Research report

Unihemispheric memory in pigeons-knowledge, the left hemisphere is reluctant to share

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Abstract

In the present study, pigeons were trained under binocular conditions in a conditional visual discrimination in which they were faced with two identical patterns arranged one above the other. In half of these stimulus pairs the animals had to peck the upper pattern, in the other half the lower one. Although only six pairs of stimuli were used, only four out of eight birds reached learning criterion. These animals needed up to 6 months of training with 3050 to 6650 trails. Then, the experiment proceeded under identical conditions using eye caps restricting vision alternatively to the left or the right eye. These monocular tests revealed that three out of four birds virtually had no knowledge of the task contingencies using their left eye (right hemisphere). Again, several thousand trials were needed to train the birds to criterion with their left eye, while they were simultaneously discriminating at a very high level with their right. These results show that memories on task contingencies are stored unihemispherically in the visually dominant left side despite extensive training with both eyes open. Additionally, it can be concluded that the subsequent read-out by the 'naive' hemisphere can be largely restricted, resulting in a 'natural split-brain' like situation in birds. It is speculated that the absence of a corpus callosum in birds restricts interhemispheric transfer of information. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Humans and many other animals display asymmetries of a large number of different brain functions [10,13,28]. Since in all central nervous systems the two halves of the brain are interconnected by numerous commissures, it is often assumed that lateralized processes are only to be demonstrated if the sensory input is restricted to one side and the subject is placed under high time pressure. Under these conditions, it is mainly the perceiving hemisphere, which guides the response, since the input to the other brain half arrives via a delayed commissural crossover. The experimenter can then simply compare the results of the left and the right stimulus conditions to draw conclusions on the differential performance levels of right and left hemispheres, respectively. This is, e.g. the logic of visual half field experiments, which have contributed importantly to our knowledge of the lateralized architecture of the human brain.

However, experiments in birds seem to tell another story. In birds, the optic nerves cross virtually completely [31], enabling unihemispheric visual stimulation by means of eye caps which are fixed to one eye during testing. With this procedure a left hemispheric superiority in learning and discrimination of visual features and a right hemispheric dominance in relational spatial orientation could be revealed in chicks [21,25,27,29], pigeons [20], marsh tits [2], and zebra finches [1]. The common aspect of all of these studies is that lateralized performance levels are observed while the animals discriminate the relevant stimuli for minutes or hours with the left or the right eye only. In some of these studies it could be shown that the right hemisphere could not access over 30 or more minutes the knowledge about the consequences of past behavior, which was present in the left half of the brain [4,8]. Although birds lack a corpus callosum, they have a hippocampal, an

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anterior, an amygdalar, a supraoptic as well as several brainstem commissures. Thus, despite the existence of these interhemispheric connections, some processes tested in the experiments cited above seem to be mainly restricted to the hemisphere contralateral to the seeing eye. Here we report that for some experimental conditions the right cannot access engrams present in the dominant left hemisphere over time spans of several months. This study makes it likely that at least for some conditions the avian brain seems to represent a natural split-brain preparation.

2. Method

Eight naive homing pigeons (Columba livia) of local origin were used. A small metal head block with a tapped hole was glued to the skull with dental cement under Equithesin anesthesia to later fix opaque hemispherical eye caps during monocular discrimination sessions. Animals were maintained at 80% of their free feeding weight throughout the study.

