

Development of the horizontal optocollic reflex in juvenile barn owls (*Tyto furcata pratincola*)

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Abstract

Adult barn owls and primates possess an almost symmetric monocular rotational horizontal optocollic reflex. In primates the reflex is initially asymmetric and becomes symmetric with time after birth. The situation in the barn owl has not been studied so far. To examine how this reflex develops in this bird, we tested juvenile barn owls from the time before they open their eyes after hatching to the time they reach adult feather length. Wide-field visual patterns presented at different rotational speeds in binocular and monocular settings served as stimuli. Symmetry and asymmetry can be discriminated if the stimulus is presented to one eye only. Asymmetry manifests itself in a weaker response for nasal-to-temporal than for temporal-to-nasal stimulus movement. The binocular horizontal optocollic responses of juvenile barn owls were adult-like at the first day at which the birds responded to the stimulus. The development of the monocular reflex depended on stimulus velocity and stimulus direction. For velocities up to 20 deg/s the monocular reflex was also adult-like at the first day at which the birds responded to the stimulus. An initially higher asymmetry for 30 deg/s compared to adults disappeared within about two weeks. The development at even higher velocities remained unclear.

Introduction

Practically all seeing animals follow with their eyes, head, body, several or all of these a wide-field visual stimulus (for reviews see e.g. Huang and Neuhaus 2008; Masseck and Hoffmann 2009; Knapp et al. 2013; Carde 2021). This following behavior is called optomotor reflex (Carpenter 1988; Gioanni 1988). The reflex may be specified as optokinetic (OKR, eye-movement based), optocollic (OCR, head-movement based) or optomotor (OMR, based on movements of the whole body). Since barn owls can rotate their eyes only by a few degrees (Steinbach and Money 1973; Du Lac and Knudsen 1990; Nieder and Wagner 2000; Iwaniuk et al. 2008; Netser et al. 2010), the rotational response of these birds while being stationary is an optocollic response. Note that if we mention the OCR in this work, we always mean the horizontal rotational OCR (hOCR), and if we mention “owl” we always mean “barn owl”, if not stated otherwise. Primates possess large eye movements, and their response to the above stimuli is predominantly an OKR (Masseck and Hoffmann 2009). The reflex is characterized by a slow-phase segment during which the subject follows the movement of the wide-field stimulus, and fast return saccades. The resulting sawtooth-like pattern of gaze is called nystagmus. It was recognized early on that the nystagmus is an innate behavior that is not fully developed at birth, matures during early postnatal life, and may be influenced in its development by environmental factors (Simon 1954; Schor 1993). While the response to binocular stimulation is typically stable and of high gain, the situation for monocular stimulation differs. Primates exhibit a symmetric horizontal OKR under monocular stimulation. In other words, the reaction upon stimulation in the nasal-to-temporal direction (N-T) is as high as the reaction upon stimulation in the temporal-to-nasal (T-N) direction (e.g. van den Berg and Collewijn 1988; Distler et al. 1999). By contrast, birds with laterally placed eyes typically show an asymmetric hOCR (e.g. Mowrer 1936; Gioanni et al. 1981; Wallman and Velez 1985) with a higher T-N than N-T gain. The reaction of adult barn owls (*Tyto furcata pratincola*) is somewhere in between, but closer to that of primates than to that of chickens (Wallman and Velez 1985; Distler et al. 1999; Wagner et al. 2021). Adult owls have a symmetric hOCR for low stimulus velocities (< 20 deg/s). The response becomes moderately asymmetric for velocities between 20 and 40 deg/s.

In primates and cats, the symmetry of the reflex develops gradually after birth or eye opening (Schor 1993; Distler and Hoffmann 2003). The reflex is initially asymmetric and becomes symmetric with time. The duration

of development is shorter for low stimulus velocities. It lasts from three to four weeks in macaques to more than two years in humans (Naegele and Held 1982; Lewis et al. 2000; Distler and Hoffmann 2003). Symmetry is observed after cortical inputs make synapses in the sub-cortical network underlying the reflex (Distler and Hoffmann 2003). It is unclear whether a similar development exists in owls.

Barn owls are altricial. They are born blind, open their eyes between post-hatching days (PHDs) 10 and 12, grow fast, can stand on their feet around PHD 20, and start to fly around PHD 60 (Bunn et al. 1982; Koepl et al. 2005; Krings et al. 2018; Roulin 2020) (Fig. 1). Feather length reaches adult values at PHD 67 (Shawyer 1998).

To study the development of the OCR in barn owls, we tested juvenile owls from PHD 9 to PHD 65. We report that the OCR in juvenile owls is adult-like and symmetric for low stimulus velocities just after eye opening. The OCR is initially more asymmetric than in adults for high stimulus velocities, and becomes adult-like within a short time after eye opening.

Material And Methods

Six tame, hand-raised barn owls participated in the experiments. The birds (codes: F, G, H, I, J, K) were taken out of the nest shortly before or shortly after the time when the eyes open and raised by hand. In this way, the owls became tame and could easily be handled by the experimenters. The birds needed thermal support until they were about 15 days old (Fig. 1). Young owls were sitting on their legs and did not walk. The birds started to stand upright and walk around day 20 (Fig. 1). While the owls were calm before they could walk, they became increasingly agile afterwards. The time between PHD 20 and PHD 30 is critical insofar, as untamed birds start to show aggressive behavior towards strange subjects from this time on (Wagner, unpublished information). Thus, it is important to keep close human contact to the juveniles from about PHD 20. The birds of this age wander around and hide, but if they are frequently handled by people, they may become very tame. The agility made it more and more difficult to record OCRs after about PHD 30, because the cooperation of the owls during the experiments became very variable.

