Research report

Do pigeons perceive the motion aftereffect? A behavioral study

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Abstract

The motion aftereffect (MAE) describes an illusory motion in the opposite direction after the sudden halt of a prolonged moving visual stimulus. Behaviorally, this illusion was mostly analyzed in humans and other mammals. Up to now, birds were never tested. Since a new neural mechanism for the MAE was recently discovered in the pigeons' midbrain, the aim of this study was to investigate if pigeons can perceive this illusion. In two successive experiments, we trained animals to discriminate black and white grating patterns with two moving directions: upward or downward, or standing still. During transfer tests, animals were shortly confronted with the static pattern after prolonged exposure to a moving stimulus. The choice behaviors of these animals were highly indicative for the perception of an MAE. The possible neuronal substrate for the movement aftereffect is discussed.
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1. Introduction

Visual illusions have always attracted the scientific interest since they beautifully expose the "hard-wired" interpretation of the visual scenery with which our perceptional system is endowed. Most illusion studies were conducted on human subjects [14,49] and mammals [5,6,8,11–13,18,25,40,45,54] not birds. And all of these experiments done on birds utilized static patterns such as the Müller–Lyer, Ponzo or subjective contour illusions (pigeons [19,20,22,30,31]; barn owls [34]; chick [47,53]). In addition, chicks were shown to achieve relative depth disambiguation [15] and amodal completion [39]. Other studies analyzed the lateralized neuronal mechanisms of geometric illusions and amodal completion (pigeon [22]; chick [38]).

Movement illusions represent a special class of illusory stimuli. Chicks have been shown to see some movement illusions like stereokinetic illusions [10] or one type of biological motion often called as the "Johansson effect" [48]. Probably the most prominent movement illusion is the motion aftereffect (MAE) or waterfall illusion which describes the illusory motion in the opposite direction after the sudden halt of a prolonged visual movement stimulus [1,36]. Behavioral studies have shown that nonhuman animals (rhesus monkey [40]; sheep blowfly [43]; cat [7]) have the ability of perceiving the MAE. As the largest group of flying vertebrates, birds constitute an interesting model to study this movement illusion. However, it is still unknown if they can perceive the MAE.

To answer this question, pigeons (*Columbia livia*) are an excellent model. Three studies had addressed the Müller–Lyer illusion using pigeons and revealed a similar pattern of perception as humans as long as inward arrows were used [20,30,31]. Further evidence [19] showed that the performance of pigeons in discriminating the length of bars located between converging contexts (Ponzo illusion) was affected by the context direction. The variation of context was able to increase the perceived difference in bar length or decrease it. Later, Güntürkün [22] indicated that pigeons could perceive the Herringbone illusion and suggested that the reduced perceptual illusion after unihemispheric lesions in brain-damaged patients [37] might be related to the asymmetry of neural circuits involved in the analysis of the illusory stimuli in the human brain. These experiments make it clear that pigeons can perceive geometric visual illusions with static patterns similar to humans.

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The neural mechanism underlying the MAE was intensely debated since this phenomenon was reported. It is usually explained by the adaptation of direction-selective visual neurons which respond selectively to moving contours in the image [4,32,33,41,50]. Recently, a new opinion emerged based on the visual responses of motion-sensitive neurons in the pretectum of pigeons [35]. These neurons responded similarly to real and illusory contours while some of them produced inhibitory or excitatory after-responses to the cessation of a prolonged motion in the preferred or null direction. Since excitatory and inhibitory receptive fields (RF) of these neurons were overlapped and possessed opposite directionalities, they could provide a neuronal substrate for the MAE perception in vertebrates.

If this conclusion applies, pigeons should be able to perceive the MAE after prolonged exposure to a moving stimulus. Two successive experiments were designed to investigate this assumption.

2. Experiment 1

2.1. Materials and methods

2.1.1. Subjects

Four female and four male adult pigeons (*Columbia livia*) with body weights of 480–570 g were employed in the experiments. The guidelines regarding the care and use of animals established by the Society of Neuroscience were applied. The animals had no previous experience with behavioral experiments. During training and tests, they were kept on a food deprivation schedule at approximately 85% of their free-feeding weight, but water was always available in the cages.