The pigeons were trained binocularly in an autoshaping procedure with a single key operant conditioning box to peck an illuminated key for food access. All following experiments were performed in a different two-key experimental chamber. Here, the two keys were vertically arranged above the food hopper with a between-key distance of 1.5 cm. Stimuli were back projected with a slide projector (Kodak Ektapro 5000). An IBM-compatible computer controlled both the experimental chamber and the projector. On both keys the same stimulus was presented in each trial. Fig. 1 depicts the six stimuli in use. All animals started under binocular conditions with the first two stimuli. Four animals had to peck the upper key when on both keys the 'inverted 1' was shown. The remaining four animals had to peck the lower key under this condition. For the second stimulus, the 'A', the conditions were inverted. Thus, the pigeons acquired that a spatial code (up or down) had to be learned in combination with a certain pattern. One session consisted of 50 trials, and the succession of the two stimuli was quasi-randomly arranged. A single correct peck elicited 2 s food reinforcement. Incorrect pecks were followed by 4 s time out with all lights off, followed by a correction trial. These correction trials were not used for the calculation of the average correct responses per session. After an animal had achieved three consecutive sessions with at least 85%, the next stimulus pair was introduced. Now the four stimuli in use alternated quasi-randomly. After again achieving 85% in three consecutive sessions with these four patterns, the third and last stimulus pair was introduced. After finally reaching criterion with all six stimuli in use, the monocular tests began.

The animals were already accustomed to wearing eye caps in their home cages and during grain-grit discrimination. However, they now for the first time started to discriminate the patterns under monocular conditions. Monocular left and monocular right seeing conditions alternated with one session conducted per day. During monocular tests each session consisted of 100 trials. Half of the pigeons started with the left, the other half with the right eye seeing condition. Monocular tests were conducted until each pigeon had achieved three consecutive sessions with more than 85% correct responses under each monocular condition. Only one animal (Nr. 51) was unable to surpass chance level for 10 weeks with its left eye.

As is evident from Fig. 1, three of the stimuli were symmetrical, while the three others were asymmetrical. This reflects an initial plan to test for asymmetries in concept formation in conjunction with spatial coding. However, as outlined in the results section, the combination of a feature and a space discrimination with multiple stimuli turned out to be so difficult for the animals that they needed more than 6 months to learn the conjunct 'stimulus & place' discrimination for the six patterns. Four pigeons did not learn this distinction at all and were discarded. We therefore abandoned the plan to introduce further training patterns and to finally test a possible 'symmetry' concept with a new set of stimuli which would have been introduced during catch trials. It is highly unlikely that our animals had acquired a symmetry concept, since their level of performance when initially faced with the second or the third pair of patterns was not importantly superior to that at the beginning of the first pair. Additionally numerous studies could show that pigeons need a large number of exemplars until switching to a more abstract cognitive strategy [32] and are not as easily trained to categorize 'symmetry' as suspected previously [14]. However, the unexpected unilaterality of left hemispheric memory with a partial absence of interhemispheric transfer are not altered by the fact that the stimuli could in principle be grouped into a symmetric and an asymmetric group.

Parallel to the monocular tests in the experimental chamber, a grain-grit discrimination was performed to analyze the individual degree of visual lateralization with an easy and established method [11]. The pigeons had to discriminate brownish-white common vetch (Vicia sativa) grains of approximately 2×3 mm axial length from small pebbles of varying size. The pebbles resembled the grains in their range of colors, shapes and size. Thirty grains were mixed with 30 g of pebbles (about 1,000 in number) in an opaque tray of $9 \times 5 \times 6$ cm. The pigeons remained in their home cages and could peck at the grain/grit mixture when the tray was inserted under an opening in the front panel of the cage. The tray was removed 30 s after the first peck, and, by counting the remaining grains, the number of grains swallowed
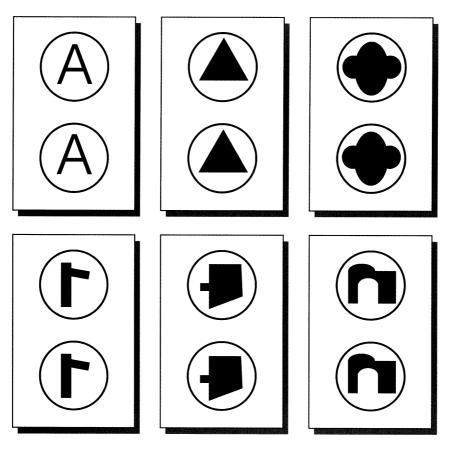
Fig. 1. The six stimulus displays used in the present study. Pigeons had to peck the upper key in the upper three pairs and the lower key in the lower three pairs.

