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RESEARCH ARTICLE

Sensitivity of the avian motion system to light and dark stimuli

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Abstract Global motion perception is important for
mobile organisms. In laterally eyed birds, global motion
appears to be processed in the entopallium, a neural struc-
ture that is part of the tectofugal pathway. Electrophysi-
ological research has shown that motion selective cells in
the entopallium are most responsive to small dark moving
targets. Here, we investigated whether this bias toward dark
targets of entopallial cells is mirrored by perceptual perfor-
mance in a motion detection task in pigeons. We measured
the detection thresholds of pigeons using random dot stim-
uli that consisted of either black or white dots on a gray
background. We found that thresholds were significantly
lower when using black dots as opposed to white dots. This
heightened sensitivity is also noted in the learning rates of
the pigeons. That is, we found that the pigeons learned the
detection task significantly faster when the stimuli con-
sisted of black dots. We believe that our results have impor-
tant implications for the understanding of the functional
role of the entopallium and the ON and OFF pathways in
the avian motion system.

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Introduction

The ability to perceive motion is essential for many ani-
mals as it serves critical functions such as segmenting
figure from ground, enhancing the extraction of 3D infor-
mation of objects and providing information about self-
motion (Nakayama 1985). Many species of birds are highly
dependent on vision for maneuvering within their envi-
ronment and often exhibit complex visual capabilities that
can sometimes exceed those of the human visual system
(Hendricks 1966; Jarvis et al. 2002; Rubene et al. 2010;
Reymond 1985; see Lazareva et al. 2012, for a review). A
large body of research suggests that pigeons, the most com-
mon model of avian vision, are highly sensitive to motion
(Spetch et al. 2006; Dittrich et al. 1998; Cook and Katz
1999; see Cook and Murphy 2012; for review). Indeed, for
pigeons, motion cues can outweigh form cues for object
discrimination and recognition (Spetch et al. 2006).

Studies of the primate visual system show that in order
to perceive the movement of objects, the visual system
combines local motion into a global motion pattern (Mor-
rone et al. 1995; see Burr and Thompson 2011; Nishida
2011). This is akin to the law of common fate proposed
by Gestalt psychologist whereby all moving elements are
grouped to perceive a single moving object (Köhler 1940).
The pooling of local motion information is often studied
using random dot stimuli (RDS), which are stimuli devoid
of any form information and require the integration of local
motion to identify a global motion pattern (e.g., Morrone
et al. 1995). Using RDS, Bischof et al. (1999) and Nankoo
et al. (2014) demonstrated that pigeons are able to group

local motion signals to extract the global motion pattern. Nankoo et al. (2014) found that pigeons are more sensitive to rotational global motion compared to radial and spiral motion in contrast to the higher sensitivity to rotation and radial motion observed in humans (see also Morrone et al. 1999). As the perception of global motion is critical for organisms to perceive the movement of other animals and objects in the environment, these species differences may help identify specific environmental pressures that shape the visual system of organisms.

Global motion in birds is likely processed primarily in the entopallium, a structure that is part of the tectofugal pathway (i.e., tectopulvinar pathway in mammals) (Karten and Revzin 1966; Karten and Hodos 1970; Engelage and Bischof 1993; Shimizu and Watanabe 2012). Nguyen et al. (2004) reported that lesions to the caudal entopallium resulted in deficits in performance in a coherent motion discrimination task, thus providing direct evidence of the importance of the entopallium for global motion perception. Similarly, Baron et al. (2007) suggested that the integration of the local components of plaid stimuli, processed by the visual Wulst (i.e., V1 equivalent) is likely to be processed upstream in the telencephalon. The Wulst projects to the entopallium, and therefore, it is likely that the entopallium is involved in combining the local components of plaid stimuli (Baron et al. 2007). Given these results, the caudal entopallium is often thought of as a functional equivalent to MT/MST of the primate visual system. Interestingly, Gu et al. (2002) argued, based on electrophysiological data, that cells in the entopallium are most responsive to small black moving targets. In addition, other nuclei have also been shown to exhibit some bias to dark objects. For instance, in two retinal recipient specialized in motion processing in the avian midbrain (i.e., the nucleus basal optic root and the nucleus lentiformis mesencephalic), cells prefer respond best to a black leading edge of a moving stimuli (Fu et al. 1998; Wang et al. 2000). Similarly, in the nucleus semilunari (i.e., a midbrain visual center), more cells prefer black objects over white background (Yang et al. 2002). Given the evidence at the neural level, it is germain to investigate whether birds' perception is also biased toward dark moving objects.

