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Research report

Limits of intraocular and interocular transfer in pigeons

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ABSTRACT

The retina of the pigeon has two areas of enhanced vision: the red field looking into the frontal binocular field and the yellow field projecting into the lateral monocular field. The entire retina projects to the tectofugal pathway, whereas the monocular areas mainly project to the thalamofugal pathway. In the present study we examine how the information received in different retinal areas and hemispheres is integrated within the pigeon brain. The pigeons' task was to discriminate between two shapes by pecking on one of the two keys located at one end of an experimental alley, while walking back and forth between two feeders. Intraocular transfer between the red and the yellow field was tested by moving the stimulus from the frontal to the lateral visual field in consecutive steps and vice versa. When the stimuli were perceived among the edge between the red and the yellow field, the pigeons showed a drastic decrease of performance that we interpret to result from a switch from the tectofugal to the thalamofugal system. There were virtually no traces of intraocular transfer of information from the tectofugal to the thalamofugal pathway, although, in a second experiment a weak intraocular transfer of information from the thalamofugal to the tectofugal system was observed. In a third experiment, interocular transfer of information between the yellow fields of the two eyes was tested. In eight out of nine birds, no interocular transfer was found. In addition, pigeons showed more difficulties to learn the task in the monocular right visual field than in the monocular left visual field, suggesting the existence of an asymmetric organization of the thalamofugal system in the pigeon brain.

1. Introduction

Rock pigeons (*Columbia livia*) and many other birds have lateralised eyes with only relatively small binocular overlap (about 25°) and a large monocular visual field extending about 120° laterally to both sides. The pigeon's eyes are specialised for frontal binocular vision at near distances during pecking, and for panoramic vision at far distances [3,10]. These two visual functions are mediated by two different retinal areas: a binocular dorso-temporal oil dropled red field and a monocular oil dropled yellow field. The red field is pointing into the lower frontal visual field, while the yellow field is covering the remaining visual field: upper frontal visual field and the lateral one [32]. In a natural situation a bird might perceive the same visual stimulus in different parts of the visual field at different times. The goal of inter- and intraocular transfer experiments is to clarify the way in which information is transmitted between the two eyes and between the lateral and the frontal visual field.

Two independent visual systems have been described in the avian brain. The tectofugal pathway that processes visual information proceeding from the entire retina, and the thalamofugal pathway which receives visual input from the yellow field. The tectofugal pathway is in large parts homologous to the extrageniculocortical pathway in mammals [2,21,14,31]. The visual input ascends from the retina to the contralateral optic tectum (OT), which projects bilaterally to the entopallium (E) via the thalamic nucleus rotundus (Rt). The thalamofugal pathway can be considered homologeous to the mammalian geniculo-cortical pathway. In pigeons, but not in chickens, this pathway mainly receives visual input from the yellow visual field [36,19], which is transmitted to the contralateral thalamic nucleus geniculatus lateralis, pars dorsalis (GLd). The GLd projects bilaterally to the telencephalic visual wulst [41,21,14].

1.1. Intraocular transfer

The first attempt to train birds in the lateral visual field in order to test intraocular transfer of information was done by Nye [34]

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who trained six pigeons in different discrimination tasks. The birds learned the task successfully if the stimuli were presented behind the pecking keys in the frontal visual field. In contrast, when the stimuli were located at 90° to each side of the axis of the beak, the pigeons did not learn the task. Nye concluded that "pigeons do not possess the neural capability required to learn to use information contained in laterally located stimuli to directly control pecking behaviour". In a previous experiment, Levine [25] had found a drop in the discrimination performance when the stimuli were shifted from a subrostral (in a plane below the pigeon's head) to an anterorostral position (in front of the pigeon head). Mallin and Delius [26] trained head-fixed pigeons to discriminate two coloured lights using jaw movements as an operant response. They found a poor intraocular discrimination transfer when the stimuli were shifted from frontal to lateral position and vice versa. However, the transfer from lateral to frontal position was slightly better (around 10%) than the reverse performance. Remy and Emmerton [36] described the existence of information transfer from the lateral to frontal visual field and a lack of information transfer from the frontal to the lateral visual field, in a light detection task, also using jaw movement as a measure. Roberts et al. [38] confirmed those results in unrestrained pigeons employing a symbolic delayed matching to sample task. The observed lack of transfer was interpreted as an absence of communication between the thalamofugal and tectofugal pathways.

In the present study we test intraocular transfer of information in free walking pigeons by presenting two patterns either in the frontal visual field or in the lateral visual field.

1.2. Interocular transfer

According to Levine [23], the earliest interocular transfer experiment was done in 1917 by Wolfgang Köhler. Patching one of the two eyes, he observed that chickens showed interocular transfer between the two eyes while discriminating two sheets of grey paper differing in brightness, which were located horizontally at ground level. However, in an experiment in which the stimuli were displayed on a vertical screen above ground level, interocular transfer was not observed [1]. Two hypotheses were proposed to explain these contradictory results: the "sensorimotor integration" hypothesis [46,45] and the "retinal locus" hypothesis [23–25,10,26].

The "sensorimotor integration" hypothesis proposes that pigeons may transfer information depending on whether the response key and the visual stimulus have the same or different spatial locations [37]. To test the "sensorimotor integration" hypothesis, pigeons were trained in three spatial tasks employing two pecking keys arranged either vertically or horizontally [46]. No matter whether the keys were arranged horizontally or vertically, if response key and stimulus were located in the same pecking key, there was a perfect interocular transfer of information. However, if response key and stimulus were located in different keys (for example: the stimulus was presented in the lower key and the pigeons had to peck in the upper key) the pigeons did not show interocular transfer.

The "retinal locus" hypothesis proposes that interocular transfer occurs when the stimuli are presented in the dorso-temporal part of the retina (red field), but not when the stimuli are presented in the other parts of the retina (yellow field) [23–25,10,26]. Levine [23–25] conducted a set of experiments using a jumping stand. The birds were placed into a rotating perch, which forced them to jump onto one of two platforms according to the presented stimuli. If the animals jumped to the incorrect platform, it collapsed and the animal dropped into a net. The correct platform remained safe until the bird was returned to its cage. They found that when the stimuli were presented horizontally in a plane below the pigeon's head (subrostral), interocular transfer between the two eyes occurred, but if the stimuli were presented vertically in front of the pigeon's head (anterostral) there was an absence of transfer. Catania [5] challenged these observations by training pigeons in brightness, colour and pattern discrimination tasks to peck on a key located in front of the pigeon head. The stimuli were projected either on the frontal key or on one of two lateral screens. Pigeons showed interocular transfer of information in both conditions. Catania proposed that the lack of interocular transfer in Levine's experiments could be explained by the amount of training and by the occlusion of the eye due to changes in the pigeon's posture. However a set of experiments replicating Levine's jumping stand [10] concluded that the absence of transfer was a genuine phenomenon which did not depend on postural habit, amount of training and task complexity. Furthermore, birds trained binocularly in the jumping stand often gave evidences of learning with only one eye when tested monocularly. Mallin and Delius [26] conducted an experiment with head-fixed pigeons using jaw movements as an operant in a colour discrimination task. They presented two coloured lights at different locations on the retina. Birds showed interocular transfer of information when the discrimination task was monocularly presented inside the red field and a lack of interocular transfer when the stimulus was monocularly presented within the yellow field.