Set-up and stimuli

The set-up and the stimuli were the same as in the work with the adult barn owls (Wagner et al. 2021). Briefly, visually induced OCRs were elicited with a rotating drum (diameter 64 cm, height 46 cm, angle subtended in elevation 70° as seen from half height) that carried the stimulus pattern. The stimulus pattern consisted either of evenly horizontally and vertically spaced squares (2.7x2.7 degrees as seen from the center of the drum) (Nalbach 1992) or of a white-and-black striped pattern (horizontal wavelength 10 degrees as seen from the center of the drum). The high-contrast pattern was diffusely illuminated from outside and had an average light intensity of 27.3 cd/m². During an experiment, the animal was positioned in the middle of the drum. Young babies up to the age of about 20 days were typically placed in a staining dish (Fig. 2a). Older birds were typically placed in a beaker with its size fitted to the size of the animal (Fig. 2b (see arrow), Fig. 2c). Other containers were also tested which all shared the property that they helped to stabilize the posture of the juveniles. The animals could move the body and the head in each of containers tested. Sheets of paper at the bottom and top of the drum masked stationary contours so that the reaction of the animals corresponded to a “stare” or “delayed” OCR (for details see Törke et al. 1996). A 16.5 cm-wide circular hole in the center of the top

of the rotating drum (see brighter circles marked by the arrow in Fig. 2b) allowed to videotape the movements of the owl's head.

Data recording

Recording of monocular and binocular OCRs took place between May 1992 and June 1993. A recording session typically lasted one hour. For recording monocular OCRs, either the right or the left eye of a bird was occluded. Different eye covers were used with the aim to adjust the cover optimally to the age of the bird (see, e.g., Fig. 2a in which the right eye is covered with black adhesive tape). All eye covers worked similarly well. In older juveniles (PHD > 50), the eye cover was fastened to a holder that had been fixed to the animal's skull under anesthesia with dental cement (for further details on surgery and anesthesia see Wagner (1993)). The surgery and the experiments were carried out under a permit issued by the Regierungspräsidium Tübingen, Germany. Recording gear was mounted shortly before an experiment and removed immediately afterwards.

Reactions were recorded without earlier training. Data for a broad variety of conditions was collected: different stimulus types (binocular, monocular N-T, monocular T-N), different ages (PHDs 11–65), and different drum velocities (5, 10, 15, 20, 30, 40, 60, 80 deg/s) (for details see results). If more than one stimulus velocity was tested on a given recording day, stimuli were presented in a pseudo-random order. Stimuli moving in clockwise and counter-clockwise direction were applied in alternation.

Stimulus position was read from a potentiometer attached to the shaft of the drum. Head rotations were recorded with a stripe of cardboard with two reflection spots at its ends. The stripe was temporarily taped to the feathers on top of the head of the owl (Fig. 2). The stripe was not moving relative to the head as assured by visual inspection. In most cases, the reflection spots were illuminated via an infrared light source and videotaped from above (Fig. 2). In other cases, the spots were painted with white color onto a black stripe or black dots onto a white stripe. The high contrast of the spots was needed for the automatic reconstruction of head position (see next section and Wagner et al. 2021).

Data analysis

As mentioned above, we measured the development of the OCR relative to hatching, by using PHDs as independent variable. In some cases, we also use the term “first day of response”, meaning the first PHD at which quantitative data were recorded and the owls responded to the visual stimulus. Optocollic reactions were automatically analyzed with a temporal resolution of 80 msec (for details see Wagner et al. 2021). The azimuthal orientation of the owl's head and the azimuthal position of the pattern were synchronously derived and stored for further processing. The horizontal angular velocity of the head was calculated from head orientation. The beginning and the end of slow-phase segments were determined by a thresholding mechanism (for details see Türke et al. 1996). The results were controlled later by visual inspection and corrected, if necessary.

We calculated the gain that characterizes the effectiveness of the hOCR as the relation of the rotational head velocity of the bird during the slow-phase segment to the angular velocity of the stimulus as derived from the potentiometer data. We thus defined the “closed-loop gain” arbitrarily (for a discussion of intricacies see Wagner et al. 2021) as:

$$\text{gain}(\%) = \frac{\text{angularvelocityofanimal'shead}}{\text{angularvelocityofstimulus}} * 100 \quad (1).$$

One slow-phase segment yielded one data point for the analysis. Slow-phase segments needed to have a duration of a least five data points to be included into the analysis.

Data fitting

We chose to fit the temporal development of the gains with a sigmoidal function. The reason for choosing this function was that in several cases the development started at a low gain value and reached an asymptotic upper value after some time. To us it seemed that the sigmoidal function yielded a simple approach, because it has only three free parameters to which a physiological meaning may be assigned. The function was defined as follows:

$$y(x) = \frac{a}{1 + e^{-\frac{b-x}{c}}} \quad (2).$$

Here $y(x)$ is the gain resulting from the fit, while x is the PHD. The upper asymptotic value a corresponds to the gain value finally reached. We shall use the abbreviated term “upper value” in the following if we refer to a . b represents the inflection point of the exponential in PHDs and is a proxy for the start of development. The factor c influences the steepness of the function and, thus, correlates with the duration of development. The aim of the fitting was to minimize the sum of the root-mean square errors (RMSE) between the data and the sigmoidal function. We chose to base the fits on the medians and not on all single data values. Controls with all data showed that results changed only marginally compared with the medians (data not shown). The “90%-PHD”, the PHD at which 90% of the upper value was reached, as well as the “90-50-difference”, i.e. the difference in days between the 90%-PHD and the PHD of the inflection point of $y(x)$ (50% of the upper value) served as further measures for the duration of development.