Nankoo et al. (2014) used RDS that consisted of white dots on black background and found significant differences in global motion processing between humans and pigeons. However, it is currently unclear whether the pigeon motion system is differentially sensitive to global motion based on luminance polarity. That is, does the bias of entopallial cells toward dark targets influence perceptual performance? In this study, we compared the detection thresholds for global motion using random dot stimuli that consisted of either black dots or white dots to address this question.
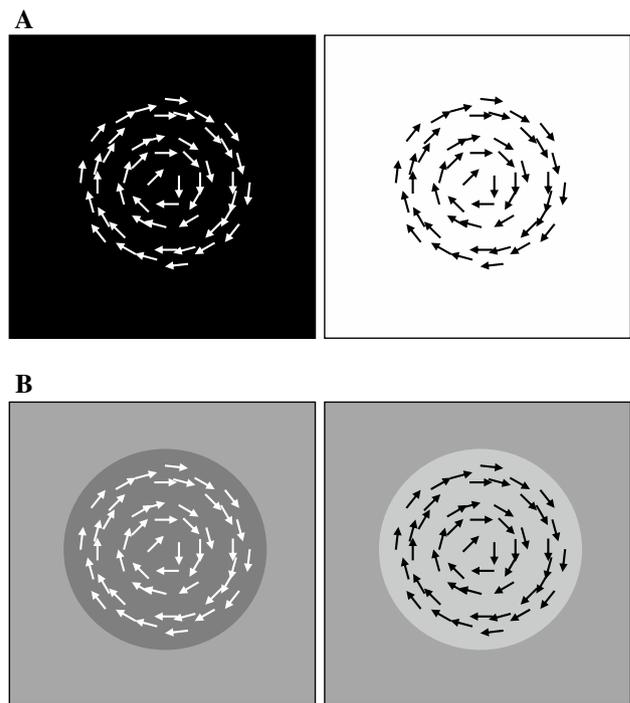
Fig. 1 **a** Light and dark random dot stimuli used in the preliminary study (see supplementary of Appendix). **b** Light and dark random dot stimuli used in this study. The mean luminance of both stimuli was equivalent. Note that this is not an exact reproduction

Method

Participants

Six pigeons (*Columba livia*) served as subjects. Four of the birds had previous experience with a motion detection task similar to that was used in this study (see Supplemental Fig. 1a). The birds were housed in individual cages under a 12-h light: dark cycle (light onset at 6:00 a.m.). All birds were maintained at approximately 85 % of their free-feeding weights. Water and grit were available ad lib in the home cages.

Apparatus

The stimuli were displayed on a 22″ Viewsonic VX2268wm FuHzion LCD computer monitor (resolution: 1680 × 1050 pixels; refresh rate: 120 Hz). The experiment was conducted in touch-screen operant chambers. The monitor was equipped with a 17″ Carroll Touch infrared touch frame. Each chamber contained two solenoid-type bird feeders on the sidewalls of the chamber. Lamps located within each feeder illuminated feeder presentations, and photocells measured the duration of head entries into the hoppers to

limit feeding durations to 1 s per food presentation. The chambers were connected to computers located in an adjacent room. These computers controlled all of the experimental contingencies and recorded the responses.

Stimuli and design

The parameters and type of motion used in this study are the same as those we have used previously (Nankoo et al. 2014). Stimuli consisted of randomly placed dots in a circular aperture that subtended 39.81° in diameter. Each dot subtended a visual angle of $0.36° \times 0.36°$, and the dot density in the display was 3 %. All visual angle measurements were based on an estimated mean viewing distance of 9 cm (Bischof et al. 1999). The dot lifetime was five frames, and each frame was updated on every second monitor refresh (16.7 ms per frame; image update rate: 60 Hz). Dots were removed when they reached their lifetime limit and replaced randomly. All signal dots moved coherently in a rotational pattern, but the dots closer to the center of the pattern moved at a slower speed and the dots closer to the edges moved at a higher speed. The configuration was set in order to maintain rigidity of the motion pattern. The average velocity was 42.93°/s.

Motion patterns were displayed on a uniform gray background (91.6 cd/m²); however, the circular aperture, on which the dots were directly overlaid, was controlled to maintain the same mean ambient luminance in both conditions (Fig. 1b). In the black-dot condition, dots were black (0.27 cd/m²) and superimposed on a light gray circle (97.4 cd/m²) and had a contrast level of 99 %. In the white-dot condition, dots were white (182.0 cd/m²) and superimposed on a dark gray circle (85.8 cd/m²) and had a contrast level of 33 %. The mean luminance of both the black dots with light gray circle (black-dot condition) and the white dots with dark gray circle (white-dot condition) was equal to the uniform gray background.

The order of the conditions was counterbalanced across birds. The coherence level was varied by changing the ratio of signal-to-noise dots within a pattern. Signal dots moved in the coherent direction, whereas noise dots moved in a random direction (Scase et al. 1996). We used the method of constant stimuli to present the different coherence levels. A total of 11 coherence levels were used: Coherences were between 0 and 100 %, in 10 % increments. The direction of motion was either clockwise or counterclockwise and remained consistent across frames within a trial. The direction of motion was counterbalanced within session.

