RESEARCH ARTICLE

Perception of complex motion in humans and pigeons (*Columba livia*)

Jean-François Nankoo · Christopher R. Madan · Marcia L. Spetch · Douglas R. Wylie

Abstract   In the primate visual system, local motion signals are pooled to create a global motion percept. Like primates, many birds are highly dependent on vision for their survival, yet relatively little is known about motion perception in birds. We used random-dot stimuli to investigate pigeons' ability to detect complex motion (radial, rotation, and spiral) compared to humans. Our human participants had a significantly lower threshold for rotational and radial motion when compared to spiral motion. The data from the pigeons, however, showed that the pigeons were most sensitive to rotational motion and least sensitive to radial motion, while sensitivity for spiral motion was intermediate. We followed up the pigeon results with an investigation of the effect of display aperture shape for rotational motion and velocity gradient for radial motion. We found no effect of shape of the aperture on thresholds, but did observe that radial motion containing accelerating dots improved thresholds. However, this improvement did not reach the thresholds levels observed for rotational motion. In sum, our experiments demonstrate that the pooling mechanism in the pigeon motion system is most efficient for rotation.

Keywords   Visual perception · Motion perception · *Columba livia* · Coherence threshold · Motion integration

J.-F. Nankoo (✉) · C. R. Madan · M. L. Spetch · D. R. Wylie
Department of Psychology, University of Alberta, P217
Biological Sciences Bldg, Edmonton, AB T6G 2E9, Canada
e-mail: nankoo@ualberta.ca

D. R. Wylie
Centre for Neuroscience, University of Alberta,
Edmonton, AB, Canada

Introduction

The ability to perceive motion is critical for survival for mobile organisms as it serves several functions such as detection of prey/predators, perception of self-motion, and separation of figure from ground (Nakayama 1985). In the mammalian visual system, motion is processed hierarchically in a feed-forward system that first extracts local signals at the lower cortical areas (e.g., primary visual cortex [V1]) and pools those signals at a higher cortical level (e.g., medial temporal area [MT+]) to create the percept of global motion (see Burr and Thompson 2011, for review). Neurophysiological studies have shown that in the monkey medial superior temporal area (MST), cells are selective for global translation motion and global complex motion (e.g., radial and rotational motion; Britten and van Wezel 1998; Duffy and Wurtz 1991; Saito et al. 1986; Tanaka and Saito 1989). These results from animal models have been substantiated by brain imagining studies that have found increased BOLD activity in the human V5/MT+ (homologue of MT/MST) in response to complex motion patterns (Morrone et al. 2000; Wall et al. 2008).

Physically, the difference among complex motion patterns is quantitative, in that it is based solely on the deviation in trajectory of the elements in the pattern (see Fig. 1 in Morrone et al. 1999). For example, if the local vectors in a radial pattern (Fig. 1a) were to be deviated by 45°, this would result in a spiral motion (Fig. 1b), whereas a deviation of 90° would result in a rotational motion (Fig. 1c). Morrone et al. (1999) and Burr et al. (2001) have shown that humans have lower detection thresholds for expansion/contraction (i.e., radial) and rotational motion (clockwise/counterclockwise rotation) relative to spiral motion. They suggest that this is evidence that specialized global detectors are tuned specifically to the cardinal directions, that

Fig. 1 Types of motion patterns used in this study. Each pattern differs from the other solely based on the direction of the local vectors. **a** Shows radial motion, **b** shows spiral motion, and **c** shows rotational motion. Note that this is not an exact reproduction (see electronic supplemental materials 1–4)

A + 45° **A + 90°**

Radial **Spiral** **Rotation**

A **B** **C**
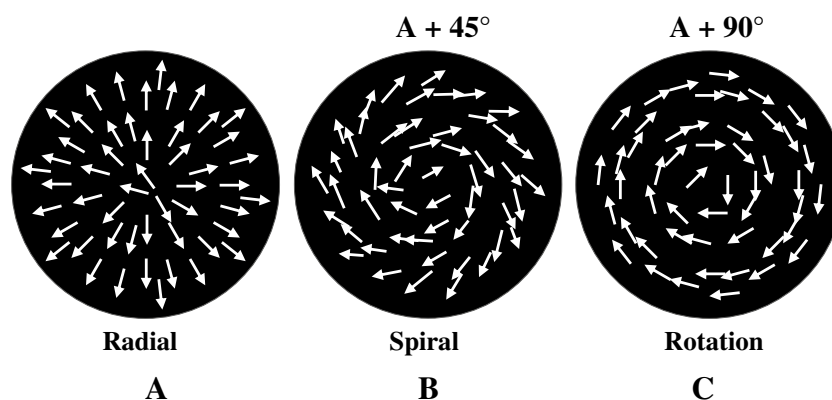
is deviations of 0° (i.e., radial expansion), 90° (clockwise rotation), 180° (radial contraction), and 270° (counterclockwise rotation) of complex motion. However, others have suggested the alternative hypothesis that there are spiral detectors that could simply be less responsive compared to radial and rotational detectors (e.g., Meese and Anderson 2002; Meese and Harris 2001; Snowden and Milne 1996). Some physiological studies with non-human primates have indeed identified neurons tuned to spiral motion in MST (Geesaman and Andersen 1996; Graziano et al. 1994). Regardless of whether there are spiral detectors, the evidence suggests that in primates, motion integration of local signals is more efficient for rotational and radial motion.

