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Research report

Evidence for physiological asymmetries in the intertectal connections of the pigeon (*Columba livia*) and their potential role in brain lateralisation

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Abstract

In pigeons, visual object processing is lateralised with a dominance of the left tectofugal system. To test the hypothesis, that avian visual lateralisation may arise, at least in part, from asymmetric interhemispheric inhibition, the intertectal modulation was quantified in 19 pigeons. Field potentials were recorded from intratectal electrodes in response to a stroboscope flash to the contralateral eye. Electrical stimulation of the contralateral tectum changed these flash-evoked potentials. This change was taken as a measure of intertectal modulation. It was found that the left-to-right tectotectal modulation was more pronounced than vice versa, supporting the hypothesis of an asymmetric modulation between the tecta of both hemispheres. It is conceivable that this lateralised interhemispheric crosstalk could constitute an important component of asymmetric visual processing.

Keywords: Tectal commissure; Visual system; Evoked potential; Electrophysiology

1. Introduction

A large number of neural systems of the human brain are functionally lateralised. Despite the ubiquity of cerebral asymmetries, an understanding of the neuronal mechanisms underlying these left–right differences is very limited. Several neuropsychological models propose that asymmetries of interhemispheric crosstalk could be among the most essential components involved in maintaining lateralisations, and different authors provide different accounts about the nature of these interactions [4,5,24,30].

The analysis of animal models could provide a powerful tool to enable detailed insights into the neuronal processes governing asymmetrical interhemispheric interactions. One of the best-analysed animal asymmetry models is the visual lateralisation in birds. Pigeons [12,13] and chicks [35,36], which are tested under monocular conditions in various visual discrimination and cognition tasks, show higher performances when using the right eye. Due to the complete decussation of the optic nerves [46] and the small amount of fibres recrossing in the supraoptic and tectal commissures [8,40], the right eye superiority in pattern discrimination is clearly related to a left hemisphere (LH) dominance. This conclusion is additionally supported by behavioural studies which demonstrate LH lesions to be of larger impact on visual performance than right hemisphere (RH) ones [6,15].

Avian visual asymmetry seems to be, in part, constituted by asymmetrical interhemispheric projections of both parallel visual pathways, the thalamofugal system in chicks [7], and the tectofugal system in pigeons [16], which are suggested to be equivalent to the geniculo-cortical and the extrageniculo-cortical visual pathways of mammals, respectively [41]. In addition to these anatomically manifested asymmetries, a lateralised tectotectal interaction via the tectal and the posterior commissures could be shown to modulate avian visual lateralisation [pigeon: 14; chicks: 28]. In pigeons, transection of these commissures results in a reversal of laterality proportional to the number of transected fibres [14]. If a cerebral asymmetry is reversed by tectal commissurotomy, it is likely that this asymmetry was previously maintained, at least in part, by asymmetrical tectotectal interactions — at least in pigeons.

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Robert and Cuénod [33] showed that in pigeons, the interaction mediated through the tectal and posterior commissures is nearly exclusively inhibitory. Hardy et al. [18], recording intracellularly from one tectum of the pigeon while stimulating the other, came to similar conclusions although they also encountered excitatory postsynaptic potentials in 25% of their cases.

In this study, we tested the hypothesis that the intertectal interaction might be asymmetrical, providing the substrate required for an asymmetrical interaction. According to the studies reviewed above, we assumed that in pigeons, the intertectal modulation should be, on average, stronger from the left dominant tectum to the right tectum. To test this hypothesis, we recorded intracranial field potentials (IFP) of one tectum opticum (TO) while stroboscopically stimulating the contralateral eye as well as electrically stimulating the contralateral TO. This was performed from both the right and the left TO in a between-subject design in order to quantify the modulation in either direction. A study investigating the asymmetry of intertectal interactions should preferably use a within-subject design. Unfortunately, electrical stimulation of the TO affects subsequent recordings from the same structure, so that a between-subject design had to be used.