Procedure

Prior to testing, the birds were trained to discriminate between the S+ (at 100 % coherence level) and S− (0 %

coherence level). Pigeons responded by pecking at the pattern. The criterion for moving on to the testing phase was 85 % correct responses over three consecutive days. Testing was carried out in two blocks: one block for each dot-polarity condition. Pigeons were trained and tested on one dot polarity before moving on to the next pattern; block order was counterbalanced across birds. One session was carried out per day and each session lasted 45 min. Pigeons completed as many trials as possible within the 45 min. Testing was carried out over a 10-day period. In each condition, across all sessions, pigeons completed an average of 144 trials per coherence level. During testing, if the birds' performance at 100 % coherence was below the training criterion for 2 days in a row, they were put back on training until they reached the training criterion; thereafter they resumed testing. This procedure was similar to Nankoo et al. (2014).

Data analysis

The birds' coherence threshold for each motion pattern was estimated using a four-parameter cumulative Weibull function (Weibull 1951) of the following form:

$$F(c) = \alpha \left(1 - e^{-(c/\beta)^\gamma} \right) + \delta \tag{1}$$

where c is the coherence level, and α, β and γ are the asymptote, spread and shape parameters of the Weibull function, respectively. δ is the y-intercept, to account for the guessing rate. The Weibull function was fit to data for each condition, for each bird, by means of the Nelder and Mead (1965) simplex algorithm set to minimize the root-mean-squared deviation (RMSD) between the function's estimation and the data. This procedure was repeated for 1000 iterations to ensure the global minima was found. The threshold was then calculated as the coherence levels corresponding to 75 % accuracy using the best-fitting parameters.

All statistical analyses were conducted using SigmaPlot (Systat Software Inc., Chicago, IL) and MATLAB (The MathWorks Inc., Natick, MA). Effects were considered significant based on an alpha level of 0.05. Paired t tests were conducted to compare the trials to criterion and threshold coherence of the two conditions.

Results

As shown in Fig. 2, the number of training sessions required to reach criterion was found to be different with birds requiring significantly less sessions to reach criterion in the black-dot condition ($M = 6.00$, SD $= 2.97$) compared to the white-dot condition ($M = 23.67$, SD $= 8.31$),
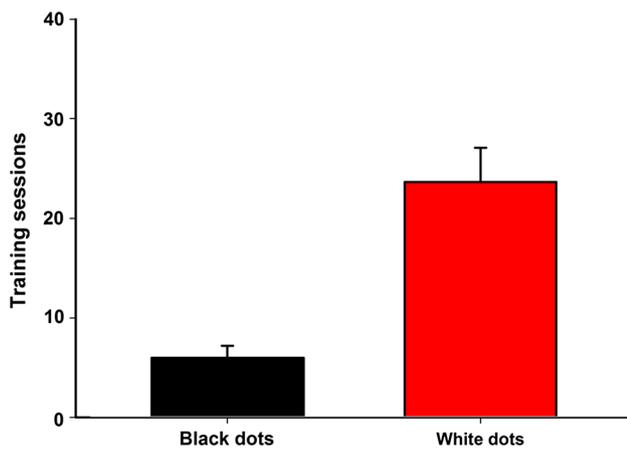
Fig. 2 Mean number of training sessions the birds took to reach criterion in each condition. *Error bars* represent standard error of the mean

$t(5) = 4.76$, $p = 0.005$, $r = 0.91$. The order of the condition did not influence the number of session required to reach criterion, $t(5) = 0.39$, $p = 0.071$, $r = 0.17$.

Figure 3a shows the performance (i.e., accuracy) of the birds as function of coherence in both conditions. The estimated thresholds (Fig. 3b) extracted from the fitted Weibull functions were significantly lower in the black-dot condition ($M = 31.19$ %; SD $= 15.0$ %) compared to those obtained for the white-dot condition ($M = 62.77$ %; SD $= 8.9$ %), $t(5) = 9.49$, $p < 0.001$, $r = 0.97$. It should be noted that these results are similar to those that were obtained when contrast was equated (Fig. A1). Additionally the mean threshold in the white-dot condition was similar to that seen for the rotation condition in Nankoo et al. (2014) ($M = 50.0$ %; SD $= 7.9$ %).

Discussion

The current study investigated the effect of luminance polarity on the perception of global motion in the pigeon. We found that pigeons' detection thresholds were significantly lower when the random dot stimuli consisted of black dots as opposed to white dots. The difference in performance was also reflected in the number of sessions required to learn the task.

