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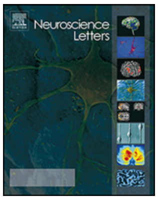

Natural split-brain?
Lateralized memory for task contingencies in pigeons

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ABSTRACT

The motion aftereffect (MAE) is an illusory motion in the opposite direction after the sudden halt of a prolonged visual moving stimulus. Birds could perceive the MAE as humans and other mammals. The present study was to investigate whether hemispheric asymmetries of visual processes affect this illusion. To this end, pigeons were trained to discriminate grating patterns which moved up, or down or stood still. The transfer tests were conducted under the binocular or monocular viewing condition. The choice behaviors of pigeons under the binocular and right-eye viewing condition (left hemisphere) were highly indicative for the perception of a MAE. However, the animals under the left-eye viewing condition (right hemisphere) did not change their choice patterns according to the different task displayed on the central stimulus key, but always stuck to the default option of pecking the response key ipsilateral to the open eye. We assume that memory for task contingencies were confined to the left hemisphere and could not be reached by the right half brain due to the absence of the corpus callosum.

Functional asymmetries of the visual system have been investigated in many species, especially in humans [2,32,35]. As a "natural split-brain" model, unihemispheric behavioral tests can be easily done in birds using eye caps since the optic nerves cross completely and the corpus callosum connecting both hemispheres is absent [39]. A large number of studies have revealed functional asymmetries of the avian visual system that the left hemisphere is superior in discriminating visual features and the right hemisphere has an advantage in relational spatial orientation (pigeon: [21,22,36]; chick: [24,29,33,34]; marsh tit: [4,5]; zebra finch: [1]; quail: [15]).

Asymmetries in the perception of illusory stimuli were first observed in patients with unilateral brain lesions and gradually attracted more research interest [3,11–13,18,23,25]. Several studies have indicated that birds can perceive optic illusions in a similar fashion as humans and other mammals (Ponzo illusion: [8]; geometric illusions: [16]; Mueller-Lyer illusion: [19]; MAE: [40]; amodal completion: [26]). However, few experiments have been conducted in birds to investigate whether there is a functional asymmetry for the illusion perception [16,26] and their underlying neural mechanism. Moreover, these studies were limited to static illusions but not moving one which represents a special class of illusory stimuli. Probably, the most prominent movement illusion is the motion aftereffect (MAE) or waterfall illusion which refers to the illusory motion in the opposite direction after the sudden halt of a prolonged visual movement stimulus. Our behavioral experiment proved that pigeons can perceive a MAE [40]. The aim of the present study was to investigate whether there was a hemispheric asymmetry for this illusion in birds.

Four female and four male adult pigeons (*Columbia livia*) with body weights of 480–570 g were employed in the experiment. These animals were previously used to analyze the MAE [40]. The guidelines regarding the care and use of animals established by the Society of Neuroscience were applied. All animals were maintained at about 80% of their free feeding weights. They were trained and tested in a cubic aluminium box (34 × 34 × 34 cm). Four pecking keys (5 × 5 cm) were arranged like an inverted 'T' on the frontal panel (Fig. 1). The moving and stationary stimuli that the birds had to discriminate were only presented on the central bottom stimulus key which was located 18 cm above the floor. Three other response keys were located on either side and directly above the stimulus key at distances of 2 cm from each other. Three response keys were illuminated red (left), yellow (top) and green (right) throughout training and testing periods. One white house-light was located in the ceiling of the chamber at a distance of 30 cm from the frontal panel. The feeder was located 12 cm below the stimulus key and 6 cm above the floor. A white feeder-light was placed 4 cm above it. The visual stimuli were produced by a computer and displayed on a monitor (HP 1530, TFT Flat Panel Display) mounted behind the back of the frontal panel. The apparatus was controlled by an IO interface with 8 outputs and 12 inputs from Frank Buschmann International Corporation via a computer. Normally, pigeons scrutinized pecking

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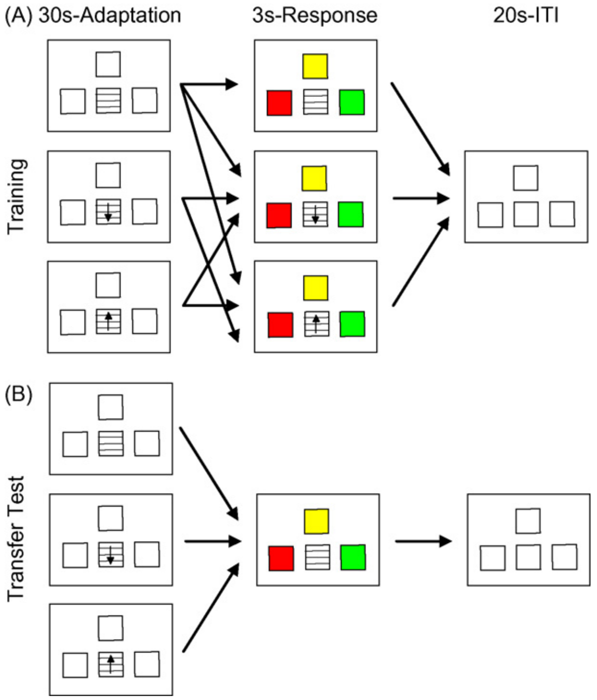