According to Remy and Watanabe [37], the "retinal locus" and "sensorimotor integration" hypotheses may not be contradictory. Retinal locus may be crucial when a task does not require sensorimotor integration. Up to now, none of the proposed hypotheses is capable of explaining all experimental results on interocular transfer. Some experimental findings suggest that other characteristics of the task, such as biological relevance, type of reinforcement, or trained response, may affect interocular transfer. For instance, transfer of information was absent in heat reinforcement, but it was present in the same task when using food reinforcement [9]. Moreover, interocular transfer in pigeons was found in colour discrimination, but it was not observed in the motor response required to show the colour discrimination [43].

Pigeons show an asymmetric information transfer between hemispheres. Nottelmann et al. [33] observed transfer of memories from the left eye/right hemisphere to the right eye/left hemisphere, but not vice versa. However, Skiba et al. [42] observed a faster shift of learned colour cues from the right to the left eye than vice versa. Most probably, cerebral asymmetries and interocular transfer of information are interrelated phenomena in birds. Interhemispheric interactions may be an important component for understanding visual asymmetries [15,35,22].

Interhemispheric information transfer in the avian and the human brain seems to be a complex phenomenon. Many questions remain unanswered and none of the proposed theories can explain all experimental results. The restricted experimental conditions of many investigations result in a very low ecological validity. Very often, the experimental conditions prevented the birds from walking freely while solving the task (examples can be found in Refs. [26,38,36,34]). Therefore, visual mechanisms that may play an important role in ecologically valid conditions like optic flow due to locomotion and head movements have not been considered. In addition, there are few experiments investigating interocular transfer between the yellow visual fields. This is probably due to the difficulties in training pigeons to solve visual tasks in the lateral visual field [37].

In the present study, intraocular transfer and interocular transfer were investigated in free walking pigeons. In the first experiment we tested intraocular transfer of information from the red to the yellow field. That is, if pigeons learn a visual task using their frontal binocular field, can they perform the same task using their lateral visual field of the same eye? In the second one, interocular transfer of information between the yellow fields of both eyes was investigated. That is, if pigeons learn a visual task within the yellow visual field of one eye, are able to perform the task with the other eye? In addition, we also examined whether pigeons were able to learn a pattern recognition task directly in the yellow visual field. Finally we tested intraocular transfer from the yellow fields to the red field in the few birds that succeeded in this later task.

2. General methods

2.1. Subjects

Ten rock pigeons (*C. livia*), males and females, aged between 3 and 7 years obtained from the aviary of the Biopsychology Department of Ruhr-University in Bochum were initially trained in a pattern recognition task. During the experiments, they were kept in individual cages on a 12-h light–dark cycle. They had *ad libitum* access to drinking water. Food was restricted to keep their weight at 85% of their free-feeding weight.

Nine of the ten pigeons successfully completed the initial training (see below) and were used in Experiment 1. Eight of them were successful and continued to participate in Experiment 2. Only three of them learned to generalize from one lateral field into the contralateral field and could be used for Experiment 3.

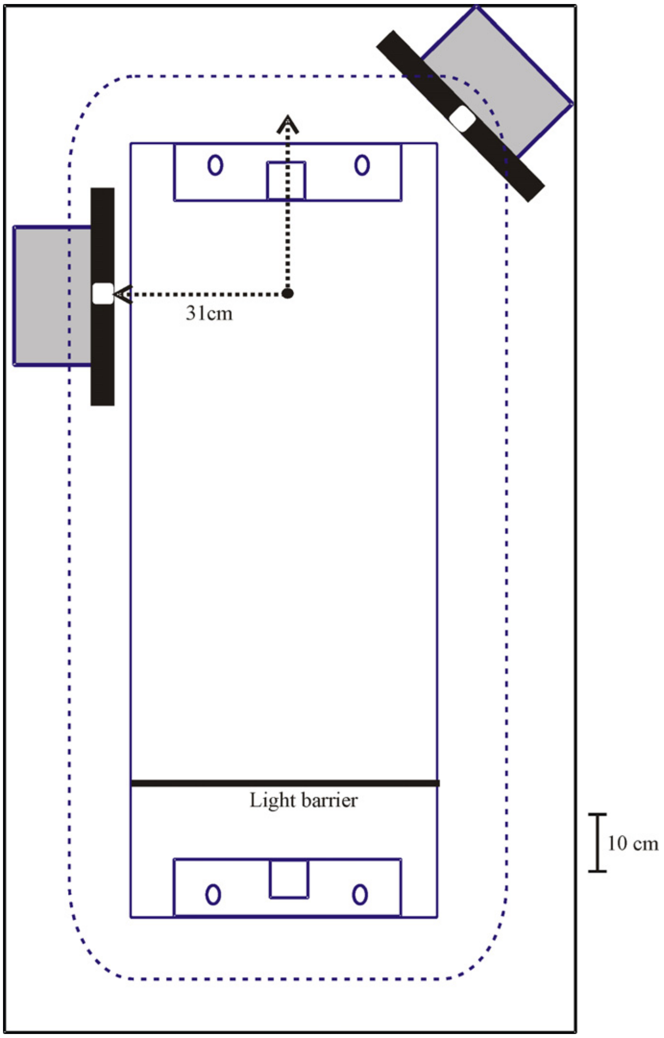

Fig. 1. Scaled drawing of the experimental arena. The position of the stimuli in degrees was calculated assigning the centre of the circumference in the equidistant point (31 cm) between two screens located in the centre and in the lateral visual field. In the diagram, the screens at the front end are located at 90° and 45° according to that definition. The bold line indicates the position of the light barrier close to the back end of the arena.

Table 1
The angular size (°) of the stimuli in the pigeon retina was calculated according to the pigeon's observation point and screen position

Observation distance (cm)	Screen position (°)										
	0	14	23	29	36	41	45	48	61	76	95
20	14.3	12.3	11.1	7.9	6.2	4.9	4.2	7.9	4.9	3.1	–
40	7.2	6.9	6.5	6	5.4	4.8	4.5	3.6	4.9	6.7	8.5
60	4.8	4.7	4.6	4.4	4.2	3.9	3.8	2	2.6	3.6	4.9
80	3.6	3.5	3.5	3.4	3.3	3.2	3.1	1.2	1.6	2	2.6
100	2.9	2.9	2.9	2.9	2.9	2.9	2.9	0.8	1	1.2	1.6
117	2.4	2.4	2.4	2.4	2.4	2.3	2.3	0.6	0.7	0.9	1.1

The observation point was the distance in cm from the pigeon to the frontal screen situated at 0°. The screen position (in degrees) was the position of the screen according to an imaginary circumference situated at 31 cm equidistant from the frontal (0°) and the lateral screen (90°). At 95° the projection of the stimuli fell out of the pigeon visual field.