2.1.2. Apparatus

The animals were trained and tested in a cubical aluminum box (34 cm × 34 cm × 34 cm) equipped with four square-shaped pecking keys (5 cm × 5 cm) and one white house-light located at the ceiling of the chamber with a distance of 30 cm to the frontal panel. The feeder was located 12 cm below the central pecking key and 6 cm above the floor. A white feeder-light was placed 4 cm above it. The four pecking keys were arranged like an inverted 'T' on the frontal panel. The central key was located 18 cm above the floor with three side keys located at its left, right and topside with distance of 2 cm to each other. The central pecking key was used to display visual stimuli. Three side keys were illuminated red (left), yellow (top) and green (right) throughout training and testing periods. 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 (Frank Buschmann International Corporation) via a computer.

2.1.3. Visual stimuli

Pigeons scrutinize pecking keys from about a distance of 55 mm before pecking them [21]. At this distance, the visual angle of the pecking key to the eyeball is 58.5°. The visual stimulus was a grating pattern consisting of black and white equal-width stripes at a spatial frequency of 0.12 cycles/° and a motion speed of 40°/s. It had two moving directions: downward, upward or standing. Which sequence of visual stimulus was chosen depended on the phases of the experiment (Table 1).

2.1.4. Training and testing

The animals were first accustomed to the chamber and the pecking procedure using an autoshaping design. Every day, they performed a single session consisting of 60 trials with 15 trials for each pecking key. For each trial, only one of four pecking keys on the frontal panel was randomly activated 5 s followed by 2 s access to food from the feeder. The central key was only illuminated plain white while three side keys were illuminated with their respective colors. During

Table 1
The combination of visual stimulus displayed on the central key at different phases of the two experiments. During the adapation phase, the animals were asked to successively peck the central key within at least 30 s to active three side keys. Subsequently, they had 3 s to peck one of the side keys to be rewarded by food delivery or be punished

Experiment	Period	Adaptation phase	Response phase
Experiment one	Training	Static (30 s)	Static (3 s)
		Upward (30 s)	Upward (3 s)
		Downward (30 s)	Downward (3 s)
	Transfer test	Static (30 s) + static (1 s)	Static (3 s)
		Upward (30 s) + static (1 s)	Static (3 s)
		Downward (30 s) + static (1 s)	Static (3 s)
Experiment two	Training	Static (30 s)	Static (3 s)
			Upward (3 s)
			Downward (3 s)
		Upward (30 s)	Upward (3 s)
			Downward (3 s)
		Downward (30 s)	Upward (3 s)
			Downward (3 s)
	Transfer test	Static (30 s)	Static (3 s)
		Upward (30 s)	Static (3 s)
		Downward (30 s)	Static (3 s)

this period, no visual stimulus was given and the animals did not need to peck any key to obtain food. After they accustomed to the chamber and learned to get food from the feeder, the training proceeded in four steps.

The first step was to train the animals to peck the activated pecking key once to obtain food. Each session consisted of 60 trials with 15 trials for each pecking key and trial length of 5 s. At this step, the central key was also illuminated plain white and only one key was illuminated in each trial. One single correct peck on the lighted key within 5 s activated the feeder. If the animals did not peck the lighted key but others, 10 s of time-out without lights started followed by 20 s of ITI (Inter-Trial Interval). Without any response, no food or punishment was delivered. When they responded correctly in all 60 trials, the next training step started. All animals quickly learned the task.

In step two, different visual stimuli were displayed on the central key to replace the plain white color. The animals had to first peck once on the lighted central key within 5 s to activate one of three side keys. Which side key was activated depended on the correspondence between the visual stimulus shown on the central key and the color/location of the side keys. For example, when the static grating pattern was shown on the central key, the yellow illuminated top key was activated; when the moving downward grating pattern was shown, the red illuminated left side key was activated; when the moving upward grating pattern was shown, the green illuminated right key was activated. When one of side keys was activated, the visual stimulus shown on the central key was left unchanged and the animals had to peck the activated side key once within 10 s to get food. This method enabled a fast learning of the correspondence between them. When correct ratios for three consecutive sessions were all at least 95% for each visual stimulus, the next training started. This part lasted at least 2 weeks.