Statistics

As in the adult study (Wagner et al. 2021), most of our data did not show normal distributions (data not shown). Therefore, we used nonparametric statistics, specifically the Mann-Whitney U test to analyze the relation of unpaired samples. Some data sets were also subjected to a correlation analysis, and some to a Wilcoxon matched pairs signed rank test (online program located at https://www.statskingdom.com/175wilcoxon_signed_ranks.html). If we refer to “adult data” in the following we mean the data as published in Wagner et al. (2021).

Results

In total, we analyzed 5357 slow-phase segments from the responses of six birds. The data resulted from a manifold of conditions: the individual birds (Table 1), clockwise and counter-clockwise stimulation, binocular and monocular stimulation, stimulus velocity and age of the birds, given in PHDs.

Table 1
Distribution of number of cases in respect to individual birds

owl	All	F	G	H	I	J	K
#	5357	1095	302	411	1454	1154	941

Since responses to clockwise and counter-clockwise stimulation were equivalent in binocular adults (Wagner et al. 2021), we pooled the responses in these two conditions for the further analyses. Table 2 shows that 1380 data points came from binocular stimulation, 2335 from monocular stimulation in the T-N direction, while monocular stimulation in the N-T contributed 1642 data points. With respect to age, we attempted to record data at certain PHDs for most velocities and at the remaining PHDs only for stimulus velocities of 10, 15 and 30 deg/s. Thus, number of cases at the different PHDs (Table 3) and the different velocities (Table 4) differ. Therefore, the much higher number of data we obtained with stimulus velocities of 10, 15 and 30 deg/s than with the other stimulus velocities should yield the most reliable results that may serve as critical benchmarks for interpretation. We chose to present the data from the other stimulus velocities in the following as well, because no other data from juvenile owls is available so far and because they illustrate the development more broadly. In this sense, we regard them as supplementary data that complete the picture (for more discussion see below). With respect to individual birds, we concentrated on certain velocities for certain birds (owl I: 10 deg/s; owls G + H: 15 deg/s, owls J + K: 30 deg/s). Owl F was tested with all velocities.

Table 2
Distribution of the number of cases on different conditions (binocular, N-T, T-N)

	binocular	owls tested	N-T	Owls tested	T-N	Owls tested
#	1380	6	1642	6	2335	6

Table 3 Distribution of number of cases in respect to age

age	11	12	13	14	15	16	17	18	19						
#	14	81	65	252	354	303	297	498	348						
owls	H, K	F, H, K	F, H	F, G, I, J, K	F, G, I, J, K	H, J, I, K	H, I, J	F, G, H, I, J, K	F, G, H, I, K						
age	20	21	22	23	24	25	26	27	28						
#	188	319	259	119	174	459	194	212	44						
owls	G, H, I, J	F, G, I, J, K	F, I, J	H, I, K	F, I, J	F, G, H, K	I, J	F, H, I	G, I, J, K						
age	29	30	31	32	33	35	36	37	38	39	40	49	50	56	65
#	102	117	14	52	186	35	124	96	27	71	80	102	55	31	85
owls	I, J	K	H	H	I, J, K	I	J, K	J	H	J	G, J	J	K	I	K

Table 4
Distribution of number of cases in respect to velocity

Velocity (deg/s)	5	10	15	20	30	40	60	80
#	172	2039	713	246	1586	302	233	66
owls	F, J, K	F, I, J, K	G, H	F, J, K				

In the following we first describe general observations of the juveniles in the stimulus set-up during the recordings, then present the temporal development of binocular responses, and finally report responses to monocular stimulation.

General observations of juvenile barn owls during recording

Tests with three owls started before the birds showed a reaction to the stimulus, and before they presumably opened their eyes. The eye lids are closed at birth. Then a small slit can be seen, but it is not clear whether the birds really see something. The latter can only be inferred from behavioral reactions, if not electrophysiological methods like EEG or invasive methods are to be used. We did not use the latter methods, but relied on behavioral testing. We tried several stimuli apart from the wide-field stimulus later used for recording optocollic data. Amongst these were stimulation with a moving stick or moving hand. During these attempts, the owls were typically sitting in the drum on different platforms. Stimulation always lasted several minutes. Since the birds had been removed from the parents at this time and were held in a comfortable environment close to the experimenters, tests with the very young birds could be repeated several times a day.

While owl K did not react to the optomotor stimulus on PHDs 9 (see video 1 in supplements) and 10, it showed the first following behaviors on PHD 11 while it was sitting in a beaker in the drum and was stimulated by wide-field motion (see video 2 in supplements; Fig. 3a-c). Likewise, owl F did not follow stimulus motion on PHD 11, but did so on PHD 12. Thus, in these two birds the very first reactions to the wide-field stimulus could be documented. Owl J was tested every day from PHD 10 on. It first reacted to the stimulus on PHD 13, but the first data available is from PHD 14. In the other three birds, testing started also at PHD 14. All six owls showed persistent reactions from PHD 14 on (see video 3 in supplements). However, periods during which the birds followed the stimulus were typically interrupted by periods during which the birds did not react (see video 3 in supplements). Also, apart from the rotational movements, sometimes translational movements of the head were observed (see video 3 in supplements). The latter were not further analyzed. Across owls, quantitative data were obtained from PHD 11 to PHD 65.

