus lateralis, pars dorsalis to the visual Wulst in the telencephalon (Güntürkün, 2000). However, the thalamofugal asymmetry is only transient and disappears about 21 days after hatch (Rogers & Sink, 1988). In pigeons, it is not the thalamo- but the tectofugal system that displays various anatomical, electrophysiological, and functional left–right differences (Folta, Diekamp, & Güntürkün, 2004; Güntürkün, 1997b; Güntürkün, Hellmann, Melsbach, & Prior, 1998; Manns, Freund, Leske, & Güntürkün, 2008). The tectofugal pathway corresponds to the mammalian extrageniculocortical system and transfers visual information through the mesencephalic optic tectum and the diencephalic nucleus rotundus to the entopallium in the forebrain. Tectofugal asymmetries in pigeons represent stable, lifelong structural, and functional left–right differences (Manns & Güntürkün, 2009).

This species's differences with respect to the critical visual pathways could be related to the fundamentally dissimilar developmental modes of chickens and pigeons. Although chickens hatch as precocial birds with a fully mature visual system (Deng & Rogers, 2002a; Rogers, 2000), pigeons are altricial and hatch with

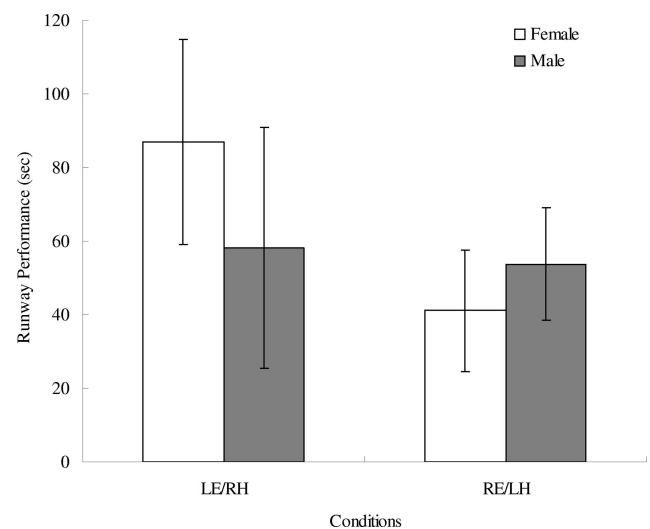


Figure 4. Mean runway performances (in seconds), with 95% confidence intervals, for the female and male quail in the left-eye/right-hemisphere (LE/RH) and right-eye/left-hemisphere (RE/LH) conditions in Experiment 2.

closed eyes and highly immature visual pathways (Manns & Güntürkün, 1997). Consequently, asymmetrical light input after hatch has no, or at least only, minor impact in chickens (Rogers, 1990). In pigeons with their slower developmental speed, however, the same manipulation can fundamentally modulate visual asymmetry at the behavioral and anatomical level (Manns & Güntürkün, 1999).

Quail are precocial and much closer related to chickens than to pigeons. As in chickens, quail display only a transitory asymmetry for a few weeks after hatch in grain versus pebble discrimination (Valenti et al., 2003). Thus, we assumed asymmetries of visually guided sexual behavior to be rather consolidated after hatch and therefore to be less modifiable. Quite contrary, our findings reveal that prolonged monocular deprivation abolishes asymmetry and dramatically increases running speed of the birds. Obviously, our 75-day monocular deprivation period in quail is not directly comparable with the 24-hr deprivation experiment in chicks (Rogers, 1990). Nevertheless, we could show that the visual system of quail can, in principle, be significantly altered by posthatch asymmetrical visual input. Our data do not allow deciding whether the absence of left–right differences in running speed of our quail is due to a true absence of a cerebral asymmetry or a floor effect that camouflages a minor existing lateralization. However, it seems that the uncovered eye system had ontogenetically consolidated an efficient control on sexual behavior, abolishing left/right differences observed in undeprived birds (Gülbetekin et al., 2007). This comparison with the Gülbetekin et al. (2007) study, however, neglects possible batch effects. Although we cannot exclude this possibility, we believe that batch effects are not very likely to abolish an existing asymmetry. We therefore assume that the absence of an asymmetry in visually guided visual tracking reflects a neural reorganization arising from our experimental manipulation. Thus, both left and right eye systems of a precocial bird probably retain an important room for plasticity after hatch.