In the third step of the training period, one correct peck on the lighted central key during the adaptation phase activated all three side keys. Thus, the animals had to peck one of them according to the correspondence with the centrally presented stimulus. This training started with a session length of 30 trials (10 trials for each grating pattern). The session length was increased by 10 trials when the discrimination ratio for each pattern reached at least 85% on three consecutive days until reaching 60 trials for each session (20 trials for each pattern). Then, the available response time was decreased from 10 s (step two) to 3 s. The animals needed at least 2 months to completely learn the correspondence between the visual stimulus and the color/location of the side key.

At step four, the threshold to activate three side keys was stepwise increased from five pecks within 5 s onto the central key to finally 30 correct pecks within 30 s. This method was taken to ensure sufficient exposure time to the
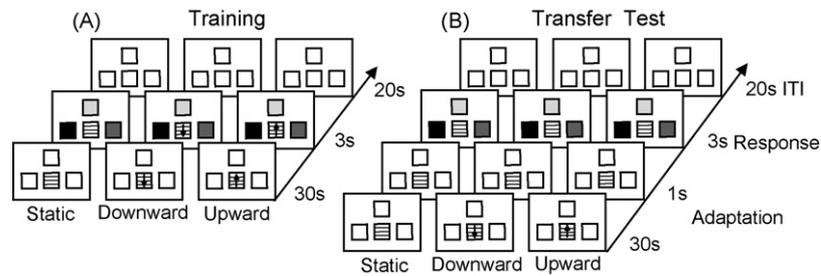
Fig. 1. Experimental setup for the training (A) and transfer tests (B) in experiment one. In the training period, a series of pecks on the lighted central key during the adaptation phase activated three side keys illuminated with different colors (red illuminated left key, yellow illuminated top key and green illuminated right key). For a centrally displayed static grating pattern, the yellow top key had to be pecked during the response phase. A downward moving grating required a peck on the red left key, and an upward pattern required a peck on the green right key. If the birds pecked the correct side key, they were rewarded. A 20 s inter-trial interval (ITI) started after the response phase. In transfer tests, a static stimulus was briefly shown after the moving grating on the central key. In humans, such a sequence induces a movement aftereffect (MAE).

illusion-inducing stimulus. The pecking counter and timer started from the first correct peck onto the central key. If the animal emitted sufficient pecks in less than the necessary time, it had to go on pecking until the time criterion was reached. If it had not pecked enough in the required time, the time span was prolonged until enough pecks were emitted. The maximal trial length was 60 s. During the response phase, the visual stimulus displayed on the central key was left unchanged while three side keys were all activated (Fig. 1A). The animal had 3 s to give a response. When the correct discrimination ratios reached at least 85% in three consecutive days, the next adaptation period before the illusion transfer tests started. The animals needed at least 1 month to finish this step.

The critical transfer tests had to be conducted without giving the animals any feedback in terms of reward or punishment. Therefore, no reward or punishment was provided irrespective of their choices in 2 out of 20 trials randomly chosen by the control program for each pattern. Using this method, they gradually adapted to the condition in the illusion test trials. This adaptation lasted several weeks until the correct ratio for each grating pattern was at least 85% on five consecutive days. When the animal reached this criterion, it started with the test sessions including the illusion test trials.

Each test session included 54 normal trials with feedback (18 trials for each grating pattern) and 6 randomly interspersed illusion test trials without feedback (2 trials for each grating pattern). In the test trial, the animals had to peck the central key at least 30 times within 30 s. Then, the central key switched to a static pattern display for 1 s before the three side keys were activated. The static grating pattern was still displayed on the central key during 3 s of the response phase until they pecked one of the three side keys. The idea behind this procedure was to induce the MAE while seeing 1 s of the static pattern (Fig. 1B). If the animal can perceive the MAE, it should peck a side key signaling the illusory movement with the opposite direction to the visual stimulus displayed at the first 30 s. Each animal was tested every 48 h.

2.1.5. Data analysis

Throughout the paper, the response latency was defined as the duration from the onset of the three side keys activation until the first response of the animal. The analysis of variance (ANOVA) and *t*-test were used to determine if there were any between-group differences in performance and the response latency. Significance was assumed when $p < 0.05$.

2.2. Results

2.2.1. Conditional discrimination training

All eight pigeons successfully mastered each task, albeit with individual differences in their acquisition speed. They needed 50–90 sessions (71.25 ± 13.04, mean $\pm$ S.D.) to learn the correspondence between the visual stimuli on the central key and the color/location of the three side keys.