2.2. Material

An experimental arena of 125-cm length and 54-cm width was constructed (Fig. 1), with a feeder and two pecking keys on either end. The two pecking keys (2.5 cm in diameter) were placed at each side of the feeder (2 cm in diameter). The lower edge of each key was 5 cm above the floor, and the two keys were spaced 23 cm apart. At one end of the arena (front end) either one (Experiments 1 and 3) or two (Experiment 2) Philips 15 in. LCD screens were mounted on a track surrounding the arena, which permitted an easy displacement of the screens around it. On the other end (back end) of the arena, a light barrier was installed to detect the bird walking between the two feeders. The monitors (Philips Soho 150S3F) have a maximum resolution of 1024 × 768 at 75 Hz, anti-glare and hard coating surface, horizontal viewing angle of 150°, and vertical viewing angle of 110°. The pigeon visual acuity in the lateral and the frontal visual field is 12.6 c/degree and 12.8 c/degree, respectively [20,40]. The angular size of the stimuli in the retina varied according to the distance and screen position from 0.6° to 14.3° (Table 1). The wide view angle of the screen together with the stimuli size (5 cm × 5 cm) ensured that the stimuli presentation were visible at any place of the experimental arena for all screen positions. The arena was placed in a symmetric experimental chamber of 190-cm length, 100-cm width and 80-cm height. On one end of the experimental chamber a video camera was placed to monitor the pigeons' behaviour in the experiment.

2.3. Training procedure

Pigeons were initially trained to discriminate between two 5 cm × 5 cm shapes: "stimulus A" and "stimulus B" (Fig. 2) by pecking once on one of the two keys. The stimuli were presented on a single LCD screen located in a central position directly behind the feeder and the two pecking keys at one end of the area. The centre of the stimulus was displayed in the middle of the screen 16 cm above floor level. The subjects were divided randomly in two groups of five pigeons each. One group of birds was trained to peck the right key

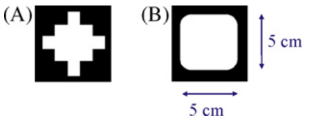

Fig. 2. Shapes presented in the discrimination task.

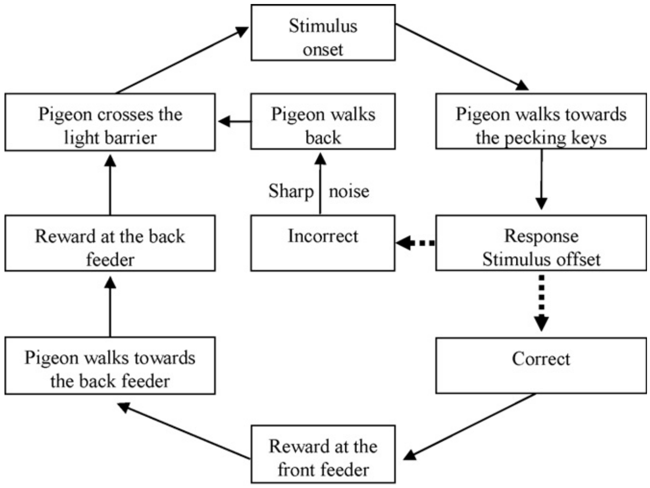

Fig. 3. Diagram of the pigeons' steps during the experimental procedure. The pigeons' task was to discriminate between two shapes by pecking on one of two pecking keys, located at one end of the arena, while walking between two distant feeders. The stimulus onset occurred when the pigeons crossed the light barrier, the stimulus offset occurred when the pigeons pecked on the response key.

when "stimulus A" was presented and the left key when "stimulus B" was presented. For the other group this pattern was reversed, that is, the left key corresponded to "stimulus A" and the right key to "stimulus B".

Pigeons were trained to progressively approximate the target behaviour in three steps. In the first step, by alternately activating the two feeders at the front and back end of the arena, the pigeon learned to walk back and forth between them to get food. In the second step, the birds learned to peck on the keys at the front end of the arena to obtain food. After 2 s of food access in the front feeder, the pigeon walked to the feeder on the back end, where it was rewarded, without pecking, for another 2 s. In the final stage of training, the walking pigeon now had to learn to peck on one of the keys, contingent to the shape presented on a screen located in the front end of the arena. Eventually, the pigeon's task was to discriminate between two shapes by pecking on one of the two keys located at the front end of the arena, while walking back and forth between the two feeders (Fig. 3). A correct response was rewarded with 2 s of food access. An incorrect response was punished with 2 s of a sharp noise. A session of training consisted of 10 "stimulus A" trials and 10 "stimulus B" trials, presented in random order. Pigeons were trained until they achieved at least 70% of correct responses in each of four consecutive sessions.

3. Experimental 1: limits of intraocular transfer in pigeons: frontal to lateral direction

3.1. Methods

Immediately after successful completion of the initial training, we started to gradually move the screen from its initial position at the front end of the arena into the lateral visual field in ten consecutive steps. At each position of the screen, the pigeons were trained until the learning criterion (70% correct responses in four consecutive sessions) was reached before the screen was moved to the next position. The animals were tested during four sessions of 20 trials each per day. The position of the screen is indicated in terms of the angle between a line pointing to the initial frontal position (0°) and the position of the screen with respect to the centre of the circular track on which the screen was moved (Fig. 1). The distance of the screen from this centre was 31 cm. Initially located at 0°, the screen was moved to the lateral side in the following steps: 14°, 23°, 29°, 36°, 41°, 45°, 48°, 61°, 76°, and 95°. For four of nine pigeons, the screen was moved from the centre to the right side of the arena. For three of the birds, the screen was moved from the centre to the left side of the arena. Due to the difficulties encountered to perform the task, the two remaining birds were tested in both sides (see Section 3.2).

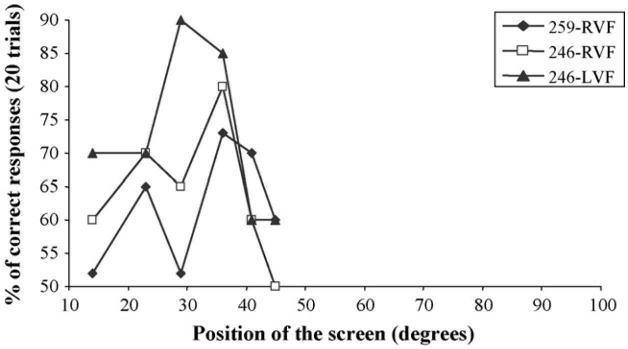

Fig. 4. Percentage of correct responses in the first 20 trials for pigeons 259 and 246, which were incapable of learning the task beyond 45° in the right and in the left visual field.

3.2. Results

Two different measures were taken in order to study intraocular transfer of information: in each new position, we measured the percentage of correct responses for the first 20 trials, and the number of trials needed to achieve a criterion of 70% of correct responses in four consecutive sessions.