This prolonged period of plasticity could be related to the differential need for visual discrimination during foraging and during sexual encounters. Although, quail display only a transient asymmetry of a few weeks after hatch in grain versus pebble discrimination (Valenti et al., 2003), adult quail display asymmetry in social recognition (Zucca & Sovrano, 2008) and visually guided sexual behavior (Gülbetekin et al., 2007). This difference between the adult quail and chicks may arise due the different developmental needs of different behavioral systems. Having a mature system for discriminating food and nonfood objects is critical for the survival of a precocial chick, whereas having a mature visual system for sexual behavior is probably not essential in the first weeks of a quail's life. This only becomes important in adulthood. Japanese quail use visual species-specific cues to discriminate the sex of conspecifics. For example, Akins (2000) showed that female sign stimuli may play an important role in the acquisition of sexually conditioned responses. Therefore, the neural components of visual system related to sexual behavior are probably formed through later stages of life and thus retain the potential for plasticity for lengthy periods of time.

Interhemispheric Inhibition

Gülbetekin et al. (2007) described a right hemisphere speed advantage in visually guided sexual tracking. In our study, running

speed of both hemispheres was comparable. However, the quail in the present study were about 30% faster than those in Gülbetekin et al.'s (2007) study. This difference could, in principle, arise by batch effects. The extent of the difference, however, makes it also possible that the long period of visual deprivation removed an existing inhibition from the undeprived side. Indeed, the intertectal commissures in birds are mostly inhibitory (Hardy, Leresche, & Jassik-Gerschenfeld, 1984; Robert & Cuénod, 1969) and contribute significantly to the maintenance of visual asymmetry in feature discrimination (Güntürkün & Böhringer, 1987; Parsons & Rogers, 1993). This system is asymmetrically organized with a higher level of inhibition transmitted from the left to the right tectum in adult pigeons (Keyser, Diekamp, & Güntürkün, 2000). However, it is conceivable that prolonged monocular deprivation can alter the extent and direction of this interhemispheric inhibition, resulting in a drastic reduction of interhemispheric inhibition on the undeprived side.

Asymmetry Is Not Abolished After Monocular Deprivation

Uncovering the deprived and closing the undeprived eye revealed two effects. First, the running speed of the quail when using the deprived eye was very slow. Second, the quail were faster with the LE/RH condition. The slow pace of the quail when they used their deprived eye was complementary to the high speed with the undeprived eye. If indeed prolonged monocular deprivation skews interhemispheric inhibition toward the deprived side, a reduced excitation pattern on the deprived and a heightened level of processing on the undeprived side could follow. In addition, it is also possible that prolonged monocular deprivation produces morphological changes within visual pathways, as shown in zebra finches and pigeons (Bagnoli, Burkhalter, Vischer, Henke, & Cuénod, 1982; Burkhalter & Cuénod, 1978; Herrmann, & Bischoff, 1986a, 1986b). Both enhanced inhibition and pathological changes within the visual system could result in a reduced running speed of our quail.

Despite the slow speed, the quail displayed LE/RH superiority. This is comparable with the study findings of Gülbetekin et al. (2007), who also revealed this lateralization pattern, although only for male quail. Similarly, Zucca and Sovrano (2008) could show that quail prefer to view a familiar conspecific with the left eye. This has also been shown for chicks (Vallortigara, 1992). Thus, in the context of running to reach a familiar sexual partner or to see a familiar companion, adult quail and chicks show a right hemispheric advantage. It is important to note that this asymmetry did not disappear, despite a prolonged monocular deprivation and concomitant major changes in the internal organization of the visual system. Thus, although these changes took place, the initially established asymmetry could still be revealed in our adult quail.

References

- Akins, C. K. (2000). Effects of species-specific cues and the CS-US interval on the topography of the sexually conditioned response. *Learning and Motivation, 31*, 211–235.
- Alonso, Y. (1998). Lateralization of visual guided behavior during feeding in zebra finches (*Taeniopygia guttata*). *Behavioral Processes, 43*, 257–263.
- Bagnoli, P., Burkhalter, A., Vischer, A., Henke, H., & Cuénod, M. (1982).