The adaptation training including the interspersed catch trials without feedback was the last procedure before presenting the critical transfer tests. The performance levels within the last 5 days in this procedure for eight pigeons were very high (Table 2, training session). The correct ratios and the response latencies did not significantly differ for the three visual stimuli (correct ratio, $F(2, 21) = 0.21$; response latency, $F(2, 21) = 0.56$; all p's > 0.57).

2.2.2. Test sessions

Each session consisted of 60 trials with 20 trials for each grating pattern including two trials for transfer tests. An illusion test trial was deemed ineffective if the animals did not immediately switch to the activated side keys in the response phase. On average, the ratio for such ineffective illusion trials was 20%. To rest our conclusion on a sound number of critical trials, test sessions continued until 30 effective illusion test trials were collected for each visual stimulus and each animal. The needed test sessions on average was 18.3 (S.D. = 1.39, $n = 8$).

The correct ratios and the response latencies within normal trials (those with feedback and without an illusion-inducing static pattern) in the test sessions (Table 2, test session) were unaffected by the presence of the interspersed critical test trials (correct ratio, $F(2, 42) = 0.0989$; $p = 0.906$; response latency, $F(2, 42) = 0.015$; $p = 0.985$). In transfer illusion test trials, the animals were faced with three contingencies (Table 1): 30 s of a static, a moving upward or downward stimulus followed by 1 s of a static pattern. The first condition (30 s of static pattern + 1 s of static pattern) was used as a control to ensure that the animals were not affected by the absence of feedback in transfer tests, but

Table 2
Correct ratios (CR) and response latencies (RL) in seconds and standard deviations (S.D.) in normal trials with feedback during training and test sessions of experiment one

Visual stimulus	Training session		Test session	
	CR (%)	RL (mean ± S.D.)	CR (%)	RL (mean ± S.D.)
Static	93.3	1.03 ± 0.26	91.8	1.03 ± 0.23
Downward	93.1	1.18 ± 0.39	92	1.19 ± 0.36
Upward	92.6	1.12 ± 0.17	91.8	1.06 ± 0.16

the other conditions were critical. In the illusion test trials, if the animals indicated that they saw a static pattern, they probably had not perceived the MAE since they indeed had seen a static pattern in the last second of the adaptation phase. This result is subsequently called the "static" result. If they pecked a side key that signaled the movement with the same direction to the stimulus displayed in the adaptation phase, they either did not perceive the MAE or only reported according to the first 30 s. We conservatively called this the "no illusion" result. However, if they decided for a side key signaling a movement with an opposite direction to the prolonged visual adaptation stimulus, they probably had perceived the MAE. This will be called the "illusion" result.

The performance of animals did not differ significantly either for the correct ratios ($F(1, 14) = 0.625$; $p = 0.442$) or the response latencies ($F(1, 14) = 4.489$; $p = 0.152$) between static grating trials with or without the additional 1 s of illusion-inducing static stimulus. Thus, the animals were not affected by the slightly prolonged trial duration and the absence of feedback. We then explored the results of those test trials with 1 s of illusion-inducing static stimulus after exposure to a prolonged moving grating. The average response ratios of eight pigeons for three possible outcomes were 44.8% (no illusion), 23.3% (static), and 31.9% (illusion). The response latencies and ratios were calculated separately for these three result types (Fig. 2). The response ratios ($F(2, 45) = 6.532$; $p = 0.003$) but not the response latencies ($F(2, 45) = 0.789$; $p = 0.46$) showed a significant difference between the three choices. Analyzing the response ratios

in greater detail, we found that the pigeons had opted significantly more often for the "no illusion" alternative than for the "static" one ($t_{30} = 3.808$, $p < 0.001$). There were no significant differences between "no illusion" and "illusion" ($t_{30} = 2.017$, $p = 0.073$). Finally, we compared the probability of pecking a side key signaling an opposite movement direction during normal trials (without a 1 s static pattern at the end of an adaptation display) and test trials (with a 1 s static pattern). The inclusion of a brief static pattern significantly increased the probability from 5% to 31.9% ($t_{30} = 6.051$, $p < 0.001$).

The average "illusion" response ratios for two moving grating patterns were 63.3% (downward) and 50% (upward). And the two stimuli were equally contributed to induce the MAE ($F(1, 14) = 1.82$; $p = 0.39$).