As is the case for primates, many birds are predominantly dependent on vision for their survival, but unlike the primate visual system, relatively little is known about the higher telencephalic areas of the avian visual system (Husband and Shimizu 2001). All vertebrates have three major visual pathways: the thalamofugal pathway (i.e., the retino-collicular pathway), the tectofugal pathway (i.e., the retino-thalamo-striate pathway), and the accessory optic system (AOS). In the mammalian brain, 90 % of the ganglion cells from the retina travel along the thalamofugal pathway. However, in the avian brain, most axons leaving the retina travel along the tectofugal pathway (Butler and Hodos 2005). Lesions to the thalamofugal pathway in humans and macaque monkeys have been shown to disrupt color perception, spatial resolution, and can even result in "blindness" (Milner and Goodale 1995; Ungerleider and Mishkin 1982). In contrast, lesions to the thalamofugal pathway have little to no deficit on visual discrimination tasks involving color, form, or intensity in pigeons. Lesions to the pigeon tectofugal pathway, however, result in deficits that are similar to the deficits found after lesions in the thalamofugal pathway of primates (Chaves et al. 1993). The organization of visual information in the pigeon tectofugal pathway is reminiscent of the organization in the mammalian extrastriate cortex as it is functionally segregated (Shimizu et al. 2010). For instance, the entopallium, a telencephalic structure that is part of the tectofugal pathway, is segregated such that the rostral portion processes form and color information, whereas the caudal region processes motion information (Nguyen et al. 2004; Shimizu et al. 2010).

Given that most birds and primates are visually dependent, comparative research between birds and primates provides an opportunity to investigate how two different visual systems solve similar problems (i.e., the problem of seeing and perceiving). Currently, there is little information on the psychophysical properties of low- and mid-level vision in birds, especially with respect to the motion integration (Lazareva et al. 2012). Bischof et al. (1999) used random-dot stimuli to investigate global motion by comparing coherent motion to random motion in pigeons and humans. They found that the pigeon visual system was much less tolerant of dynamic noise compared to the human visual system. It should also be noted that Bischof et al. (1999) used planar motion (specifically up, down, left and right global motion) and they did not observe any differences in performance based on direction of motion. In this study, we investigate whether the pigeon visual system is more sensitive to certain complex motion patterns relative to others by measuring the detection of complex motion embedded in noise (Pelli and Farell 1999) using similar patterns to those used by Morrone et al. (1999). We also measured the detection thresholds in humans to allow a direct comparison of the psychophysical properties of the motion system in the primate and avian visual systems.

Experiment 1

Methods

Participants

Six adults with normal or corrected-to-normal vision participated in the experiment. Participants included three authors and three graduate students from the University of Alberta who had only cursory knowledge of the purpose of the experiment.

Six pigeons with previous unrelated touch screen experience served as subjects. 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

For both humans and pigeons, stimuli were displayed on a 22″ Viewsonic VX2268wm FuHzion LCD computer monitor (resolution: 1,680 × 1,050 pixels; refresh rate: 120 Hz). Participants' head position was fixed with a chin rest. For pigeons, 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 side walls 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 stimuli consisted of randomly placed dots in a circular aperture that subtended 39.81° in diameter. The dots were white and subtended a visual angle of 0.36° × 0.36°. The white dots were presented on a black background. The dot density in the display was 3 %. In one condition (i.e., radial), each dot moved 0.72° per frame, which means that the speed was 42.93°/s. In the two remaining conditions (i.e., Rotation and Spiral), dots closer to the center of the pattern moved at a slower speed, while the dots closer to the edges moved at a higher speed in order to maintain rigidity of the motion pattern. However, the average velocities in these two conditions were matched to that of the radial condition. We used a lifetime of five frames, and each frame was updated on every second monitor refresh (16.7 ms per frame; image update rate: 60 Hz). Viewing distance was set at 45 cm for human participants, whereas for pigeons, we scaled down the physical measurements of the stimuli (including dot size) by a factor of 5 to account for viewing distance in the operant box (Bischof et al. 1999). Dots were removed when their position on the current frame reached the edge of the circular aperture or if they reached their lifetime limit. New dots were generated following Gaussian probability functions (SD = 4.22°), such that dots were most likely to be generated near the center of the circular aperture for spiral and radial patterns. Note that in the rotation pattern, dots never exceeded the edge of the aperture