Typically, very young birds were placed in a staining dish or a beaker, supported by soft paper for comfort, but otherwise free to move during the recording (see video 3 in supplements). It was obvious that very young birds (approximately up to PHD 13) had problems with stabilizing the head. Nevertheless, high-gain responses were observed. The head was above the upper rim of the dish, with the lower jaw often touching the rim. In this situation, the head rotated, following the rotation of the stimulus. From about PHD 14, the birds could hold their head (Fig. 2a). Although the birds were not yet standing on their feet, now the head did no longer touch the rim of the staining dish. The birds were calm and typically followed the stimulus. Again, after a few more days (around PHD 20), the birds were also standing on the feet (Fig. 2b). At this time, the birds became more agile, and they sometimes started to negotiate the staining dish. Thus, we started to keep the birds in a beaker that was adapted to the size of the birds, and did no longer use the staining dish (Fig. 2c). Note that the birds were free to move in the staining dish or the beaker and were not restrained in any other way than being placed in a container. While the birds tolerated well being seated in a beaker, the responses of the birds became more variable, especially after PHD 30. The untrained birds often behaved in an agitated way, for longer periods they seemed to show no interest in the stimulus pattern and seemed to be distracted (see video 4 in supplements). Nevertheless, it was possible to record data after PHD 30 and up to PHD 65, the last day of juvenile life covered in this work.

Binocular optocollic responses of juvenile barn owls

Binocular data were obtained from all owls and for all stimulus velocities (Table 2). Binocular stimulation with a wide-field pattern very reliably elicited the OCR in juvenile owls of all ages. The birds showed persisting reactions for all stimulus velocities tested (Fig. 3a, d, g, j, m). Specifically, gains were adult-like from the first day of responding to the stimulus for all stimulus velocities tested (Fig. 4). In the following, we discuss five typical examples that provide a picture of the variability of the responses (Fig. 3a, d, g, j, m), and present a quantitative analysis (Figs. 4, 5).

The typical reaction of an owl to visual wide-field stimulation was that it followed the stimulus by head rotation. Stimulus movement in the counter-clockwise direction elicited a counter-clockwise head rotation during the slow-following phase (Fig. 3d). Opposite (clockwise) head turning was observed with opposite (clockwise) stimulus movement (Fig. 3a, g, j, m). A slow-phase segment ended with a saccadic turn in opposite direction to the slow-phase movement. The angular velocity of the head was almost constant while the owl followed the stimulus. This may be concluded from the almost linear change of head azimuth with time (Fig. 3a, d, g, j, m).

The gains were often 80% or higher, and only 1 out of 19 slow-phase segments shown for binocular stimulation in Fig. 3 had a gain below 70% (see numbers close to the single slow-phase segments in Fig. 3a, d, g, j, m and Fig. 4).

Before analyzing the typical behavior of the birds presented so far, we point to some rare behavior. For example, a special situation is shown in Fig. 3g. Here, after the first following movement with a high gain and low-amplitude saccade, the owl ceased to follow the stimulus for about 3 secs, before it started the next following movement (see arrow in Fig. 3g). As may be seen from the gain values noted in Fig. 3g (83.6 and 72.2), the period during which the owl was not following the stimulus was not included in the analysis. Another peculiarity occurred in the sequence shown in Fig. 3m. Here, the return saccade starting at 3.68 s was followed by a head movement that was much faster than the stimulus movement for more than half a second (3.92 to 4.64s, see arrow in Fig. 3m). Then a movement in the opposite direction occurred with a low velocity (4.72 to 4.96), before the bird started to follow the stimulus with a gain of 86% at 5.12s. Both, the fast head rotation from 3.92 to 4.64s and the movement in the opposite direction were also not included in the analysis. In the other 3 examples shown (Fig. 3a, d, j), the owl followed the stimulus during the total time sequence shown, as it did in the vast majority of cases. Note, however, that the amplitudes of the following movements varied considerably. We did not further analyze amplitudes and durations of the slow-phase segments, but concentrated here on the development of gains.

The quantitative analysis of the data sets for stimulus velocities of 10, 15, and 30 deg/s (Fig. 4) demonstrated that adult-like gain values were reached very early. The median gains reached an adult-like value from the first day of responding. For example, the first day of responding for 30 deg/s was on PHD 11 in owl K (Fig. 4f). Already at this day, the gain was not statistically different from the gain at PHD 33 (Mann-Whitney U-Test, number of cases PDH 11: 6, PHD 33: 11, $U = 32$, $z\text{-score} = 0.05025$, $p = 0.96012$). The data of all owls (data were recorded with owls F, K, J) showed a similar picture (Fig. 4e). Median gains stayed pretty much constant during the whole period of recording from PHD 11 to PHD 40. The data recorded in the whole period were pooled and tested against the data from adult birds as published in Wagner et al. (2021). There was no difference between the two data sets (Mann-Whitney U-Test, number juvenile: 407, number adult: 73, $U = 15073$, $z\text{-score} = 0.1989$, $p = 0.8424$; see also Fig. 5). The time course of development was fitted by a sigmoidal function (which was chosen as it describes also the monocular data (Figs. 6, 7), see Material and methods). The function fitting the 30 deg/s data demonstrated that the 90%-PHD corresponded to the first day of responding (Fig. 4e, f).