Eight of the nine birds learned the task in the lateral visual field by moving the screen in successive steps from 0° (frontal visual field) to 95° (lateral visual field). Pigeon 246 was tested first from the frontal to the left visual field (LVF); afterwards the same bird was tested from the frontal to the right visual field (RVF). In both cases the bird failed to reach the criterion when the screen was moved beyond 45° after 600 trials of learning. Pigeon 259 was also incapable or learning the task beyond 45° on the right side. However, after 380 trials of training on the left side at 45°, the animal achieved the criterion and the screen was moved step by step until 95° were reached. Summarizing, pigeon 259 in the right visual field and pigeon 246 in both visual fields were unable to learn the task beyond 45° (Fig. 4). Four pigeons (51, 321, 333, and 347) successfully learned the task in the right visual field. Another four birds (251, 512, 988, and 259) learned the task in the left visual field. Regardless of the individual differences, all birds showed a consistent and drastic decrease of performance at 45°. Note, that this was the case even though the differences between successive screen positions were much smaller in this region than they were in the frontal and lateral regions.

3.2.1. Percentage of correct responses

For data analysis, the results of four birds for each visual field were considered. In seven of the ten positions the overall average percentage of correct responses for the first 20 trials was above 70%. At 29° and 36° it was close to 70%: 67% and 68%, respectively. However, at 45° the average percentage of correct responses for the first 20 trials dropped to almost chance level (58%) (Fig. 5). Data were analysed by means of a 10 × 2 mixed ANOVA. The first factor was the within-subject factor of screen position with 10 levels. The second factor was the between-subjects factor of visual field with 2 levels. The data analysis revealed a significant effect for screen position ($F_{(9,54)} = 2.55$, $p = 0.01$). A pair-wise comparison accounted for significant differences between the 45° position and positions 14°, 41°, 61° and 76°. Significant effects were also found between position 14° and positions 29° and 36° (Fig. 5), and between position 48° and

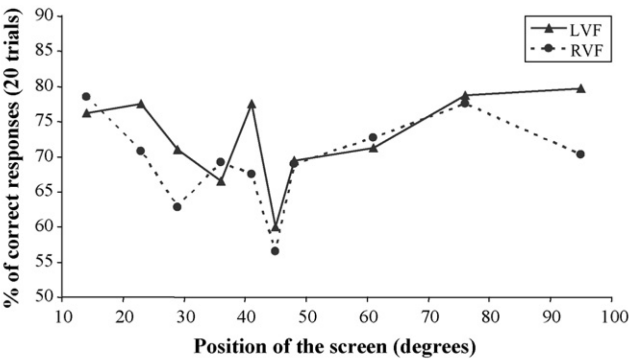

Fig. 5. Average percentage of correct responses in the first 20 trials of training at each position of the stimuli in the left visual field (LVF), and in the right visual field (RVF).

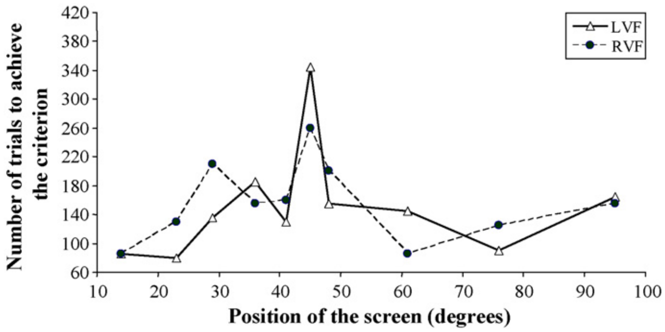

Fig. 6. Average number of trials needed to achieve the criterion at each position of the screen for birds trained in the RVF and in the LVF.

76°. No significant effects were found for the factor encoding the visual field ($F_{(1,6)} = 0.49$, $p = 0.51$) and for the interaction between the two factors ($F_{(9,54)} = 2.56$, $p = 0.91$).

3.2.2. Number of trials for achieving the criterion

The number of trials needed to reach criterion at each position of the screen was also analysed for the eight birds, which completed the training. Up to 45° eccentricity, moving the screen to the next position required an average of 144 trials; while at 45° the animals needed an average of 302 trials to achieve the criterion (Fig. 6). A data analysis was performed with the number of trials needed to reach the criterion at each position of the screen. A screen position × visual field ANOVA revealed a significant effect for screen position ($F_{(9,54)} = 2.13$, $p = 0.04$). The post hoc test accounted for significant differences between 45° and positions 14°, 23°, 36°, 41°, 61°, and 76°. Significant effects were also found between 95° and positions 14°, 23°, and 61° (Fig. 6). No significant effects were found for the visual field ($F_{(1,6)} = 0.32$, $p = 0.59$) and the interaction between screen position and visual field ($F_{(9,54)} = 0.01$, $p = 0.91$).

3.3. Discussion

Eight of the nine birds learned the discrimination task in the lateral visual field by moving the stimuli step by step from 0° to 95° which contradicts Nye's [34] results. He found that pigeons were not capable of colour and brightness discrimination in the lateral visual field after moving the stimuli from the frontal to the lateral side in a sequence of 18° steps. Nye concluded that pigeons lack the neural capabilities to learn a task in the lateral visual field. Other evidence showed that pigeons are capable of learning a discrimination task in the lateral visual field [38,36,26,10,3], however none of those experiments tested free moving animals while moving the stimuli to the side in consecutive steps. The main differences between Nye's experiments and the present one are the number of steps used to move the screen to the 90° position and the amount of training at each step. In the present experiment pigeons were trained in more steps and probably more intensively at each single step.

Even though we chose much smaller step sizes around 45° than for the rest of the range of screen positions, the animals showed a dramatic decrease in performance at 45° degrees. Remarkably, at 45°, performance consistently decreased to values below 65% in all pigeons and the animals needed on average twice as many trials than in other positions to achieve the criterion. In addition, pigeon 246 in both visual fields and pigeons 259 in the RVF did not manage to learn the task beyond 45°. We hypothesize that this dramatic decrease of performance is due to the switch from perceiving the stimuli with the frontal binocular red field to perceiving the stimuli with the lateral monocular yellow field that we interpret to result from a lack of communication between the thalamofugal and tectofugal pathways.

The major disadvantage of testing information transfer in free walking birds is that it is hard to establish the exact point at which each pigeon observed the stimuli, furthermore the angular size of the stimuli in the retina changes across the observation distance and the screen position (see Tables 1 and 2). However, the stimulus presentation occurred when the pigeons crossed the light barrier that was located at a distance of 118 cm from the frontal screen. The frontal binocular field of the pigeon, in the horizontal plane has a maximum extension of 27° [27,28]. The edge of the frontal binocular field of a bird located at 118 cm in the centre of the arena corresponds to a stimulus location of 40° in the experimental arena. Consequently, a 5 cm × 5 cm stimulus presented at 45° falls entirely in the lateral visual field (Table 2). If birds saw the stimulus at closer distances to the screen, the performance reduction would be observed at earlier screen positions (Table 2). Thus, pigeons 512, 51, and 321 showed the lowest percentage of correct responses at positions 29° and 36° and performance was back up at high discrimination values (65%) at 45°. This difference can be well explained by assuming that the position in the arena from which the pigeon inspected the stimuli to make a decision is different for the different birds. At the position at which the pigeon passes the light barrier that triggers stimulus onset, the stimulus moves from the red field into the yellow field at the 45° screen position. However, as the bird gets closer to the front end of the arena, this critical screen position changes, for example a bird observing the stimuli at around 100 cm from the screen would show a decrease of performance when the screen is situated at 36°, whereas a bird observing the stimuli at around 80 cm from the screen would show difficulties when the screen is situated at 29°. Since the stimulus was presented when the pigeons crossed the light barrier at 118 cm, this is the maximum observation point from which the pigeons can solve the task. As discussed above, at this position birds may solve the task perceiving the stimuli using their yellow visual field.