- Effects of early monocular deprivation on choline acetyltransferase and glutamic acid decarboxylase in pigeon visual Wulst. *Brain Research*, 247, 289–302.
- Bullock, S. P., & Rogers, L. J. (1986). Glutamate-induced asymmetry in the sexual and aggressive behavior of young chickens. *Pharmacology, Biochemistry and Behavior*, 24, 549–554.
- Burkhalter, A., & Cuénod, M. (1978). Changes in pattern discrimination learning induced by visual deprivation in normal and commissurotomy pigeons. *Experimental Brain Research*, 31, 369–385.
- Buschmann, J. -U. F., Manns, M., & Güntürkün, O. (2006). Let there be light! Pigeon eggs are naturally exposed to light during breeding. *Behavioral Processes*, 73, 62–67.
- Clayton, N. S., & Krebs, J. R. (1993). Lateralization in Paridae: Comparison of a storing and non-storing species on a one-trial associative memory task. *Journal of Comparative Physiology*, 171A, 807–815.
- Clayton, N. S., & Krebs, J. R. (1994). Memory for spatial and object-specific cues in food storing and non-storing birds. *Journal of Comparative Physiology*, 174A, 371–379.
- Deng, C., & Rogers, L. J. (2002a). Factors affecting the development of lateralization in chicks. In L. J. Rogers & R. J. Andrew (Eds.), *Comparative vertebrate lateralization* (pp. 206–246). Cambridge University Press, Cambridge.
- Deng, C., & Rogers, L. J. (2002b). Social recognition and approach in the chick: Lateralization and effect of visual experience. *Animal Behavior*, 63, 697–706.
- Dharmaretnam, M., & Rogers, L. J. (2005). Hemispheric specialization and dual processing in strongly versus weakly lateralized chicks. *Behavioral Brain Research*, 162, 62–70.
- Fersen, L. Von, & Güntürkün, O. (1990). Visual memory lateralization in pigeons. *Neuropsychologia*, 28, 1–7.
- Folta, K., Diekamp, B., & Güntürkün, O. (2004). Asymmetrical modes of visual bottom-up and top-down integration in the thalamic nucleus rotundus of pigeons. *Journal of Neuroscience*, 24, 9475–9485.
- Gülbetekin, E., Güntürkün, O., Dural, S., & Çetinkaya, H. (2007). Asymmetry of visually guided sexual behavior in adult Japanese quail (*Coturnix japonica*). *Laterality*, 12, 321–331.
- Güntürkün, O. (1997a). Avian visual lateralization: A review. *Neuroreport*, 8, R3–R11.
- Güntürkün, O. (1997b). Morphological asymmetries of the tectum opticum in the pigeon. *Experimental Brain Research*, 116, 561–566.
- Güntürkün, O. (2000). Sensory physiology: Vision. In G. C. Whittow (Ed.), *Sturkie's avian physiology* (pp. 1–19). Orlando, FL: Academic Press.
- Güntürkün, O., & Böhringer, P. G. (1987). Reversal of visual lateralization after midbrain commissurotomy in pigeons. *Brain Research*, 408, 1–5.
- Güntürkün, O., Hellmann, B., Melsbach, G., & Prior, H. (1998). Asymmetries of representation in the visual system of pigeons. *NeuroReport*, 9, 4127–4130.
- Güntürkün, O., & Kesch, S. (1987). Visual lateralization during feeding in pigeons. *Behavioral Neuroscience*, 101, 433–435.
- Güntürkün, O., & Kischkel, K. F. (1992). Is visual lateralization sex dependent in pigeons? *Behavioral Brain Research*, 47, 83–87.
- Hardy, O., Leresche, N., & Jassik-Gerschenfeld, D. (1984). Postsynaptic potentials in neurons of the pigeon's optic tectum in response to afferent stimulation from the retina and other visual structures. *Brain Research*, 311, 65–74.
- Herrmann, K., & Bischof, H. -J. (1986a). Effects of monocular deprivation in the nucleus rotundus of zebra finches: A nissl and deoxyglucose study. *Journal of Experimental Brain Research*, 64, 119–126.
- Herrmann, K., & Bischof, H. -J. (1986b). Monocular deprivation affects neuron size in the ectostriatum of the zebra finch brain. *Brain Research*, 379, 143–146.
- Keyser, 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 lateralization. *Brain Research*, 852, 406–413.
- Kuo, Z. Y. (1932). Ontogeny of embryonic behavior in *Aves*: III. The structural and environmental factors in embryonic behavior. *Journal of Comparative Psychology*, 13, 245–271.
- Manns, M. (1998). The ontogeny of visual lateralization in the pigeon (*Columba livia*): development and plasticity of the system. Unpublished doctoral thesis, Ruhr-Universität Bochum, Bochum, Germany.
- Manns, M., Freund, N., Leske, O., & Güntürkün, O. (2008). Breaking the balance: Ocular BDNF injections induce visual asymmetry in pigeons. *Journal of Neurobiology*, 68, 1123–1134.
- Manns, M., & Güntürkün, O. (1997). Development of the retinotectal system in the pigeon: A cytoarchitectonic and tracing study with cholera toxin. *Anatomy and Embryology*, 195, 539–555.
- Manns, M., & Güntürkün, O. (1999). Monocular deprivation alters the direction of functional and morphological asymmetries in the pigeons (*Columba livia*) visual system. *Behavioral Neuroscience*, 113, 1257–1266.
- Manns, M., & Güntürkün, O. (2009, January 20). Dual coding of visual asymmetries in the pigeon brain—The interaction of bottom-up and top-down systems. *Experimental Brain Research*. [Electronic version published ahead of print]
- Mench, J. A., & Andrew, R. J. (1986). Lateralization of food search task in the domestic chick. *Behavioral Neural Biology*, 46, 107–114.
- Parsons, C. H., & Rogers, L. J. (1993). Role of the tectal and posterior commissures in lateralization of the avian brain. *Behavioral Brain Research*, 54, 153–164.
- Prior, H., Wiltshko, R., Stapput, K., Güntürkün, O., & Wiltshko, W. (2004). Visual lateralisation and homing in pigeons. *Behavioral Brain Research*, 154, 301–310.
- Robert, F., & Cuénod, M. (1969). Electrophysiology of the intertectal commissures in the pigeon II. inhibitory interaction. *Experimental Brain Research*, 9, 123–136.
- Rogers, L. J. (1982). Light experience and asymmetry of brain function in chickens. *Nature*, 297, 223–225.
- Rogers, L. J. (1990). Light input and the reversal of functional lateralization in the chicken brain. *Behavioral Brain Research*, 38, 211–221.
- Rogers, L. J. (1995). *The development of brain and behavior in the chicken*. Wallingford, CT: CAB International.
- Rogers, L. J. (2000). Evolution of hemispheric specialization: Advantages and disadvantages. *Brain and Language*, 73, 236–253.
- Rogers, L. J., & Andrew, R. J. (2002). *Comparative vertebrate lateralization*. Cambridge, England: Cambridge University Press.
- Rogers, L. J., Andrew, R. J., & Johnston, A. N. B. (2007). Light experience and the development of behavioral lateralization in chicks: III. Learning to distinguish pebbles from grains. *Behavioral Brain Research*, 177, 61–69.
- Rogers, L. J., & Sink, H. S. (1988). Transient asymmetry in the projections of the rostral thalamus to the visual hyperstriatum of the chicken and reversal of its direction by light exposure. *Experimental Brain Research*, 70, 378–384.
- Rogers, L. J., Zappia, J. V., & Bullock, S. P. (1985). Testosterone and eye-brain asymmetry for copulation in chickens. *Cellular and Molecular Life Sciences*, 41, 1447–1449.
- Skiba, M., Diekamp, B., & Güntürkün, O. (2002). Embryonic light stimulation induces different asymmetries in visuo-perceptual and visuo-motor pathways of pigeons. *Behavioral Brain Research*, 134, 149–156.
- Ulrich, C., Prior, H., Duka, T., Leshchins'ka, I., Valenti, P., Güntürkün, O., & Lipp, H. P. (1999). Left-hemispheric superiority for visuospatial orientation in homing pigeons. *Behavioral Brain Research*, 104, 169–178.
- Valenti, A., Sovrano, V. A., Zucca, P., & Vallortigara, G. (2003). Visual lateralisation in quails (*Coturnix coturnix japonica*). *Laterality*, 8, 67–78.