2.3. Discussion

This first experiment indicates that pigeons can perceive the MAE. This conclusion rests on the observation that the animals pecked a side key signaling "illusion" perception after the prolonged visual stimulus in about 32% of the critical test trials. This kind of choice was extremely rare in normal trials when no static pattern was briefly shown at the end of the adaptation phase (see also Table 2). However, the illusory and non-illusory choices were almost equally happened on average for the eight pigeons in the critical trials. This could be due to two different reasons. First, it is possible that pigeons see, if at all, only a weak movement illusion. Second, the pigeons were not specifically trained to make their choices according to the movement they perceived at the end of the adaptation phase. Even if pigeons would perceive a strong MAE, their perception would be composed by a lengthy exposure to a grating moving in one direction followed by a brief exposure to an opposite movement. Since the transfer tests provided no feedback to the animals, their indecision to peck according to the first or the last perceived movement could not be solved. To avoid this confusion, we changed the procedure in the second experiment such that the animals were instructed to make their choices according to the last perceived movement on the central key.

3. Experiment 2

3.1. Materials and methods

The same animals, apparatus and visual stimuli described in the experiment one were also employed here, but seven different combinations of visual stimuli were used during the transition from the adaptation phase to the response phase (Table 1). Two different visual stimuli were successively shown on the central key. The important difference to the experiment one was that the pigeons had to respond to the second stimulus displayed on the central key not the first one. Every day, the animals were given one session consisting of 70 trials with 10 trials for each combination. Note that during the training period, the critical sequence of a moving display followed by a static stimulus for inducing the MAE at the transfer tests was not shown. For example, at the training period, when the sequence "downward (30 s, adaptation phase)–upward (3 s, response phase)" was shown on the central key, the correct peck on the green illuminated right side key indicating the motion upward would deliver food; but if the animal pecked one of another two side keys, all lights were switched off for 10 s (Fig. 3A).

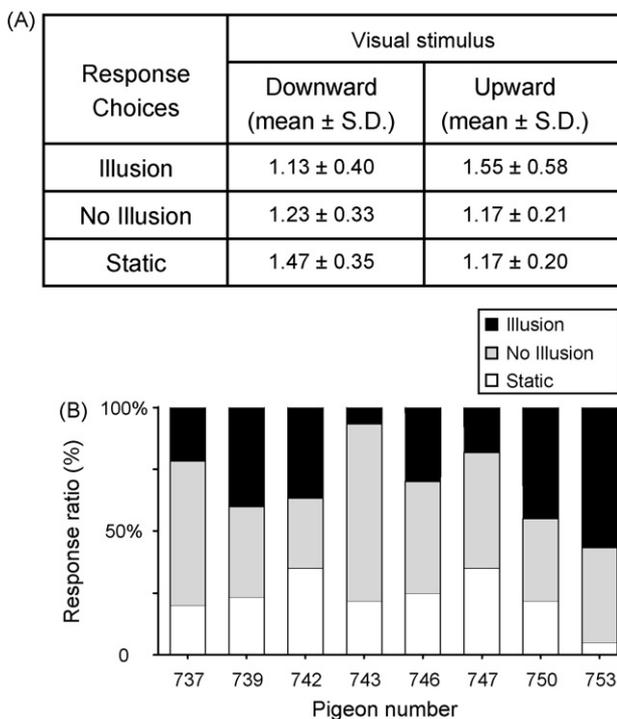| (A) Response Choices	Visual stimulus	
	Downward (mean ± S.D.)	Upward (mean ± S.D.)
Illusion	1.13 ± 0.40	1.55 ± 0.58
No Illusion	1.23 ± 0.33	1.17 ± 0.21
Static	1.47 ± 0.35	1.17 ± 0.20