2. Materials and methods

2.1. Subjects and surgery

A total of 19 adult naive homing pigeons (*Columba livia*) of local origin and unknown sex were used (in pigeons, gender seems to have no effect on lateralisation [17]). All experiments were performed in accordance with the ECC directive of 24 November 1986 (86/609/EEC). Approximately 1 week before the experiment, the pigeons were anesthetised (40 mg/kg ketamin and 8 mg/kg xylazin, i.m.) and a small metal head block was glued to the skull with dental cement. In addition, on each side of the skull, the outer bone layer lining the tectum was trephined. The walls of the trephined areas were covered with dental cement, and the hole was covered with a plastic lid. The pigeons were then returned to their home cage, with ad libitum water and food access for a recovery period of approximately 1 week. On the day of the experiment, the pigeons were deeply anesthetised using 1 mg/kg of ethylurethane (diluted at 20% in saline). The inner bone layers were removed, to expose the two tecti, but the durae matrae left intact. The tecti were covered with liquid paraffin to prevent drying of the tissue. A thin stainless steel reference wire was introduced under the skin to the back of the head. The recording side was chosen pseudorandomly. The upper and lower eye lids of the side contralateral to the recording were fixated in their opened position using super glue. The pigeon was then fixated in a stereotactic device using the head block. The body temperature was maintained using an electrical heating pad.

2.2. Electrodes and histological marking

To record the IFPs, monopolar stainless steel electrodes (150 μm diameter) were covered with Isonel 31 and a bare tip length of 500 μm was exposed. For electrical stimulation, bipolar stainless steel electrodes were used (bare tip 500 μm, diameter 150 μm, electrode spacing 500 μm). All electrodes were coated with DiI (1,1′-dioctadecyl-3,3,3′3′-tetramethylindocarbocyanine-perchlorat) in saturated ethanol solution using a paintbrush under microscopic visual control and allowed to dry before use. This method adapted from Snodderly and Gur [43] was used to facilitate histological localisation of the recording and stimulation site.

2.3. Stimulation and recording

Eight animals were recorded from the left and 11 from the right side (referred to as left and right pigeons, respectively). IFPs were recorded from the surface of one lateral TO while giving a stroboscope flash to the contralateral eye (Fig. 1). Using a hydraulic microdrive, the recording electrode was advanced under visual control until it caused a visible dip in the surface of the TO. The stroboscope was

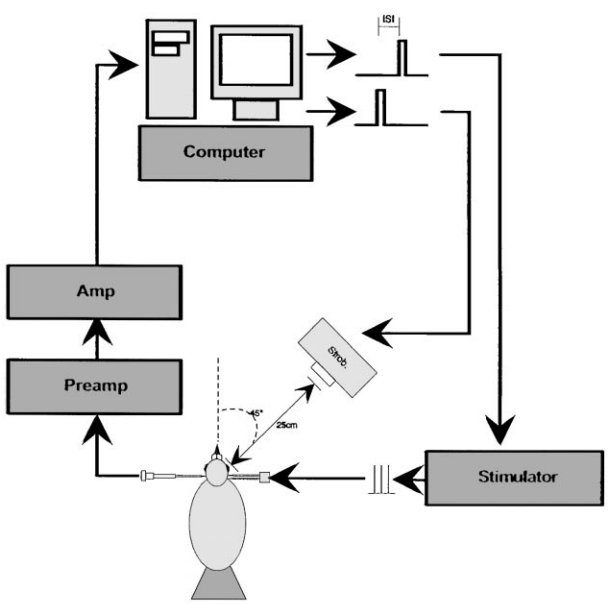

Fig. 1. Arrangement of the experimental setup. A computer controls a stroboscope delivering a flash of light to one eye, as well as a stimulator leading to an electrode in the tectum of the same side. A time interval separates the flash from the electrical stimulation. This interval is referred to as ISI. A second electrode in the opposite tectum records the resulting potential. This potential is amplified, filtered, aligned based on the time of occurrence of the flash of light and averaged within each condition to create the evoked potentials used for the analysis.

placed 25 cm from the eye of the pigeon, at an angle of 45° in the horizontal plane. In addition, for all animals, in some trials, an electrical stimulation was delivered to the TO contralateral to the recording side through a bipolar stimulation electrode inserted 500 μm into the contralateral TO. The stimulation was a train of three square pulses (0.1 ms duration each at 1000 Hz) with an amplitude of 0.2, 0.5 or 1 mA. Ten stimulation conditions were tested: (1) only the stroboscope (Strob only); (2) only the contralateral TO stimulation, but no stroboscope (TO only); (3–10) both the stroboscope and the contralateral TO stimulation were used, with an interstimulus interval (ISI) of −2 (TO stimulation starting 2 ms before the stroboscope), 5 (TO stimulation 5 ms after the stroboscope), 7.5, 10, 12.5, 15, 17.5 or 20 ms. These intervals had been selected in prestudies by scanning the intervals in which effects can be observed. For each of the stimulating amplitudes, a randomised sequence of the 10 conditions was measured with an interval of 3 s between each condition. This sequence was repeated 10 times. The response at the recording electrode was amplified, filtered, and an evoked potential for each condition was computed by averaging the 10 repetitions of each condition on a computer. The same was then repeated for the two remaining amplitudes. The order of the three amplitudes was pseudorandomised. A total of 300 trials were therefore performed (three amplitudes × 10 conditions × 10 repetitions). The experiments were controlled by a PC running Experimenters Workbench (Datawave Technology).