Fig. 1. Experimental setup for the training (A) and transfer test (B). During training and transfer test, each trial consisted of three phases. Two successive visual stimuli were shown on the central stimulus key during the transition from the adaptation phase to the response phase. A series of pecks on the stimulus key during 30 s of the adaptation phase activated three response keys illuminated with different colour. And then the pigeons had to peck one of response keys according to the displayed stimulus during the 3 s of response phase (static grating = yellow top key; downward moving grating = red left key; upward moving grating = green right key). Two illusion-inducing stimulus sequences were only used in the transfer test (B), in which a moving pattern (upward or downward) during the adaptation phase was followed by a static pattern during the subsequent response phase. If a MAE occurs, the animals should perceive the static pattern moving in the opposite direction to the movement one. The correct peck was rewarded with 3 s food. Incorrect choice was punished with 5 s time-out. Each trial was followed by 20 s ITI (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article).

keys from a distance of 55 mm (as measured from the center of two eyes) before pecking them [10]. The visual stimulus was a grating pattern consisted of black and white stripes of equal-widths with a spatial frequency of 0.12cycles/° and the motion speed was 40°/s. This pattern moved upward, downward or stood still.

In the training period, all birds were initially trained under the binocular viewing condition to correctly peck the central stimulus key at least 30 times within 30 s (Fig. 1A). This paradigm ensured sufficient exposure time to one of three visual stimuli (static grating, upward moving grating and downward moving grating) in the adaptation phase. The pecking counter and the timer started from the first correct peck onto the stimulus key. Subsequently, 3 s response phase started with a static, or a downward moving or an upward moving grating displayed on the central key. But a moving pattern during the adaptation phase was never followed by a static pattern during the response phase because such sequence might induce an illusory movement into the opposite direction. Therefore, it was only used at the illusion test trials (Fig. 1B). The response phase was also characterized by the activation of three differently coloured response keys surrounding the central stimulus key. It is important to stress that the pigeons were trained to peck one of response keys according to the stimulus displayed during the 3 s of the response phase (static grating pattern = yellow top key; downward movement = red left key; upward movement = green right key). If the birds pecked correctly, they were rewarded with 3 s access to food. Otherwise, they were punished with 5 s of darkness. A 20 s inter-trial interval started after the response phase. Each training session included 70 normal trials with feedback (10 trials for each stimulus combination).

The pigeons were trained binocularly until the correct discrimination ratios for the task reached at least 85% in three consecutive days. In parallel, they were accustomed to wearing eye caps in the home cages. Subsequently, 10 sessions of monocular training for each eye were given before the first transfer test, with which the birds gradually adapted themselves to do the task with one eye in the chamber. No learning criterion was applied for these monocular training sessions.

In the testing period, each session included 70 normal trials with feedback as the training session. In addition, 6 randomly interspersed illusion test trials without feedback were given. These test trials consisted of three different stimulus sequences with each type being shown twice (adaptation phase followed by response phase: static–static; moving up–static; moving down–static; Fig. 1B). If a MAE occurs, the animals should perceive the static pattern in the response phase moving in the opposite direction compared to the movement pattern in the adaptation phase. Therefore, their choices of the response key should indicate this illusory perception. For example, a choice of the green right response key indicating upward movement after viewing the sequence “downward (30 s, adaptation phase) – static (3 s, response phase)” would be an indicator of perceiving a MAE. However, if the animals would peck the yellow top key (= ‘I saw a static pattern’), they probably did not perceive a MAE and responded only according to what was indeed displayed. Pecking the red left response key (= ‘I saw a downward movement’) signalled that the animals reported the stimulus displayed at the first 30 s and would not indicate a MAE. Each bird was alternatively tested under the binocular, left-eye or right-eye viewing condition every two days. Test sessions continued until 10 effective test trials were collected for each illusion-inducing stimulus sequence under three viewing conditions. A test trial was deemed ineffective if animals did not immediately switch to the activated response keys during the response phase.

All pigeons successfully learned the task under the binocular viewing condition, albeit with individual differences in their acquisition speed. Totally, they needed 50–90 sessions (71.25 ± 13.04, mean ± S.D.) before the correct discrimination ratios reached atleast 85% in three consecutive days. In the subsequent monocular training, the birds were trained for 10 sessions (700 trials) in each eye condition. No test trials for MAE were used in these sessions and the animals did not need to reach a learning criterion. But the average performance levels of eight pigeons at the last session were 39.6% for left-eye, 54% for right-eye and 87.5% for the binocular viewing condition.

For the transfer tests under the monocular viewing condition, pecking ratios on the top (yellow) response key were significantly lower than that on the left and the right response keys ($p < 0.001$, χ^2 test). The static stimulus sequence (30 s of static pattern during the adaptation phase + 3 s of static pattern during the response phase) was only used as a control to ensure that animals were not affected by the absence of the feedback in transfer tests. Therefore, the further analysis was only conducted on pecking responses of the left and right response keys for two stimulus sequences (30 s of grating moving downward + 3 s of static pattern, 30 s of grating moving upward + 3 s of static pattern). Pecking ratios on the ipsilateral and the contralateral response key to the exposed eye showed a significant difference ($F(1, 63) = 42.58$, $p < 0.001$, One Way Analysis of Variance). And birds pecked the ipsilateral key more often than the contralateral one ($t_{62} = 13.911$, $p < 0.001$). Between two monocular viewing conditions, the left-eye exposed birds were more likely to peck the ipsilateral left response key than the contralateral right one ($t_{30} = 4.072$, $p < 0.001$) no matter what stimulus was shown on