Similar observations were made for a velocity of 15 deg/s for which data from owls G and H were available. The earliest recording in owl H, at PHD 13, already yielded data (median gain value 87.8) that was statistically not different from the data at PHD 32 (median gain value 91.1) (Mann-Whitney U-Test, number of cases PDH 13: 15, PHD 32: 20, $U = 141$, $z\text{-score} = 0.28333$, $p = 0.77948$). Again, this was confirmed, if the data of owls G and H were pooled (Fig. 4c), and also here the juvenile and adult data were not different from each other (Mann-Whitney U-Test, number juvenile: 211, number adult: 11, $U = 1046.5$, $z\text{-score} = -0.5224$, $p = 0.6015$; see also Fig. 5).

The data for a stimulus velocity of 10 deg/s were mainly based on recordings with owl I (Fig. 4b), with some data also from owls F, J, and K (Fig. 4a). Again, the very first recordings, on PHD 14, showed a median gain (84.3) close to that measured at PHD 29 (85.4) or PHD 33 (92.2), and much higher than that determined at PHD 56 (72). However, for 10 deg/s stimulus velocity, the juvenile data yielded significantly lower gains than measured in adults (Mann-Whitney U-Test, number juvenile: 634, number adult: 64, $U = 9867$, $z\text{-score} = -6.7781$, p

= $1.218 \cdot 10^{-11}$; see also Fig. 5). The reason for this difference is not clear. For all other stimulus velocities tested, the juvenile and the adult responses were not different (Fig. 5).

Median gains with binocular stimulation were close to 100% for velocities up to 20 deg/s (Fig. 5). The median gains decreased to 70% for velocities up to 60 deg/s and to about 40% at a stimulus velocity of 80 deg/s (Fig. 5). Gain values did not change in the course of development, apart from some extraordinary recording days, where median values were either below (Fig. 4a, b, PHDs 17 and 18) or above (Fig. 4e, PHD 36) the rest of the values. The differences between the 1st and the 3rd quartiles were between 14.3 and 24.2 percent of gain in absolute terms or, relative to the median gain values, between 15 and 29 percent. In total, binocular gains measured in juvenile birds were not statistically different from adult gains for 6 out of 7 stimulus velocities tested that ranged from 5 to 60 deg/s (Fig. 5).

Monocular optocollic responses of juvenile barn owls

While an adult-like response behavior was observed from the first PHD of responding for binocular stimulation, the response pattern for monocular stimulation was more complex. Major differences occurred in the responses to N-T and T-N stimulation. First, at the first PHD at which the bird responded (PHD 11 in owl K, stimulus velocity: 30 deg/s), the responses to both T-N and N-T stimulation were short and of low gain (Fig. 3b, c; see Fig. 6i, j for a quantitative analysis of the reaction with a stimulus velocity of 30 deg/s). This changed fast for the responses to T-N stimulation not only for low stimulus velocities (10 deg/s, Fig. 3n, Fig. 6d), but also for 30 deg/s (Fig. 3e, h, k; Fig. 6j). By contrast, gains to N-T stimulation remained low for several days. These gains gradually increased during development. At PHD 19 responses to N-T stimulation were of high gain for a stimulus velocity of 10 deg/s (Fig. 3o: single gain values 81.5 and 85, quantitative analysis in Fig. 6c: median gain: 76.8), but still low for 30 deg/s (Fig. 3i: single gain values: 26 and 31, quantitative analysis in Fig. 6i: median gain: 47). At PHD 27, gains for N-T stimulation had increased also for a stimulus velocity of 30 deg/s (Fig. 3l: single gain values: 71, 56, 71, 70.7, 64.5, quantitative analysis in Fig. 6i: median gain: 66).

The fitting of the responses offered a possibility to gain insight into the duration of the development. The inflection points of the fit function as determined from the data were all between 9 and 13 PHDs. This suggested to us that the development started at similar times for all velocities and conditions. The duration of development may be derived from the 90 – 50 differences and the 90%-PHDs that are both related to the factor c of the fitting function. These two parameters varied a lot with stimulus velocity (range 10–26 PHD for 90%PHD, Fig. 7b). They yielded highly correlated values (7 data points, correlation coefficient: 0.988, $p < 0.00003$). In the following we use the 90%-PHDs as a measure for the duration of the development (Fig. 7b). The 90%-PHDs for N-T stimulation were 26, 17, and 24 for stimulus velocities of 10, 15, and 30 deg/s, respectively (Fig. 7b). The responses to T-N stimulation were high from very early on. The 90%-PHDs for T-N stimulation were between PHD 11 and 14 for all stimulus velocities tested (Fig. 7b). In other words, the 90%-PHD was reached almost immediately after the first day of responding (Fig. 7b). The longest time necessary to reach 90% of the final values with T-N stimulation was three days which occurred for a stimulus velocity of 30 deg/s (Fig. 7b).

The fitting of the data did not only make it possible to quantify the duration of development, but also helped to obtain insight into the differences in upper gain values for the different stimulus types (binocular, monocular T-N, monocular N-T). For binocular stimulation sufficient data for fitting was available for 10, 15 and 30 deg/s.

The comparisons showed that the upper values for binocular stimulation were very close to the upper values for T-N stimulation (compare dashed and dotted lines in Fig. 7a). Larger differences were seen between the responses to binocular and T-N stimulation on the one and the responses to N-T stimulation on the other side (Fig. 7a). The upper values for N-T responses were significantly lower than the upper values for T-N responses (7 pairs of upper values, Wilcoxon Matched Pairs signed rank test, $z=-2.418$; $p = 0.016$).