2.4. Histology

After the experiments, the pigeons were deeply anesthetised with 5 ml/kg equithesine, i.m. They were perfused intracardially with 0.9% NaCl followed by 4% paraformaldehyde. Brains were removed, postfixated, cryoprotected for 24 h with 30% sucrose in 0.12 M phosphate-buffer solution and cryosectioned in 100 μm frontal sections. Because DiI is ethanol-soluble, great care is needed to avoid any ethanol-containing substances. Sections were mounted and cells were marked with diamidino-phenylindol (DAPI, Sigma, 5×10^{-7}% aqueous solution). This fluorescent dye has the advantage of being water-soluble and not interfering with the DiI marking of the tracks. Sections were then inspected using an Olympus BH-2 fluorescent microscope, using the filter module DM U for DAPI and DM G for DiI. The DAPI and DiI pictures were overlaid using digital techniques. The position of the electrode track was reconstructed according to the Karten and Hodos [19] atlas of the pigeon brain.

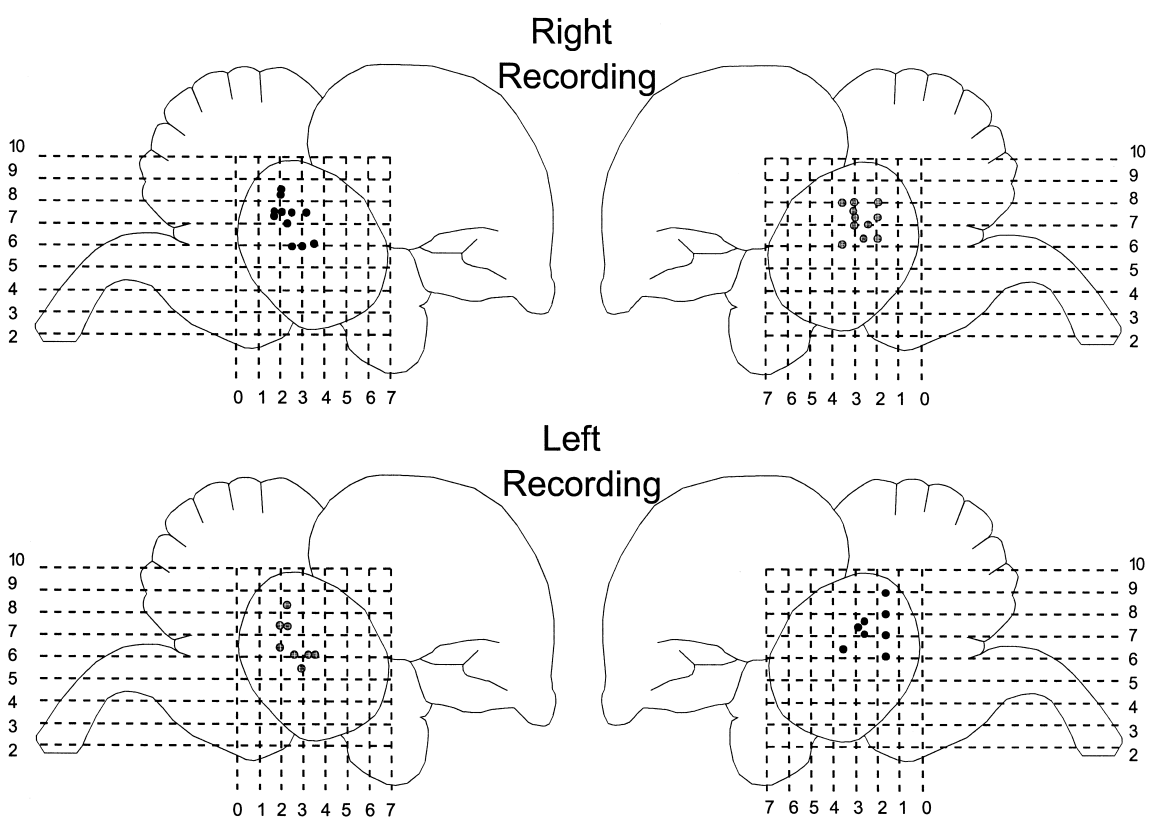

Fig. 2. Location of stimulation (open circle) and recording (black circles) sites in the 11 ''right'' animals (upper drawing) and eight ''left'' animals (lower drawing) based on the histological reconstruction.