Various researchers have reported that cells in the pigeon visual system are more responsive to motion stimuli that consisted of black dots (Gu et al. 2002; Fu et al. 1998; Wang et al. 2000; Yang et al. 2002). Here we demonstrate behavioral differences in global motion detection that are congruent with the preference of black dots at the cellular level. These results have major implications with respect to how the avian visual system processes light and
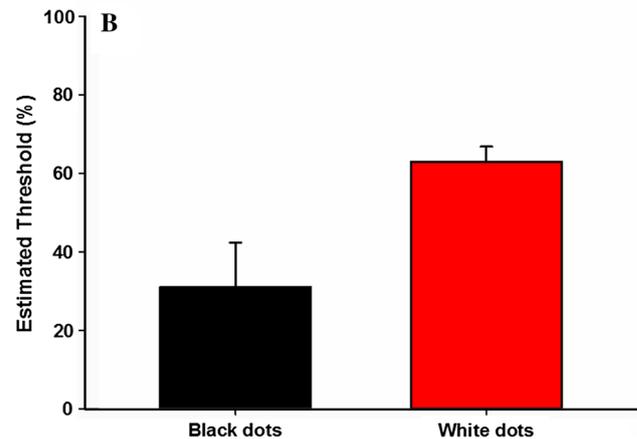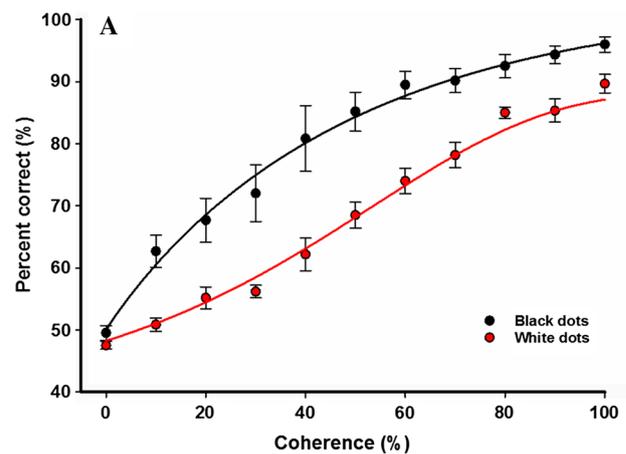
Fig. 3 a Percent correct as a function of coherence level for each condition. *Lines* represent the Weibull function fit for each condition; *markers* represent the observed mean percentage correct. **b** Estimated threshold (coherence level corresponding to 75 % correct) for each condition. *Error bars* represent the standard error of the mean

dark moving objects. At the retinal and early cortical levels of the visual system, luminance information follows along two pathways: the ON pathway and the OFF pathway. The ON pathway responds to light increments, whereas the OFF pathway responds to light decrement (Schiller 1995). Currently, little is known about how the ON and OFF pathways function in the avian brain, but based on our result it appears that there is a substantial difference between the pathways at the level of global motion processing.

Differences between the ON and OFF pathways have been reported in various neuroanatomical and neurophysiological studies in the mammalian brain (Balasubramanian and Sterling 2009; Jin et al. 2011; Komban et al. 2011; see Lu and Sperling 2012; for review). However, the evidence suggests that in the mammalian motion system, the ON and OFF pathways are combined at the global level of motion processing, possibly at the level of MT/V5. Edwards and Badcock (1994) used random dot stimuli to investigate

the interactions of the ON and OFF pathways on local and global motion perception in humans. They noted that motion when a dot's polarity was changed (i.e., white to black or vice versa) on each frame global motion perception was abolished. This suggests that there was no integration of the light and dark dots at the local level. However, when Edwards and Badcock (1994) used a stimulus consisting only of light dots, the addition of dark dots as noise raised the thresholds for global motion. This can only be due to an integration of the light and dark dots. In other words, the visual system treated light and dark dots as equivalent, and therefore, this suggests an integration of ON and OFF signals at the global level of motion processing (Edwards and Badcock 1994; see also Xing et al. 2010). While our experiment cannot distinguish whether the light–dark asymmetry first occurs at the local level, it does suggest that the difference between ON and OFF pathways is present at the global motion level in the avian brain.

The importance of luminance polarity on motion perception in birds cannot be overstated. The heightened sensitivity to motion with black dots may be related to an adaptation of the visual system to the birds' environment. Studies have shown that objects in the foreground are often darker than the background and that this relative difference is congruent with the larger number and higher density of OFF cells, relative to ON cells, in the primate visual system (Ratliff et al. 2010). It may be that diurnal birds are more sensitive to dark moving objects because during flight other organisms will tend to be darker in contrast to the sky. Investigating whether the heightened sensitivity to dark moving object is specific to diurnal birds would be an interesting avenue of future research.

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