was calculated. Additionally, the experimenter counted the number of pecks issued by the animals during the 30 s testing procedure. The pigeons habituated to the procedure for 1 week before the experimental data were recorded for subsequent analysis. The animals were tested on alternate sessions with sight restricted to the left or the right eye by means of eye caps. Each pigeon completed 20 sessions, that is, ten sessions under each monocular condition. On each day only one session was conducted. For each session three measures of the pigeon's performance were assessed: (a) the number of grains eaten; (b) the number of pecks, as an index of the activity level of the animal; (c) the percentage of pecks leading to swallowing of grain, which gives a measure of the discrimination performance of the animals. This percentage was calculated as the number of grains eaten multiplied by 100 and divided by the number of pecks.

3. Results

Only four out of eight animals learned the conjunction of 'stimulus' and 'space'. Therefore, only data from these four animals are given below. The results of the grain-grit discrimination are given in Table 1 and show

clear right eye superiority for all four animals. The following account is descriptive since no statistics were needed to analyze data sets.

The four successful pigeons needed a very large number of sessions until being able to reach criterion with six different stimuli. The number of trials until criterion varied between 3050 and 6650 trials (Table 1). A representative learning curve is provided for pigeon 54 which reached criterion after 4000 trials (Fig. 2).

After switching to monocular conditions, the performance of the monocular right condition was only slightly below the level of the last binocular session for all birds (Fig. 3). All of them started with a discrimination success rate higher than 75%. Their performance slowly increased until reaching learning criterion with three consecutive sessions with 85% correct after 300–1900 trials. Pigeon 51 was close to reaching this criterion when we had to stop testing after 2400 trials due to problems with the headblock.

The situation for left-eye performance was, with one exception, dramatically different. After switching to monocular conditions, left-eye performance dropped to chance level or was slightly higher than chance (Fig. 3). For pigeon 51 this left-eye situation did not improve despite testing for up to 2400 trials. The other birds

Table 1
Performance of the animals in the grain-grit and the conjunction task under monocular and binocular conditions

Animal	Grain-grit (left eye) % correct	Grain-grit (right eye) % correct	Conjunction task trials to criterion (binocular)	Conjunction task trials to criterion (left eye)	Conjunction task trials to criterion (right eye)
49	49.3	76.1	6650	100; 1100	100; 1100
51	47.4	70.9	3050	–; –	100; –
54	47.4	55.8	4000	2100; 3200	100; 300
55	55.4	77.6	4000	900; 1200	100; 1900

The two numbers given for the monocular conditions of the conjunction task are, first, the number of trials needed to reach once 75% correct and, second, the number of trials until reaching 85% in three consecutive sessions. Each session of the conjunction task under monocular conditions consisted of 100 trials.
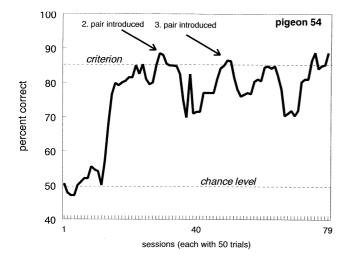

Fig. 2. Learning curve of pigeon 54 during binocular training. After three successive sessions with more than 85% correct choices the new pairs were introduced. After introduction of the second pairs, the birds had to discriminate four stimulus displays. After introduction of the third pair this number increased to six. Note that sessions during binocular training consisted of 50 trials each. Monocular tests started after three successive sessions with more than 85% using the six stimuli shown in Fig. 1.

finally succeeded after 1200–3200 trials. Pigeon 54 slowly increased its left eye performance until reaching criterion after 3200 trials. This is about the same number it had needed previously under binocular conditions. Pigeon 55 was faster and could, after 1000 trials, reach even slightly higher scores than with the right eye.