3. Results

For the 11 ''right'' pigeons (i.e., recorded from the right side) and for the eight ''left'' pigeons, the position of the recording and stimulating electrode could unambiguously be reconstructed with the help of the DiI marking. The reconstruction is shown in Fig. 2.

The evoked potentials obtained after averaging the 10 individual IFPs of each condition showed a large amount of variety between pigeons. A typical example is shown in Fig. 3. To sum the impact of the stroboscope on the brain activity over time without arbitrarily selecting a ''peak'' for analysis, the potentials were analysed based on an integration of their IFPs over time. For the stroboscope-only condition, the voltage as a function of time after the stroboscope flash ($t = 0$) will be defined as $S(t)$. The amplitude of the response will be characterised by the value S defined as follows:

$$S = \int_{30\,\mathrm{ms}}^{80\,\mathrm{ms}} |S(t)|\,\mathrm{d}t$$

(The time before $t = 30$ ms was discarded because at long ISIs, it would contain the stimulation artefact and therefore be meaningless.)

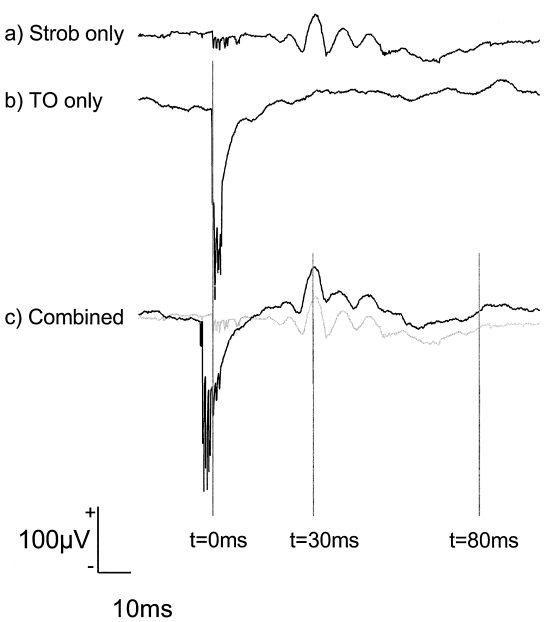

Fig. 3. Evoked potentials obtained from the right tectum of animal 567 in three different conditions. Each potential represents the average of 10 individual sweeps. (a) Potential obtained in the stroboscope-only condition, i.e. using only the stroboscope flash. (b) Sweep obtained in the TO only condition, i.e. using the electrical stimulation (1 mA) of the tectum but no stroboscope. (c) Overlay of the potential obtained in the condition in which both the stroboscope and the electrical stimulation were used (black, 1 mA, ISI = 2 ms) and the stroboscope-only potential (light grey) as represented in (a). The effect of the electrical stimulation can be interpreted as the area between the two potentials in condition (c). The interval 30–80 ms used to calculate this area is represented as vertical lines.

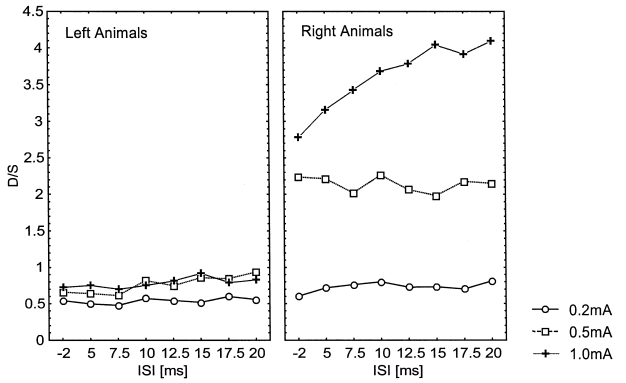

Fig. 4. Average D/S values represented as a function of the side of recording (right vs. left), the ISI (varying from -2 to 20 ms) and the amplitude of stimulation (0.2, 0.5 and 1 mA).