Figure 7a also shows that the differences in the upper values for T-N and N-T responses increased with stimulus velocity. This resulted in an increase of the T-N/N-T factors with stimulus velocity (Fig. 7c). A comparison with the adult T-N/N-T-factors showed that the juvenile T-N/N-T factors derived from the fits are very similar to the measured T-N/N-T-factors in adults for velocities up to 20 deg/s, while they are slightly larger for higher velocities.

While the upper values of the fits yielded data that reflected the final result of development, it was also interesting to examine the temporal change of the gains and specifically the T-N/N-T factors during development. To this end, we pooled data from three distinct age periods (PHD 11–18, PHD 19–25, and PHD 26–65) and compared the results with the result from the adults (Fig. 7d-f). While this approach coarsens the time resolution of the data compared to the data shown in Fig. 6, the resulting curves are less bumpy and allow better insight into the underlying mechanisms than the plots shown in Fig. 6. Figure 7d demonstrates that the T-N gains were high from early on. T-N gains for a stimulus velocity of 60 and 80 deg/s decreased in the last period (Fig. 7d). Note, however, that the latter data points are based on low numbers (Table 4). In the course of development, gains for N-T stimulus did not change much for stimulus velocities up to 20 deg/s and also not for 40 and 60 deg/s (Fig. 7e). The gain for a stimulus velocity of 30 deg/s increased in the last period ranging from 26–65 PHDs compared to the gains in the earlier two periods and reached an adult-like value (Fig. 7e). Figure 7f summarizes the data shown in Fig. 7d and e and demonstrates that the measured factors T-N/N-T for velocities up to 20 deg/s were close to 1 and adult-like from the first period on. By contrast, there were developmental changes of the factors T-N/N-T for velocities above 20 deg/s. The values were larger than the adult values for the first two time-averaging periods from PHD 11–18 and PHD 19–25. The T-N/N-T factors derived from the measured gain data reached adult-like values for the last analysis period (PHD 26–65) (Fig. 7f) consistent with the T-N/N-T factors derived from the fitted data shown in Fig. 7c.

Discussion

We shall discuss our data in the following with respect to methodology and behavioral variability, compare the development observed in barn owls with that in other species, and speculate about the underlying neural network.

Methodology and behavioral variability

We have already discussed methodology in the work on the adult barn owls (Wagner et al. 2021). Since the methods used in the current study were the same as for the adult study, the considerations detailed in the earlier study hold also for this study.

Similar to what was reported by Simon (1954), very young birds up to about PHD 13 supported their head by the rim of staining dish. According to our observations this did not influence the reaction of the birds to the

stimulus, and binocular gains were adult-like from PHD 11 on. In contrast to Simon (1954) we did not see a leaning of the head to one side, if one eye was occluded. This may be a difference between a bird with lateral eyes, as the chicken is (Simon 1954), and the barn owl with frontal eyes.

One may consider it a weakness of our data that the data base varies considerably between the different stimulus velocities. To take care of this, we based the conclusions on the data obtained with stimulus velocities of 10 deg/s, 15 deg/s, and 30 deg/s. The data recorded with the other stimulus velocities completed the picture. This also means, however, that the development for stimulus velocities above 30 deg/s remains an open question.

What we did not discuss in depth in the earlier study on adult owls (Wagner et al. 2021) is behavioral variability. Behavioral variability was obvious in our data. Although the optomotor behavior is a strong reflex that very reliably elicits responses, the responses are variable. For example, in pigeons the responses differ whether the head is fixed or free (Gioanni 1988), or whether the animal is in the resting, standing, walking or flying condition (Maurice et al. 2006). To guarantee an alert status, sometimes amphetamines were administered (Gioanni 1988). We did not do this. Since we used untrained birds, the variability we observed in the responses of the juveniles was not surprising. Variability may be reduced in experiments with trained owls (van der Willigen et al. 1998; Nelson and Takahashi 2010; Kettler et al. 2017; Zahar et al. 2018), where it is possible to test whether a subject is under stimulus control (Green and Swets 1966). This was not possible in our experiments with the juvenile owls in which we obtained data just after opening of the eyes.

The variability within one daily recording was determined by calculating the difference between the gains representing the 1st and 3rd quartile. The variability was typically around 25% of gain. For low stimulus velocities, for which the gain was close to 100%, a variability of 25% corresponds to a coefficient of variation of 0.25. This value is similar to the variability observed in sound-localization tasks (Wagner 1993; Hausmann et al. 2009). A coarse reconstruction of the data presented by Wallman and Velez (1985, their Fig. 3), Distler et al. (1999, their Fig. 2), and Maurice et al. (2006, their Fig. 4) showed a similar variability in juvenile chickens, macaques and adult pigeons in tests of OMRs. In spite of its variability, the data presented here are similar to the data obtained in adult owls (Wagner et al. 2021). Thus, we believe the data on juvenile owls to be sufficiently established to allow for a comparison with studies of the development of the optokinetic response in other species.

Development of optocollic responses in barn owls compared with other species

The ontogenetic change in optocollic gains of owls showed up as a fast process that depended on stimulus velocity and stimulus type. This is similar to the changes observed in primates (Roy et al 1989; Distler et al. 1999; Distler and Hoffmann 2011) and cats (Distler and Hoffmann 1992, 2003). The time course in the owl was similar to that in monkeys (Distler et al. 1999; Distler and Hoffmann 2011). Adult-like binocular responses were seen in juvenile owls from the first day at which the birds responded to the stimulus. Monocular responses to stimulation in the T-N direction attained adult-like values also within a few days and certainly less than a week after the eyes opened. By contrast monocular responses to N-T stimulation took a few days longer to reach adult-like values. However, this process was also completed around PHD 26.