Pigeons may also turn their head to observe the stimuli within their yellow visual field, close inspections of the video recordings did not reveal any indication of head turns. Samples of frame-by-frame motion analysis of the walking birds revealed a parallel trajectory of the peck edge and the eye, which discarded head turns. It was also possible to observe that pigeons normally walk from the back end to the frontal end of the arena across the centre of the experimental arena, and at around 30 cm from the screen the birds changed their trajectory toward the pecking key situated at 20 cm to the screen.

The amount of training required when the stimulus is moved into the 95° position is significantly higher than in positions 14°, 23°, and 61°. At this position the screen was located 20 cm away from the pecking keys. Pigeons have a panoramic visual field that extends 122° into each lateral visual field [21]. A stimulus located at 95° with respect to the centre of the track on which the screen moves, appears at an eccentricity of 130° on the pigeon's visual field when the bird is located right at the pecking key and is therefore outside of the pigeon's visual field. Hence, at this position pigeons may need to memorize the response before arriving at the pecking keys. This memory component could be responsible for the difficulties to achieve the criterion at 95°.

4. Experimental 2: interocular transfer between the two yellow fields

4.1. Methods

Eight pigeons (*C. livia*) that completed the previous experiment were tested for interocular transfer of information between the yellow fields. The same discrimination task described in the first experiment was used. Although, to avoid a possible memory effect (see Section 3.3), the stimuli was located at 90° rather than in the 95° position. Before trying to train the pigeons to discriminate the stimuli in the contralateral eye, we tested their spontanenous behaviour by means of non-reinforced catch trials. To accustom the pigeons to the lack of punishment and reward, four catch trials per session, inserted on the trained side, were randomly presented during eight sessions. Then, 10 catch trials in each hemisphere were collected by introducing two catch trials on the trained side and two catch trials on the untrained side into each session. All reinforced trials were still on the trained side.

Additionally, we also examined whether pigeons were capable to learn a pattern recognition task in the naïve yellow visual field. The pigeons were now trained to discriminate the two stimuli at the 90° location in the naïve hemisphere over 10

Table 2
Position of the centre of the stimuli in the pigeon visual field in degrees according to the pigeon's observation point (cm) and screen position (°)

Observation distance (cm)	Screen position (°)									
	14	23	29	36	41	45	48	61	76	95
20	21.8	33	42	49	54.5	66	42	54.5	62.2	67.4
40	**11.3**	18	24.2	29.9	35	37.8	38.5	46.9	58.5	73.8
60	7.6	**12.2**	16.7	21	25	27.3	27.7	32.3	38.5	46.9
80	**5.7**	**9.2**	**12.7**	16	19.3	21.2	22.2	24.2	27.7	32.3
100	**4.6**	**7.4**	**10.2**	**13**	15.6	17.2	17.4	19.2	21.4	24.2
117	**3.9**	**6.3**	**8.7**	**11.1**	**13.5**	14.8	15	16.3	17.9	19.8

The numbers in bold represent the positions where the centre of the stimuli falls within the red visual field. Calculations were made taking in consideration that pigeons walked across the centre of the experimental arena.

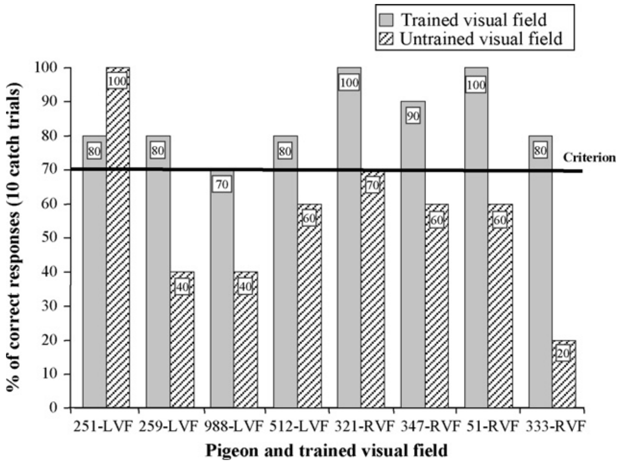

Fig. 7. Percentage of correct responses for each pigeon in 10 catch trials in the trained visual field and 10 catch trials in the naïve visual field.

experimental days, with 80 trials per day. Most of the birds did not learn the task in the naïve hemisphere during those 10 experimental days (see results part bellow). For this reason and considering the long lasting and time consuming task ahead, we continued the training in the naïve hemisphere just in two birds on each side until reaching a criterion (70% of correct responses) or for 5760 trials (72 days of training), however due to the difficulties encountered to learn the task (see results part bellow) in the RVF, eventually four birds continued the training in the naïve RVF and two birds in the LVF. Pigeons 51 and 347 initially trained in the RVF where retrained in the LVF, while pigeons 988, 251, 512, and 259 initially trained in the LVF were retrained in the RVF.

4.2. Results

Three types of data were analysed to investigate interocular transfer of information: the percentage of correct responses for the catch trials, the learning curves of all birds over the first 800 trials (10 days of training) in the untrained hemisphere, and the learning curves of six pigeons that were continued to be trained for 5760 trials (72 days of training) or until reaching the criterion in the untrained hemisphere.

4.2.1. Percentage of correct responses for the catch trials

The average of correct responses in the reinforced learning trials (220 trials per bird) for the LVF was 81.75% and for the RVF 84.5%. There were no significant differences between the LVF and the RVF. Regarding the catch trials (10 trials per bird in each hemisphere), most showed a drop of performance in the untrained hemisphere in comparison to the trained hemisphere. Pigeon 251 was the only exception; it had 80% correct responses in the trained (left) visual hemifield and 100% in the untrained (right) hemifield (Fig. 7). The average percentage of correct responses in the catch trials for all pigeons was 85% in the trained hemisphere and 56.25% in the untrained hemisphere. A hemisphere × visual field mixed ANOVA (2 × 2) revealed significant differences between the trained and the untrained hemisphere ($F_{(1,6)} = 11.10$, $p = 0.02$), and non-significant effects for the visual field ($F_{(1,6)} = 0.69$, $p = 0.44$) and the interaction ($F_{(1,6)} = 0.19$, $p = 0.68$).