In trials with stimulation of the contralateral TO stimulation, the IFP reflects the impact of the stroboscope and of the intertectal modulation. The intertectal modulation should, therefore, be contained in the difference between trials with and without electrical stimulation, and will be calculated as the area between the trace with (defined at $ST(t)$, with $t = 0$ the time of stroboscope onset) and without TO stimulation (i.e., $S(t)$). The measure D (standing for ''difference'') was defined as:

$$D = \int_{30\,\mathrm{ms}}^{80\,\mathrm{ms}} |ST(t) - S(t)|\,\mathrm{d}t.$$

To make it possible to compare the values D between different recordings that might differ in electrode properties, the value D was divided by S, to create the value D/S that reflected the proportional effect of the contralateral stimulation on the response to the stroboscope. Since these integrals were computed based on the absolute values of the curves, D reflects an intertectal modulation and does not reflect the effect direction.

3.1. Effect of the ISI and the amplitude of stimulation

Fig. 4 summarises the D/S values obtained as a function of the side of recording, the amplitude and the ISI. First, the effect of stimulation amplitude and ISI will be analysed regardless of the side of recording. Both amplitude and ISI had significant effects on the D/S in the $N = 19$ animals. To measure the effect of stimulation amplitude, the data were averaged over the eight ISIs. A Friedman ANOVA [$N = 19$, $df = 2$] then yielded a significant effect with $\chi^2 = 20.63$ and $p < 0.00003$. The 1 mA condition showed the largest effects. To assess the effect of ISIs, the data were averaged over the three amplitudes. The Friedman ANOVA [$N = 19$, $df = 7$] performed on those averages gave $\chi^2 = 34.43$ and $p < 0.00001$. Here, the 20 ms condition showed the largest effect. Hence, the 1 mA 20 ms condition was the most effective stimulation

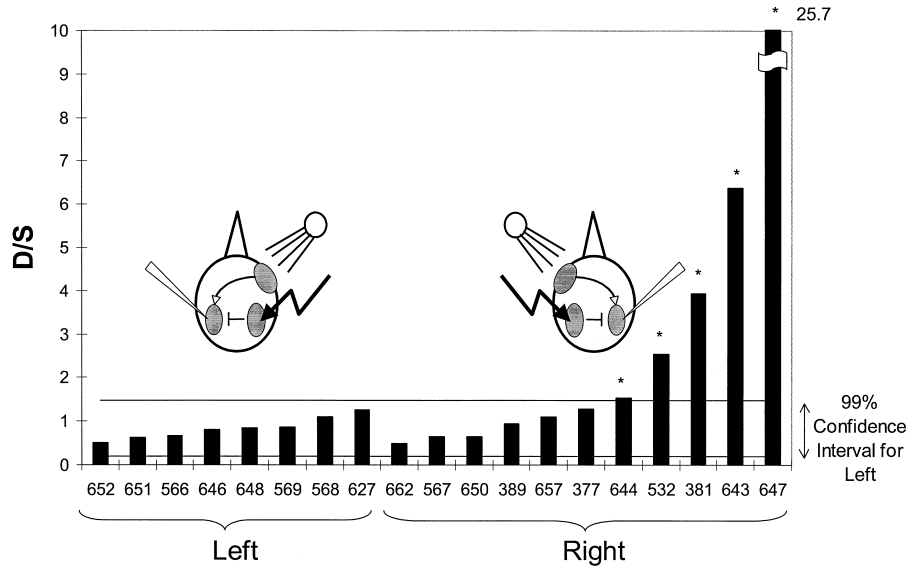

Fig. 5. D/S for ISI = 20 ms and 1 mA for each of the 19 animals. The animals are arranged in order of increasing D/S, separately for right and left animals. The two horizontal lines at $D/S = 0.20$ and $D/S = 1.47$ represent the upper and lower limits of the $p = 0.99$ confidence interval of the distribution of the left animals. The stars (*) on the animals 644, 532, 381, 643 and 647 signal that their respective D/S value falls outside the confidence interval of the left animals. The ''25.7'' on top of the bar of animal 647 represents its D/S value. The odds of having 5/11 right animals falling outside the confidence interval are $p < 5 \times 10^{-10}$.

condition. Since the effect of the side of stimulation was assumed to be most apparent in that stimulation condition, subsequent analysis will be restricted to the 1 mA 20 ms condition.