Fig. 2. Response latencies (A) and percent response ratios (B) for three possible choices in experiment one: illusion (reporting an illusory movement into the direction opposite to the adaptation phase), no illusion (reporting the factual movement direction during the adaptation phase) and static choice (reporting the factually displayed static grating) during the transfer tests.
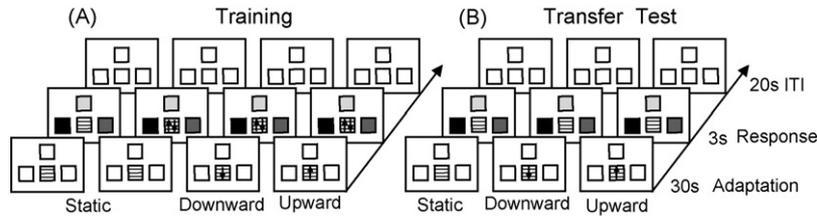
Fig. 3. Experimental setup of the training (A) and transfer tests (B) in experiment two. The critical difference to the experiment one was that the animals had to choose a side key not according to the first central stimulus for 30 s on display (adaptation phase), but according to the subsequent 3 s stimulus (response phase). Please refer to Table 1 for the seven different combinations of visual stimuli that were used.

For the adaptation period before the transfer tests, no reward or punishment was provided irrespective of their choices in 1 out of 10 trials randomly chosen by the control program for each stimulus combination. The test session included 63 normal trials with feedback (9 trials for one stimulus combination) and 6 randomly interspersed illusion test trials without feedback (2 trials for one illusion-inducing stimulus combination) (Fig. 3B). A choice of the side key indicating upward movement after seeing the sequence "downward (30 s)–static (3 s)" would be an indicator of perceiving the MAE at the transfer tests. Each animal was tested every 48 h.

3.2. Results

3.2.1. Conditional discrimination training

The critical difference to the experiment one was that the pigeons now had to respond to the second stimulus displayed on the central key. On average, the animals needed 63.13 (S.D. = 14.9, $n = 8$) sessions to learn the new task.

The adaptation training including the interspersed catch trials without feedback was applied before presenting the transfer tests. The correct ratios and the response latencies within the last 5 days were calculated separately according to the first stimulus (Table 3, training session). No significant differences were obtained with regard to response latencies ($F(2, 21) = 0.15$; $p = 0.86$) between them. However, the correct ratios for the static pattern were higher than those for the other two moving stimuli ($F(2, 21) = 12.58$; $p < 0.001$). But the correct ratios between two moving stimuli did not significantly differ ($F(1, 14) = 0.75$; $p = 0.39$).

3.2.2. Test sessions

For each grating pattern, 2 illusion test trials were conducted within one session. In order to collect 20 effective critical trials, the average number of needed sessions was 12.9 (S.D. = 0.99, $n = 8$). The correct ratios and the response latencies in the normal trials (those with feedback and without the illusion-inducing static pattern) of the test session (Table 3, test session) were

unaffected by the presence of the interspersed illusion test trials (correct ratio, $F(2, 42) = 0.217$; $p = 0.806$; response latency, $F(2, 42) = 0.24$; $p = 0.788$).

For three choices—"no illusion", "static" and "illusion", the response latencies and ratios for each choice were calculated separately (Fig. 4A). The response ratios ($F(2, 45) = 55.96$; $p < 0.001$) but not the response latencies ($F(2, 45) = 0.648$; $p = 0.528$) showed significant differences between the three choices. And the "illusion" choices were recorded significantly more often than the "no illusion" alternatives ($t_{30} = 3.821$, $p < 0.001$). The average response ratios for the three choices were 32.8% (no illusion), 6.8% (static) and 60.4% (illusion) (Fig. 4B).

The average illusion response ratios for two moving stimuli were 62.9% (downward) and 58.8% (upward). These two visual stimuli contributed equally to induce the MAE ($F(1, 14) = 0.12$; $p = 0.75$).

(A)

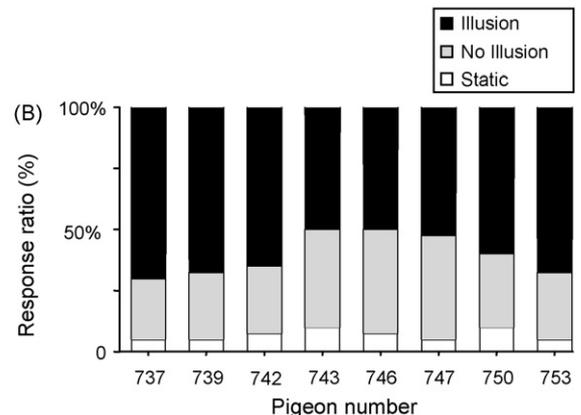|	Visual stimulus	
Response Choices	Downward (mean ± S.D.)	Upward (mean ± S.D.)
Illusion	1.31 ± 0.19	1.32 ± 0.38
No Illusion	1.06 ± 0.19	1.32 ± 0.27
Static	1.23 ± 0.24	1.36 ± 0.31

Fig. 4. Response latencies (A) and percent response ratios (B) for three possible choices in experiment two: illusion (reporting an illusory movement into the direction opposite to the adaptation phase), no illusion (reporting the factual movement direction during the adaptation phase) and static choice (reporting the factually displayed static grating) during the transfer tests.