- Vallortigara, G. (1992). Right hemisphere advantage for social recognition in the chick. *Neuropsychologia*, *30*, 761–768.
- Vallortigara, G., & Andrew, R. J. (1994). Differential involvement of right and left hemisphere in individual recognition in the domestic chick. *Behavioral Processes*, *33*, 41–57.
- Vallortigara, G., Pagni, P., & Sovrano, V. A. (2004). Separate geometric and nongeometric modules for spatial reorientation: Evidence from a lopsided animal brain. *Journal of Cognitive Neuroscience*, *16*, 390–400.
- Vallortigara, G., Regolin, L., & Pagni, P. (1999). Detour behavior, imprinting and visual lateralization in the domestic chick. *Cognitive Brain Research*, *7*, 307–320.
- Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*, *28*, 575–633.
- Vallortigara, G., Rogers, L. J., & Bisazza, A. (1999). Possible evolutionary origins of brain lateralization. *Brain Research Reviews*, *30*, 164–175.
- Vallortigara, G., Snyder, A., Kaplan, G., Bateson, P., Clayton, N. S., & Rogers, L. R. (2008). Are animals autistic savants? *PLoS Biology*, *6*, 208–214.
- Ventolini, N., Ferrero, E., Sponza, S., Della Chiesa, A., Zucca, P., & Vallortigara, G. (2005). Laterality in the wild: Preferential hemifield use during predatory and sexual behavior in the black winged stilt (*Himantopus himantopus*). *Animal Behavior*, *69*, 1077–1084.
- Wiltschko, W., Traudt, J., Güntürkün, O., Prior, H., & Wiltschko, R. (2002). Lateralization of magnetic compass orientation in a migratory bird. *Nature*, *419*, 467–470.
- Yamazaki, Y., Aust, U., Huber, L., Hausmann, M., & Güntürkün, O. (2007). Lateralized cognition: Asymmetrical and complementary strategies of pigeons during discrimination of the “human concept.” *Cognition*, *104*, 315–344.
- Zucca, P., & Sovrano, V. A. (2008). Animal lateralization and social recognition: Quails use their left visual hemifield when approaching a companion and their right visual hemifield when approaching a stranger. *Cortex*, *44*, 13–20.

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