3.2. Right *vs.* left animals

The D/S values for the eight left and 11 right animals were analysed separately for the stimulation with the largest effect, i.e., 1 mA, 20 ms condition. Fig. 5 shows the D/S values in that condition for the 19 animals. Table 1 resumes the relevant statistical measures for the right and left animals separately.

As can be seen in Table 1, the values of the eight left animals were relatively small and homogenous, whereas the right animals were strikingly more heterogeneous with a higher proportion of large D/S values. To assess what proportion of animals showed significantly higher values when recorded from the right tectum, a $p = 0.99$ confidence interval (mean $\pm$ 2.5758 S.D.) for the D/S values for the left animals was calculated and was equal to [0.20; 1.47] (see Fig. 5). Five out of the 11 right animals fell outside this confidence interval. If the two samples belonged to the same population, the probability of any given right animal to be outside the confidence interval of the left animals would be $p = 0.01$. Using a cumulative binomial distribution with $p = 0.01$, the probability of 5 or more ''successes'' out of 11 is smaller than 5×10^{-10}. This result is highly significant and allows us to reject the hypothesis that the right and left animals belong to the same population. This difference in the distribution is independent of the ISI chosen for analysis. If the average over the eight ISIs is analysed at 1 mA instead of the 20 ms condition, then there are still four out of the 11 animals falling above the confidence interval. The probability of 4/11 is $p = 3 \times 10^{-6}$, and is thus indicative of a robust difference in distribution.

Table 1
Statistical measures for the D/S values in the most effective stimulation condition (1 mA, ISI = 20 ms) for the two sides of recording
Note that the right animals have a higher mean D/S as well as a higher range and standard deviation.

	Valid *N*	Mean	Minimum	Maximum	S.D.	Skewness	Kurtosis
Left	8	0.84	0.50	1.26	0.25	0.59	−0.14
Right	11	4.11	0.50	25.66	7.37	2.99	9.31

4. Discussion

The aim of this series of experiments was to investigate whether the interhemispheric connections in pigeons function in an asymmetrical manner. It was hypothesised, that the interaction from the dominant left to the subdominant right side should be stronger than the other way around. The data were in perfect agreement with this hypothesis. The interaction from the left tectum onto the right one and vice versa was quantified by measuring how much the electrical stimulation of the TO contralateral to the recording side would affect a visual-evoked potential. It was found that the right-to-left interaction (as measured in ''left'' animals) was quite homogenous and moderate, whereas the left-to-right interaction was very heterogeneous, with a substantial part (5/11 of the ''right animals'')

having values higher than the confidence interval of the modulation from the other side. This significant left–right difference could play an important role in the functional asymmetry of the pigeon and could provide a physiological basis for the observation that visual lateralisation is reversed by an intertectal commissurotomy in the pigeon [14]. Functionally, it is possible that the stroboscope flash in the present study could experimentally substitute a salient visual event in the natural environment of the animals. Since the tectotectal interaction seems to be of mainly inhibitory nature [18,33], it is conceivable that this intertectal asymmetry creates a functional architecture in which visual stimuli reaching both TO are mainly processed by the left dominant hemisphere, because left tectal processes are modulated and inhibited to a smaller extent from the right side than the other way around. Behavioral studies in chicks [10] and pigeons [12] indeed show that some visual discrimination tasks are memorised and processed predominantly by LH structures, despite binocular acquisition.

The right–left difference in amplitude of intertectal modulation could be explained by the ontogenesis of the pigeon. Pigeons, like most birds, have an asymmetrical posture in the egg [20]. Their right eye faces the shell, and their left eye faces their body. Since the shell of the egg is translucent, the right eye receives more light than the left eye. This difference plays a crucial role in the development of the behavioral asymmetry, for dark incubated pigeons lack this behavioral asymmetry [11,34]. Since dark incubation or posthatch monocular deprivation also prevents or modifies the establishment of anatomical asymmetries in the tectofugal system [11,22,23], it is likely that the embryonic light stimulation asymmetry represents a crucial trigger for the formation of neural left–right differences. Probably, the ontogeny of the electrophysiological intertectal asymmetry follows the same developmental framework. If the right eye receives more light, activity-dependent synaptic processes should reach higher levels in the left tectum as compared with the right one. In each TO, two inputs have to compete for synaptic space between: (1) inputs from the ipsilateral hemisphere and the contralateral, directly connected retina and (2) inputs from the contralateral optic tectum. Higher embryonic retinotectal activity of the left TO may provide it with an advantage in this competition, resulting in a stronger capacity for left-to-right tectal modulation, as found in our experiment. Since the direct tecto-tectal connections are not homotopically organised [3,45], it is conceivable that asymmetries in tectotectal modulation have widespread effects on most contralateral tectal processes. For the same structural reason, we found no systematic relationship between position of recording and stimulating electrode and amplitude.