Since the binocular responses were adult-like from the beginning, we like to argue that possible changes in eye positions (of which we are not aware that they occur) cannot explain the initial low N-T gains. Although we also cannot prove this, we speculate that the optomotor circuit matures (see next section). Symmetry of the monocular hOCR was reached for a stimulus velocity of 30 deg/s by a stable high gain in the T-N direction and a temporally increasing gain in the N-T direction. This is similar to what was observed in frontally-eyed mammals (Naeyele and Held 1982; Distler and Hoffmann 1992, 2003; Distler et al. 1999). By contrast, the adult-like T-N/N-T factors for stimulus velocities above 30 deg/s were mainly due to decreased gains in the T-N direction. This is contrary to what was expected from the above cited studies in cats and primates. Since the data for 40, 60, and 80 deg/s are less reliable, because they are based on relative low numbers, many more data is necessary to find out whether this constitutes a second way to reach symmetry.

The only studies on the OMR of young birds we found in the literature were those by Simon (1954) and by Wallman and Velez (1985). Simon (1954) demonstrated that the asymmetry of the monocular responses increased with time. This is similar to what Wallman and Velez (1985) reported. The latter authors argue that an increased asymmetry in the older chickens may be related to the lateral position of the eyes in this bird and that asymmetry may be the more functional state in lateral-eyed animals. We observed much more symmetric monocular responses in both juvenile (this study) and adult (Wagner et al. 2021) owls than Wallman and Velez (1985) observed in chickens. However, the asymmetry in chickens was weaker for lower than for higher stimulus velocities (Wallman and Velez 1985), similar to what we observed in owls.

The neural circuits underlying optocollic, optokinetic, and optomotor responses

The visually induced wide-field responses are driven by a sub-cortical network (Grasse et al. 1984; Schor 1993; Wallman 1993; Distler et al. 2002). The network receives direct input from the retina, subcortical inputs via the optic tectum, and indirect inputs from the cortex or its avian analogue, the visual Wulst (for reviews see Wallman 1993; Wylie et al. 2014). Important nuclei in mammals are the nucleus of the optic tract (NOT) and the terminal nuclei (Schor 1993; Masseck and Hoffmann 2009). The homologous nuclei in birds are the nucleus lentiformis mesencephali (LM) and the nucleus of the basal optic root (nBOR), respectively (Rio et al. 1983; Wiley et al. 2005). It is known for cats that the OKR in response to high velocities is mainly controlled by cortical input in both N-T and T-N directions, while OKR to low velocities is mediated in the N-T direction by the cortex and in the T-N direction by both the cortex and subcortical pathways (Montarolo et al. 1981; Grasse et al. 1984). In young kittens the NOT receives only input from the contralateral retina, and these inputs drive the responses with T-N stimulation. In older kittens the NOT receives also a cortical input. This input makes functional synapses in NOT at the time when symmetry of the OKR is first seen (Distler and Hoffmann, 1992).

We like to speculate that in the owl inputs to LM from both the nBOR and the visual Wulst interact to generate the OCR in the N-T direction as they do in the pigeon and the chicken (Gioanni et al. 1983; for a review see Wallman 1993). The maturational changes observed here most likely reflect an input from the Wulst. In this respect, it would be interesting to know whether the bilateral projections from the visual Wulst to several midbrain and diencephalic nuclei (Wirth and Wagner 2019) are already present at this time. In the chicken, McKenna and Wallman (1985) observed that directional sub-regions in nBOR are not present at hatching but develop rapidly within the first postnatal weeks. We also saw a rapid development in juvenile owls. However, while the development in the lateral-eyed chicken increased asymmetry (Wallman and Velez (1985), the

developmental changes in the owl increased symmetry. It would also be interesting to know whether response properties of optomotor neurons in barn owls are similar to those in frontal-eyed mammals (Distler and Hoffmann 2011), similar to what Wylie et al. (1994) demonstrated for saw-whet owls, to lateral eyed birds (Morgan and Frost 1981, Crowder et al. 2003), to specialists like hummingbirds (Gaede et al. 2016), or have established their own specific distribution.

Abbreviations

PHD: post-hatching day

90%-PHD: PHD at which 90% of the upper (asymptotic) value of the fit function is reached

90-50-difference: difference in days between the PHD of the inflection point of the fit function (50%) and the 90%-PHD

deg: degrees

hOCR: horizontal optocollic response

LM: nucleus lentiformis mesencephali

nBOR: nucleus of the basal optic root

N-T: nasal-to-temporal

OCR: optocollic response

OKR: optokinetic response

OMR: optomotor response

RMSE: root-mean square error

T-N: temporal-to-nasal

Declarations

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Figures



Figure 1

Post-natal development of the barn owl. Six stages of development are shown from left to right together with the related age and major developmental steps. d= post-hatching day.



Figure 2

Juvenile barn owls in the set-up. a) Young bird sitting in a staining dish with white stripe carrying reflecting spots and right eye covered with black adhesive tape. b) Twenty-one day (d) old bird sitting in a beaker (arrow) with white stripe with black dots on the top of the head. Frame number, gearwheel and the border of the mask (arrow) are also shown. c) Barely visible older bird with bright reflecting spots mounted on a stripe of cardboard that was fixed to the head with black adhesive tape. The bright (a, c) or dark (b) spots were used for reconstruction of head azimuth.