4.2.2. Learning curve

Seven of the eight birds still scored below the criterion (70%) after the first 10 days of training (800 trials). At this point, the percentage of correct responses was around chance level for all birds except for pigeon 251 which showed clear signs of interocular transfer and reached the criterion within the third day, with percentages of correct responses above 70%. Pigeons 51 and 347, trained initially in the RVF, learned the task in the LVF after 5120 (64 days of training) and 2400 trials (30 days of training), respectively. Pigeons 988 and 259, trained initially in the RVF, were incapable of learning the task in the LVF after 5760 (72 days of training). Another attempt to retrain a bird in the LVF, was made with pigeon 512. Even though this bird reached the required criterion in several sessions, the behavioural results were very unstable (Fig. 8). The analysis of the video recordings of pigeon 512 during the training revealed that this pigeon reached the criterion in sessions during which it was turning the head towards the screen, whereas this behaviour was not observed in any other pigeon.

4.3. Discussion

Only one out of eight birds showed spontaneous interocular transfer. Otherwise, the performance level for the catch trials in the untrained hemisphere was around chance level (50%), whereas in the trained hemisphere birds obtained data above criterion level (70%). In consonance to previous experiments [26,24,10] our results confirm a lack of interocular transfer when the stimuli are perceived within the yellow visual field. The only exception, pigeon 251, gave correct responses in 100% of the catch trials; therefore it showed clear interocular transfer of information. We did not observe any differences during the experimental procedure that could explain those results. Inspection of video recordings of the animal training excluded that pigeon 251 was twisting the head to observe the stimuli within the frontal visual field. In addition, the animal reached the learning criterion after only three sessions of training in the naïve hemisphere (Fig. 8). Most probably the bird did not reach the criterion earlier due to an extinction phenomenon after being exposed to catch trials without punishment or reward. Further observations confirmed that pigeon 251 scored a higher percentage of correct responses in the RVF than in the LVF. Those results could be a consequence of individual differences in hemispheric lateralisation of pigeon 251. Although most individuals of a species show similar direction bias in several behaviours (for example, pecking behaviour in pigeons and handedness in humans) as a consequence of brain lateralisation, it is common to find a percentage of individuals with a different direction bias [16,44].

Birds initially trained in the RVF relearned the task in the LVF only after very extended training, whereas birds initially trained in the LVF (except pigeon 251 which transferred information) did not relearn the task in the RVF at all. Learning to discriminate between two shapes in the lateral visual field while walking between two feeders in an open arena has been demonstrated to be a very demanding task for the pigeons. Long distances between the discriminative stimuli and the response site may increase the difficulties of a discrimination task [45].

5. Experimental 3: limits of intraocular transfer in pigeons: lateral to frontal direction

5.1. Methods

Pigeons 51, 251, and 347, which in the interocular transfer experiment learned the task in the initially “naïve” hemisphere, were used for testing intraocular transfer of information from lateral to frontal direction. In order to have similar conditions as in Experiment 1, the screen was initially located at 95°. The animals were tested during 4 sessions of 20 trials each per day. The pigeons were retrained at each position of the screen, until achieving the criterion (70% of correct responses in four consecutive sessions). Then the screen was moved to the next position. The same screen positions as in the Experiment 1 were used, and the data of the current experiment were directly compared to the ones obtained in the first experiment.

Additionally, as a measure of the learning effect during the initial training, pigeons 988, 259, and 512 were tested in the same task exclusively at 0°. These pigeons shared the same training history as pigeons 51, 251, and 347. Training at this position had taken place at least 1 year before for all pigeons. Therefore, testing these birds at 0° provides a valuable measure of the effect of the initial training that might confound the transfer of information from the lateral back to a frontal stimulus position.

5.2. Results

Moving the screen all the way from the lateral to the frontal position (lateral–frontal condition) took a total amount of 800, 900, and 1180 trials (average = 960 trials) for pigeons 251, 51, and 347, respectively. In Experiment 1 moving the screen from the frontal to the lateral visual field (frontal–lateral condition) took a total amount of 1260, 1820, and 900 trials (average = 1326.6 trials) for pigeons 251, 51, and 347, respectively (Fig. 9). A one tailed t-test analysis between the number of trials needed at each position to move the screen from frontal to lateral direction and vice versa, confirmed that pigeons 251 and 51 needed significantly less sessions of training in the lateral–frontal condition than in the frontal–lateral condition ($t = 2.29$, d.f. = 9, $p < 0.05$ and $t = 2.29$, d.f. = 9, $p < 0.05$, respectively). Whereas pigeon 347 did not show significant differences between the frontal–lateral and lateral–frontal condition ($t = 1.02$, d.f. = 9, $p > 0.05$). At position 45°, the birds needed on average 140 trials in the lateral–frontal condition and 273 trials in the frontal–lateral condition, although a Wilcoxon test revealed no significant differences ($z = -1.06$, $p = 0.28$) probably due to the limited sample of birds.

The percentage of correct responses during the first 20 trials at each new stimulus position is similar in the frontal–lateral condition and in the lateral–frontal condition (Fig. 9). No significant differences were found for any of the three pigeons. In both conditions, a decrease of performance close to chance level was observed at 45° for all three pigeons. In addition pigeon 251 showed percentages of correct responses close to chance level at 61°, 48°, in the lateral–frontal condition and at 39° and 48° in the frontal–lateral condition.

The three animals directly tested at 0° screen position, showed a percentage of correct responses around chance level for the first 400 trials. The training criterion was achieved after an average of 1587 trials. In the initial frontal training at 0°, birds required an average of 1740 trials to achieve the criterion (Fig. 10). A Wilcoxon statistic analysis revealed no significant differences between the initial and the later training. We conclude that the birds had not