The single exception was pigeon 49 for which left- and right-eye performance was about equal throughout the whole study. This animal was also the fastest to reach criterion under monocular conditions (1900 trials for each eye), although it had needed the most trials to criterion binocularly (6650 trials). It is unclear why this animal deviates in its behavioral pattern from the other birds. As shown in Table 1, its visual asymmetry in grain-grit discrimination is substantial. It is conceivable that the large number of trials needed to reach criterion binocularly is the reason for its equal left and right

performance, since both hemispheres had a chance to learn the contingencies during this very long time.

4. Discussion

Using an experimental set-up in which the animals had to learn a combination of object and spatial cues we could show that most birds which under binocular conditions had finally reached criterion after 3000–6000 trials, had virtually no knowledge of the task contingencies using their left eye. Some of these pigeons then needed up to further 3200 trials to learn the task with the left eye while they were meanwhile performing excellent using their right. In principle, previous studies in birds had also demonstrated limitations of interocular transfer (for a review see Remy and Watanabe [22]), especially using conditional discrimination procedures [30]. In the present experiment, however, the animals had experienced a pretest session of up to 6 months with thousands of trials in which both hemispheres had unrestricted access to the experimental contingencies. After the switch to monocular testing, three out of four animals again needed several thousand trials to slowly acquire with the right hemisphere what was obviously known to the left. Therefore, to our knowledge, the present communication is the strongest evidence ever that memory traces can be unilaterally organized despite binocular training and the existence of intact commissures. Additionally it makes it likely that the read-out of unilateral engrams is restricted in an animal, which has no corpus callosum.

An alternative explanation for the unilateral memory hypothesis might be that the birds had problems discriminating the stimuli using their left eye. The results of the grain grit task make this explanation very unlikely. As usual for most pigeons right eye performance was higher than left eye performance in the grain grit task [11]. However, the left-eye scores of the animals of the present study are at the upper half of what pigeons usually achieve in this task [11]. Additionally, pigeons are known for their ability to discriminate easily
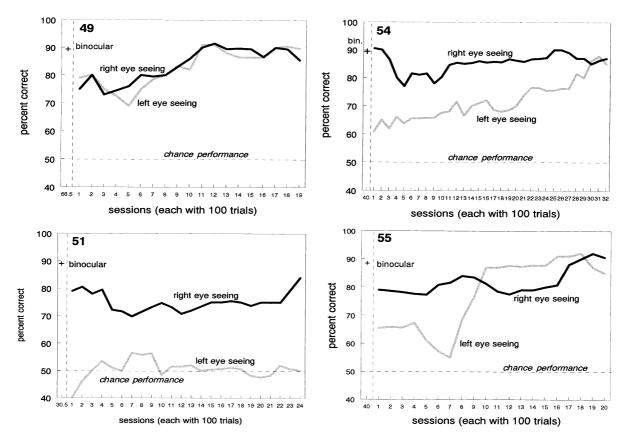
Fig. 3. Monocular trials of the four animals under study. The last binocular session is shown with a ' + '. Note that test sessions consisted of 100 trials each.

under both monocular conditions patterns like the one used here [9,12]. Thus, it is unlikely that the problem of the left eye/right hemisphere system was due to perceptual limitations. A further possibility might be that under left-eye seeing conditions the animals had used a purely spatial strategy and completely ignored the pattern information. A detailed analysis of the choice reactions showed that all animals had pecked the lower key more often during beginning of the binocular sessions. Under left eye conditions, the birds switched back to this habit. However, it is unlikely that pecking the lower key is a spatial strategy. It is more parsimonious to assume that this is a convenient default option since the lower key is closer to the beak height of the birds and since they can switch more rapidly to the food hopper directly situated below. Videotapes taken at different times of the experiment showed in addition that the animals made no obvious lateral head movements in front of the keys which might had pointed to each hemisphere trying to attend to specific cues of the display. Taken together, neither perceptual limitations nor hemisphere-specific strategies are likely explanations for the present results.