Figure 3

Examples of OCRs of juvenile barn owls. a-o) The responses to different stimulus types at different ages and different velocities for different birds as notified in the insets or on top of the middle plots are shown. Dashed lines represent a reference position on the wide-field pattern, plotted in the range between +/- 100 degrees. Note that the dashed lines between +100 and -100 degrees and the saw-tooth-like appearance of stimulus position

are due to wrapping. Solid lines signify the position of the owl's head in azimuth. The numbers close to the individual slow-phase segments specify the gain during the respective segment. The arrows in (g) and (m) point to rare events as explained in the text.

Figure 4

Dependence of binocular gains on age. Median data (triangles) and 1st to 3rd quartiles (lines) are shown for different days of recording (x-axis), and different stimulus velocities, including all (a, c, e) or only data of an individual bird (b, d, f). The respective fit function is shown by the dotted line. Adult data (Wagner et al. 2021) are documented for comparison in each plot on the right. The numbers specify the number of cases for each condition.

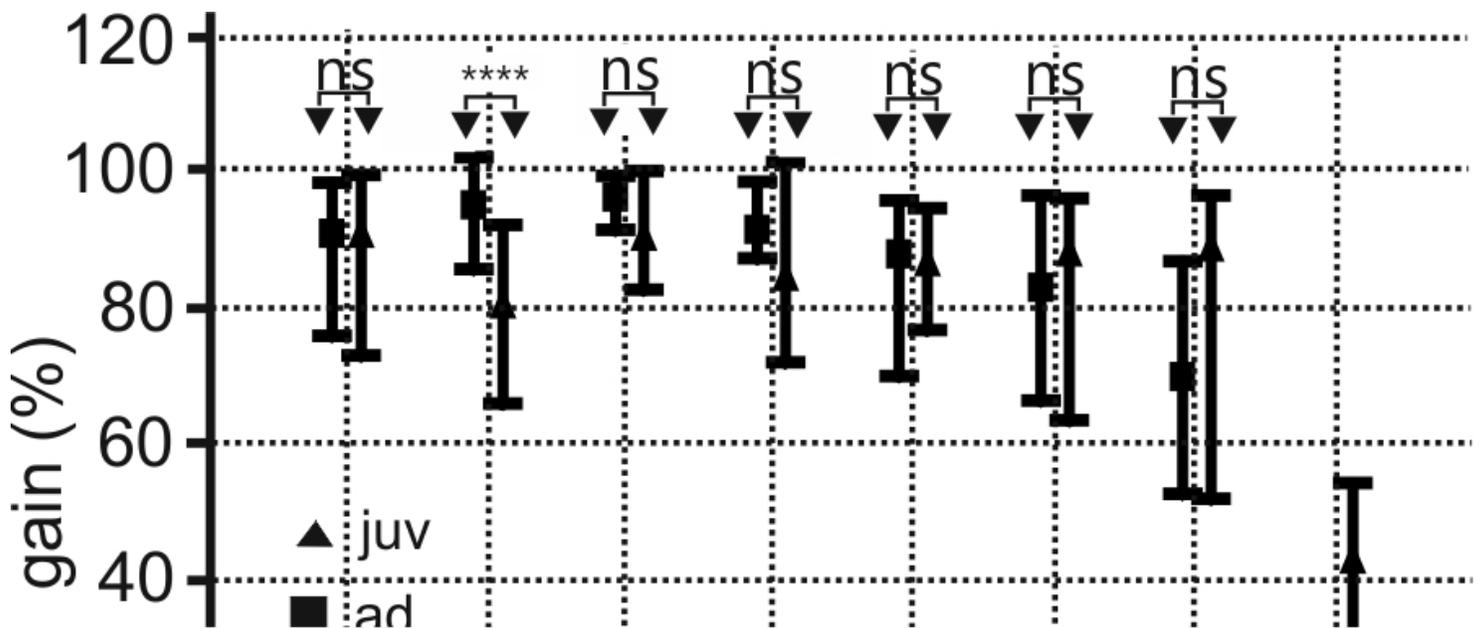


Figure 5

Comparison of juvenile and adult binocular OCRs. The median data together with the 1st and 3rd quartiles are shown. Note that the rotational speeds are not plotted on a linear axis. The numbers between 0 and 20% gain

specific the respective numbers of cases. The data of juveniles and adults are not different (ns) for 6 out of 7 velocities and highly significantly different (****) for 10 deg/s. For 80 deg/s only juvenile data was available.

Figure 6

Dependence of monocular gains on age. a-n) All monocular data is shown as it was recorded for different velocities (row) and either N-T (left column) or T-N (right column) stimulation together with the fit functions (dotted lines). Specifications are as explained in the legend to Fig. 4. Note the lower gains and the delayed development for N-T responses compared with T-N responses.

Figure 7

Quantification of asymmetry. a) Fit parameter “asymptotic upper value”, b) First day of response and 90%-PHD days. The “first day of response” (for a definition see text) refers to both T-N and N-T conditions and is documented for each stimulus velocity. The 90%-PHDs are separately plotted for T-N and N-T stimulation. d, e) Data from three developmental periods (PHDs: 11-18, 19-25, 25-65). c, f) Asymmetry factors T-N/N-T in juveniles (juv) derived from the fits (c) and from the data (f) in comparison to the measured adult factors (ad).

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