Table 3
Correct ratios (CR) and response latencies (RL) in seconds and standard deviations (S.D.) in normal trials with feedback during training and test sessions of experiment two

Visual stimulus	Training session		Test session	
	CR (%)	RL (mean ± S.D.)	CR (%)	RL (mean ± S.D.)
Static	92.8	1.31 ± 0.26	91.1	1.39 ± 0.32
Downward	87.1	1.31 ± 0.32	86.5	1.26 ± 0.31
Upward	88	1.38 ± 0.25	87.1	1.36 ± 0.25

3.2.3. Discussion

In the experiment two, the animals were instructed to give the response according to the second visual stimulus on display. This difference in the procedure produced a major change in the pattern of results. While the "illusion" and "no illusion" choices occurred equally in the experiment one, the response ratios to the "illusion" choices were significantly higher in the experiment two. Thus, it meant that the pigeons in the experiment one had indeed been confused between two options since the instructions were unclear at this point. According to the results of experiment two, it provided considerably stronger evidence that pigeons can perceive an MAE after a prolonged exposure to a moving stimulus.

4. General discussion

To our knowledge, this study represents the first behavioral evidence for the motion aftereffect (MAE) in pigeons. It therefore accords with the electrophysiological results of Niu et al. [35] which identified a cellular correlation of the MAE at midbrain level in pigeons. As we know, the birds can perceive geometric illusions in static displays (pigeon [19,20,22,30,31]) as well as illusory contours defined by contrast gradients (pigeon [35]; barn owl [34]; chick [47,53]). The present study extents this list for the first time to the domain of movement illusions.

Several reports indicated that in humans 20 s of prolonged visual stimulation can subsequently elicit an MAE [27,35]. Thus, 30 s of prolonged visual stimulus was used in the current experiment in order to induce an MAE in pigeons.

A classic explanation for the MAE assumes a neural adaptation process in which the direction-selective neurons coding for a particular movement reduce their responses after prolonged exposure to a constantly moving stimulus [4,32,33,41,43]. Under normal conditions, the outputs of neurons tuned to different directions are balanced when looking at a stationary scene. However, the adaptation to the prolonged moving stimulus leads to a decrease of output in that direction. It is also this adaptation which finally elicits a perception of movement into the opposite direction after seeing a static display. Niu and colleagues [35] proposed a new neural mechanism for the MAE based on the single cell recordings from the avian nucleus lentiformis mesencephali (nLM) of the pretectum. According to their data, motion-sensitive pretectal neurons have overlapped excitatory and inhibitory receptive fields with opposite directionalities [9,16,17]. Thus, they could show that the inhibitory after-response subsequent to a prolonged motion stimulus was identical to the inhibitory response due to the exposure to a movement into the opposite direction of the preferred one. This arrangement could be a powerful cellular mechanism to create illusory motions with the opposite direction to the previous stimulus. Since the nLM projects via the visual thalamus to the forebrain [23,24,51], it is possible that the MAE is integrated at telencephalic level to guide goal-directed behavior as analyzed in the present study.

The avian nLM corresponds to the nucleus of the optic tract (NOT) in the pretectum of mammals which also is involved in generating optokinetic nystagmus (OKN) [29,52]. Usually, it is suggested that the MAE in humans is based on cortical processes [2]. Brain imaging data showed that cortical areas sensitive to visual motion are activated during the waterfall illusion [26,28,46] and the activity level is related to the occurrence and strength of the MAE [3,42,44]. However, based on electrophysiological [35] and behavioral (present study) evidences in pigeons, it might be conceivable that in humans the MAE or the waterfall illusion also starts at midbrain level although its final perception is based on cortical mechanisms.

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