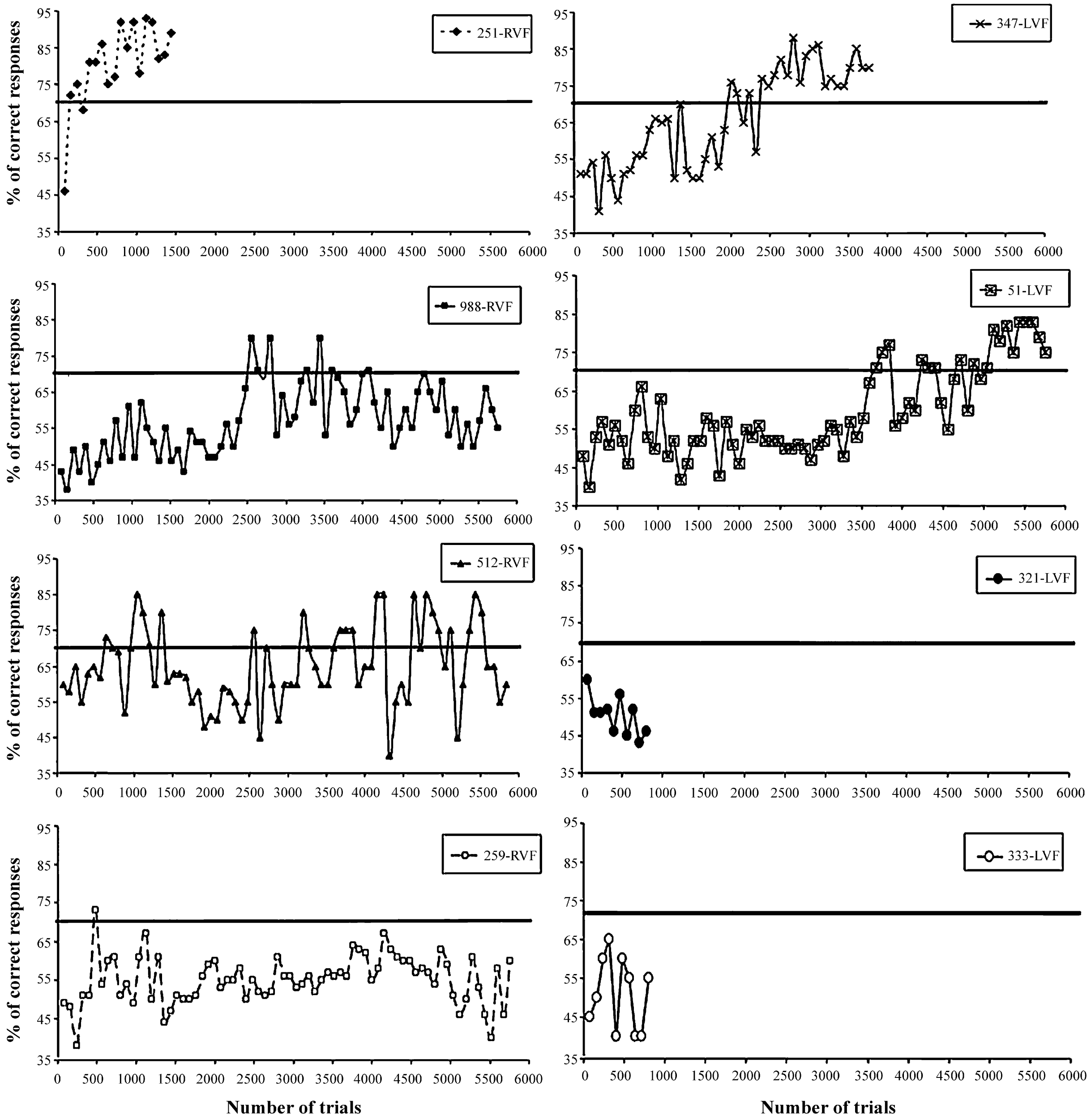

Fig. 8. Learning curve of the originally untrained hemisphere. Each point represents 80 trials (1 day) of training. Pigeons 251, 259, 512, and 988, trained initially in the LVF, were retrained in the RVF, while pigeons 51 and 347, trained initially in the RVF, were retrained in the LVF. Birds 333 and 321 were only trained during 800 trials. The bold line represents the criterion.

retained the discrimination performance they had demonstrated about a year ago in this position. The better discrimination performance in the lateral–frontal condition can therefore not be attributed to the initial training in the frontal visual field.

5.3. Discussion

Moving the screen from the lateral to the frontal visual field took less training than vice versa for two of the analysed pigeons. The third animal did not show significant differences between both directions. This animal was in fact exceptionally good in the frontal to lateral condition. In the video recordings, no sign of turning the head towards the screen was observed.

At the 45° stimulus position, the birds' initial percentage of correct responses was close to chance level in both conditions. In addition, a significant increase of the number of trials to achieve the criterion at this position was observed in both directions. However, birds needed on average only half of the trials in the lateral–frontal direction than in the frontal–lateral direction to reach the criterion. We assume that at the 45° position pigeons switch from one visual mechanism to another, which may result in the observed decrease of performance. Three factors can explain the better performance of the pigeons in the lateral–frontal direction. First, there is a higher level of intraocular transfer in lateral to frontal direction than vice versa. Second, pigeons have previous experience solving the same task in the frontal visual field. Third, the decreasing spatial contiguity between stimuli and response keys could facilitate the task.

The initial learning in the frontal visual field took place at least 1 year earlier for all pigeons. To estimate the effect of the frontal initial training in the results, we tested at 0° pigeons 988, 259, and 512 which did not manage to relearn the task in the "naïve hemisphere" (see experiment 2). Surprisingly, during the first 400 trials of training all pigeons performed at chance level and they needed more than 600 trials to achieve the criterion, although they had no problems performing the task with the screen located at 90°. The result suggests that pigeons had forgotten the task in the frontal visual field. Furthermore, the spatial contiguity has less influence when the stimulus is presented in the frontal screen, but the pigeons needed still to be retrained.

Taking all data together, we can conclude that we observed a weak intraocular transfer from the lateral to the frontal visual field and no traces of intraocular transfer from the frontal to the lateral visual field. Although, further investigations are needed in order to confirm the observations from lateral to frontal direction in walking birds.

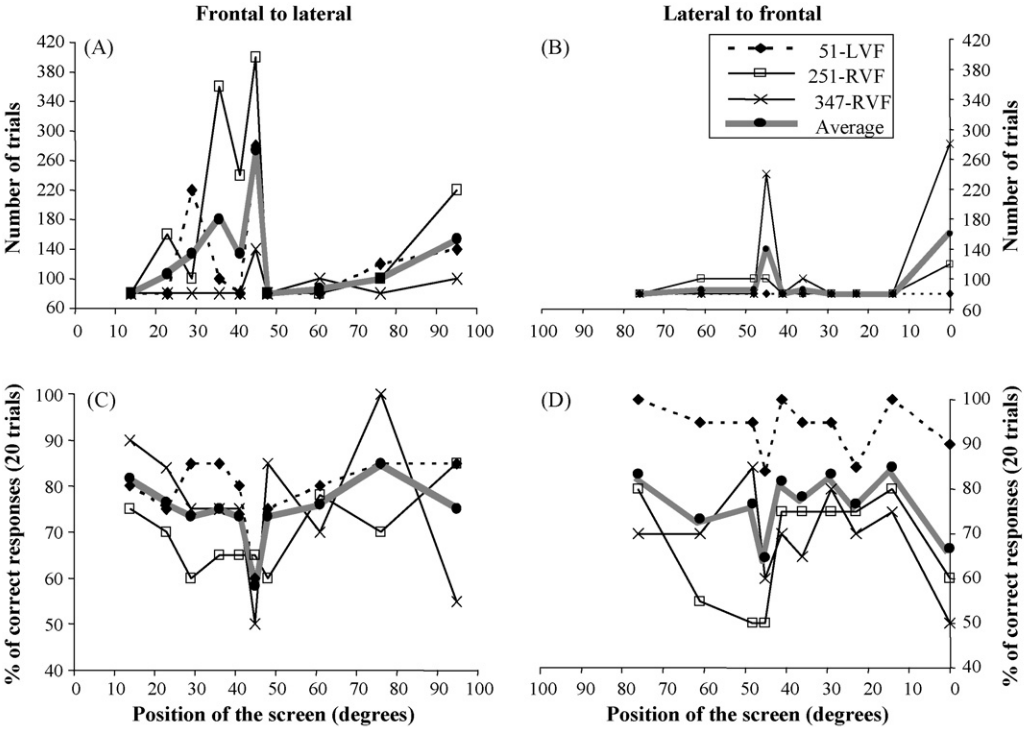

Fig. 9. Number of trials needed to achieve the criterion at each position from frontal to lateral (A) and lateral to frontal (B) for pigeons 251, 51, and 347. Percentage of correct responses for the first 20 trials at each position for moving the stimuli from frontal to lateral (C) and from lateral to frontal (D) in 10 consecutive steps for pigeons 251, 51, and 347.