It is, however, conceivable that the right hemisphere could in principle learn the task but had problems to remember the spatial contingencies over lengthy periods

of time. Although avian right hemispheric mechanisms seem to be specialized to extract relational spatial coding properties [27], at least in some bird species memory for space seems to be distributed within 24 h to the left-brain side for long-term storage and subsequently 'forgotten' in the right-brain [2,3]. If this were also true for pigeons, their right hemisphere would have suffered from a continuous loss of knowledge about the spatial domain of the task. This might explain why three out of four birds were virtually at chance level at the onset of monocular left eye (right hemisphere) testing. This continuous right-to-left hemispheric transfer of spatial memory might also explain why these animals needed so long to learn the task when using the left eye only. However, a storage of spatial memory in the left hemisphere cannot explain why the birds were virtually unable to use this left hemisphere engrams when being tested with the right hemisphere, although all commissures were intact. Thus, it is of importance to distinguish between the hemispheric location of a memory trace and the actual read-out of an engram via commissural systems. At least for the conjunct learning of spatial and pattern cues in pigeons, memory traces seem to be mostly left hemisphere-based while the read out through the right hemisphere is importantly limited. In the following, we will argue that this limited interhemi-

spheric access is probably due to the absence of a corpus callosum in birds.

Since the pioneering work of Myers and Sperry [18], studies in mammals could show that interhemispheric access to memory stores is mainly achieved over the corpus callosum. In an elegant series of studies, Doty and colleagues demonstrated that indeed the major forebrain commissures are needed for transfer of learned visual cues [6,7,15,23]. In their absence, however, brainstem commissures are able to mediate at least some exchange on the total memory load and even might enable access to some common memory traces laid down subcortically [7,15,17]. The presence of the corpus callosum does not necessarily imply that any kind of information is quickly transferred between the hemispheres. As shown by Dee and Fontenot [5] asymmetries of performance levels can persist even though a delay of several seconds is imposed between lateralized perception and response. In a different line of studies Wittling and collaborators [33,34] could even show that using continuous unilateral stimulation, which leaves plenty of time for the perceived images to disseminate throughout both sides of the brain, sympathetic and emotional reactions to movies could only be elicited after right-hemispheric stimulation. Similarly, Risse and Gazzaniga [24] had shown in a patient undergoing a Wada-session that haptic information acquired by the right hemisphere during left hemisphere anesthesia could not be verbalized after the end of the session.

Taken together, these studies show that: (1) in humans and other mammals memory traces can be unilaterally organized; (2) the corpus callosum is needed for the read-out of most of these unilateral memories by the other hemisphere; (3) subcortical commissures can mediate access to a limited aspect of memory processes; (4) the presence of the corpus callosum does not necessarily imply that any kind of unilateral information can immediately be accessed by the other half of the brain.

Against this background, the present data show that the absence of a corpus callosum in birds results in a different functional architecture between birds and mammals. While both store some of their memories unilaterally, the development of the corpus callosum has enabled placental mammals to access these traces interhemispherically more efficiently. Although birds are also able to transfer some information between left and right [22,26] this study outlines how limited these transfers can be. This limitation probably forces birds to execute motor responses based on unihemispheric processes [19].

Our data make a further point clear. Beginning with Levy [16] it is often speculated that the reduction of the redundancy of bilaterally distributed mnemonic and cognitive capacities is the key purpose of cerebral asymmetries. One of the functions of the corpus callosum might then be to prevent the establishment of bilateral engrams and to subsequently aid the interhemispheric read-out [6]. Our results show that an animal without a corpus callosum nevertheless produces unilateral engrams, although the lack of a callosum then reduces the transfer of information from one hemisphere to the other.

Acknowledgements

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