It is tempting to interpret the fact, that the left-to-right modulation was measured to be much more variable than the right-to-left modulation within the same embryonic framework. Different from precocial chicks in which the retinotectal pathway is mature at hatch [26], altricial pigeons hatch with an immature visual system [1,2]. In pigeons, the first retinal axons arborize in deeper tectal layers at embryonic day 15/16, and thus only 1–2 days before hatch [21]. However, this applies only to the maturationally advanced rostral tectum. In the more slowly developing caudal tectal portions, retinal input is only able to exert its effects after hatch [21]. In chicks, the arborization of retinal axons in deep tectal layers marks the critical timepoint in which the first functional retinotectal synapses are established [8,25,28,29], an event which occurs up to 5 days before hatch in these animals. If indeed in pigeons parts of the retinotectal system become functional only shortly before hatch, individual differences in maturational speed or the amount of light exposure in the egg could induce important differences in the amount of tectal light stimulation asymmetry. These could explain the high variability of left-to-right modulation which was not observed, vice versa.

The strength of the LH to RH connections could correspond to the distribution of behavioral asymmetry as described by Güntürkün [12] in a grain-grit discrimination test with 67 animals. If one considers pigeons with an asymmetry of no more than 15% to be symmetrical, then 3% of the pigeons were found to be inverted (RH dominant), 63% to be symmetrical and 34% to show the typical LH dominance. In the present experiment, using a conservative classification of the 11 ''right'' animals based on the $p = 0.99$ confidence interval, we found 64% of symmetrical and 36% of typically asymmetrical (LH to RH interaction > LH to RH interaction) pigeons. The two distributions show striking similarities that may possibly underline the role played by the asymmetry of the intertectal connection in the behavioral asymmetry.

It should be noted that the proportions of left- and right-eyed animals seem different for other species and depend on the precise lateralisation criterion applied. In addition, lateralisation is highly task-dependent, as a LH lateralisation in chicks and pigeons exists for visual discrimination tasks, whereas a RH advantage in chicks is evident in response to novelty or spatial cues [44]. Very likely, these conditions are specific for pigeons and probably do not apply to chicks. In chicks, behavioral visual lateralisation is also triggered by an embryonic asymmetry in posture [34], but affects the formation of asymmetrical projections of the thalamofugal [36,37,39] and not of the tectofugal system [38]. Additionally, pharmacological manipulations of the thalamo- but not of the tectofugal system in chicks affect visual discrimination in a lateralised way [6]. Taken together, seemingly similar functional asymmetries in chicks and pigeons turn out to be based on different neural systems. The tectotectal asymmetry of the present study could therefore be specific for the tectofugal asymmetry in pigeons.

To our knowledge, the present study presents the first evidence for asymmetries in interhemispheric interaction

with local electrophysiological recordings. Evidence for asymmetries in the intertectal interactions of the pigeon cannot be directly generalised to other species. Indeed, the fact that the main locus of asymmetry is different in chicks (thalamofugal) and pigeons (tectofugal) indicates that even within avians, the precise mechanisms underlying asymmetries are likely to be different. Nevertheless, the present study indicates that asymmetric interhemispheric interactions are a possible component in asymmetric neural systems. Several neuropsychological models propose that the mechanisms of interhemispheric crosstalk could also be among the most essential components to maintain cerebral asymmetries in humans (for review, see Ref. [4]). The most widespread view to explain asymmetries by commissural mechanisms is either large-scale [9,32] or module-specific reciprocal inhibition [5,24,27,30]. This effect is assumed to induce a lateralisation by a stimulus-specific activation of one hemisphere which then inhibits the other brain-half during task processing [31,42]. The present results could be embedded within this general framework, even if the detailed mechanisms with which asymmetries of interhemispheric interaction are accomplished may widely differ between species and systems.

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