6. General discussion

Intraocular transfer of information between the frontal red field and the lateral yellow field was tested by gradually moving the stimuli from the frontal into the lateral visual field and vice versa. Performance basically dropped to chance level at a location of the stimulus that corresponds to a retinal position at which the projection of the stimulus leaves the red-field and enters the yellow field. Intensive training was required to relearn the task in the new location. In summary, information transfer between the frontal and the lateral visual field was not found in free walking pigeons, a result that corroborates findings obtained from head-fixed and non-walking pigeons [38,37,34,26].

In addition, we found a weak intraocular transfer from the lateral to the frontal visual field in walking birds. Mallin and Delius [26] also observed a weak intraocular transfer in a colour discrimination task in head-fixed pigeon's. Remy and Emmerton [36] found a clear intraocular transfer of information in birds discriminating whether a light was on or off. Similar results were observed in a matching to sample task [38]. In both tasks the animals utilize their working memory, whereas in a colour or a pattern discrimination tasks, birds need to make their choices according to a previously learned correct colour or shape. Hence, this difference in memory components may explain the weak transfer observed in these two tasks. While performance is clearly task dependent, there seems to be a general tendency in these data, that intraocular transfer is better in the lateral–frontal direction than in the frontal–lateral direction. This is understandable from an ecological point of view. Information first received within the yellow field system needs to be transferred into the frontal visual field in order to switch atten-

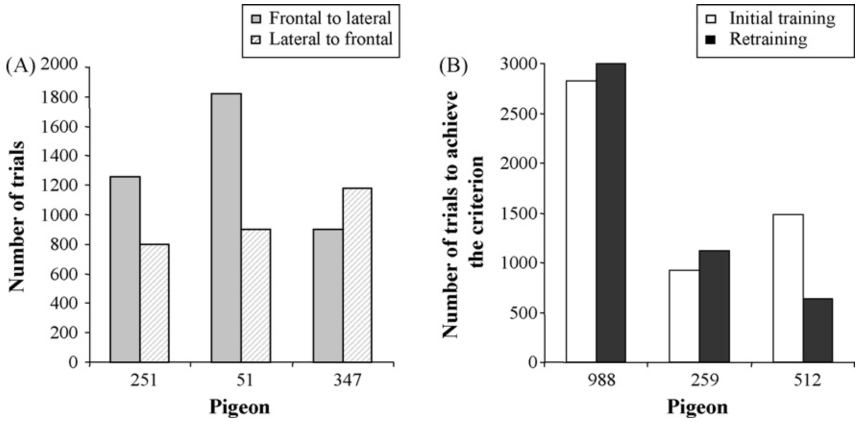

Fig. 10. Number of trials needed to train pigeons 251, 51, and 347 in the lateral to frontal direction and vice versa (A). Number of trials for learning the task in the 0° position in initial training and in the 1 year later retraining for pigeons 988, 259, and 512 (B).

tion to interesting or important environmental stimuli into an area of the visual field in which they can be manipulated (e.g. where food can be picked up). Also, note that our experimental design did require a certain degree of information transfer between the yellow and the red field, because in our task birds perceived the pattern within the yellow field but directed the pecking response to a point in the red field.

Birds have been observed fixating objects within the lateral visual field [6]. These fixation movements may be required to focus the stimuli with the fovea centralis, an area of high ganglion cell density within the yellow visual field. Indeed, the monocular acuity in the lateral field of pigeons is about the same in the binocular frontal field [20,17]. In the experimental task as soon as the birds learned the task in the lateral visual field, they did not show difficulties to transfer information from one position to another within the lateral visual field, but transfer from frontal to lateral visual fields was lacking.

We also investigated interocular transfer of information between the two yellow fields in our free walking pigeons. Pigeons initially trained in the LVF were tested in the RVF, and vice versa. In eight of the nine pigeons, no traces of interocular transfer of information were observed. Only one pigeon was capable of performing the task spontaneously in the untrained visual field. Our results confirm, in a more ecological situation, previous experimental findings in which a lack of interocular transfer was found when the stimuli were perceived within the yellow visual field [10,23,26]. However, several studies demonstrate the existence of interocular transfer of information within the red visual field [10,26,23–25]. Due to the almost complete decussation of the optic nerve in pigeons [47], interhemispheric transfer of information received in the red visual field is required for local coarse stereopsis [30,29]. By contrast transfer between the lateral visual fields might not be a requirement for the birds. The lateral visual field serves vision at longer distances, monitoring predators and cospecifics [11,8], as well as to detect food at farther distances than 10 cm [3]. In natural conditions an alert response can be activated without transfer of visual information. The trigger of the motor response after processing a possible alert signal in one of the two hemispheres could be enough for the bird to exhibit the appropriate behaviour in a given situation. In the present experiment, birds exposed to catch trials in the untrained hemisphere exhibited pecking behaviour, but they were not able to discriminate between the two stimuli. Whereas if the stimulus was not presented, the birds remained static until a new stimulus appeared.

In pigeons, a number of studies have demonstrated a right eye/left hemisphere dominance for object recognition in the frontal binocular field [18,12,13]. In contrast, we observed no such asymmetry. In the intraocular transfer experiment, two animals trained in the right visual field never learned the task beyond 45°. Furthermore, in the interocular transfer experiments (excluding a bird that was capable of transfer) after long lasting training, birds initially trained in the RVF relearned the task in the LVF, whereas birds initially trained in the LVF (except the animal capable of information transfer) did not relearn the task in the RVF. A left hemisphere dominance of the thalamofugal visual pathway was observed in a pattern discrimination task in an open arena [4] social recognition in chicks, and novel stimuli detection [3,44,7,39]. A lateralised brain may allow dual attention to short distance tasks like feeding (using the right eye/left hemisphere system) and long distance tasks like vigilance for predators (left eye/right hemisphere system) [39].

In summary, information transfer was not observed from the frontal to the lateral visual field of the same eye. Interocular transfer between the yellow fields of the two eyes was absent. A weak transfer from the lateral to the frontal visual field of the same eye was observed. At first glance, it is surprising to find that the two hemispheres of the pigeon's brain work in many aspects as independent brains, however a closer look reveals that they are perfectly adapted animals capable of solving environmental demands minimizing brain complexity. Pigeons show interocular transfer of information within the red visual field of the eyes that serves local stereopsis, but no interocular transfer of information between the yellow fields. Information transfer from the lateral to the frontal visual field of the same eye may be useful to fixate relevant stimuli within the red visual field, but intraocular transfer from the frontal to the lateral visual field has no obvious function and may not provide any advantage.

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