Table 1 Number of training sessions required to reach criterion for each motion pattern in Experiment 1

Bird ID	Number of sessions			
	Radial (Rad)	Spiral (Spi)	Rotation (Rot)	Block order
41	48	16	3	Rad-Rot-Spi
26	39	24	5	Rad-Spi-Rot
971	64	36	5	Spi-Rad-Rot
34	6	63	6	Spi-Rot-Rad
74	36	29	16	Rot-Rad-Spi
978	19	37	24	Rot-Spi-Rad

and thus were only removed if they reached the lifetime limit.

Three types of global complex motion were used: radial, spiral, and rotation (Fig. 1; also see electronic supplemental materials 1-4). The three conditions were counterbalanced across participants (see Block Order in Table 1). 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 randomly assigned 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. For pigeons, we used: 0, 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100 %. For humans, we used: 0, 1, 2, 4, 6, 8, 10, 15, 20, 25, and 30 %. The use of different levels of coherence for pigeons and humans are based on the findings of Bischof et al. (1999) who found that motion integration in pigeons were poor relative to humans. For radial patterns, the direction of motion moved inward (i.e., contraction) or outward (i.e., expansion). Likewise, rotation patterns rotated either clockwise or counterclockwise and spiral patterns rotated inward clockwise or outward counterclockwise. The direction of motion within a trial remained consistent across frames, but was counterbalanced within the session.

Procedure

Humans

Participants were tested using a two-alternative forced choice paradigm. At the beginning of each block of trials, participants were told which type of pattern they would be trying to detect. As illustrated in Fig. 2, participants began the trial by "clicking" a gray start stimulus (i.e., moving the mouse cursor over the stimulus and depressing the left mouse button). Thereafter, the S+ (motion containing coherence motion) and S− (noise pattern; identical to 0 % coherence) were presented simultaneously. The participants were then required to click on the S+. No feedback
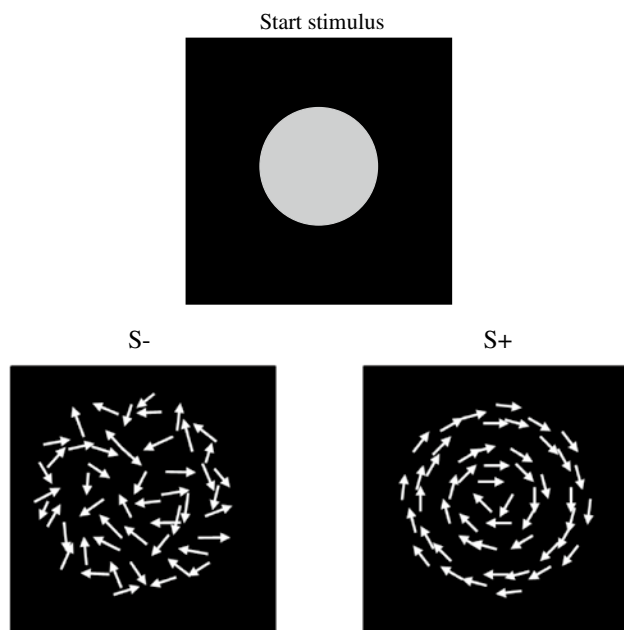
Start stimulus

S−   S+

Fig. 2 Illustration of the stimulus presentation protocol. First, the start stimulus is presented. After a peck (or mouse click for humans), two motion patterns are shown: one with coherent motion (S+) and one with no coherence (S−). In this example, the coherence is at 100 %, meaning that all the dots moved in the same direction

was given. The left/right position of the S+ and S− was counterbalanced.

Testing was carried out in three blocks: one block for each type of motion pattern. In each condition, a total of 40 trials per coherence level and 20 trials per direction were presented for both the given pattern and the random control. This yielded a total of 440 trials within a block. Participants were allowed to take a brief break between blocks.

Pigeons

The procedure for the pigeons was similar to that described above, but with a few modifications. 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 three blocks: one block for each type of pattern. Pigeons were trained and tested on one motion pattern before moving on to the next pattern. One session was carried out per day and each session lasted 45 min. The pigeons were allowed to complete as many trials as possible within the session. Testing was carried over a 10-day period. In each condition, across all sessions, the pigeons completed an average of 144 trials per coherence. 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 reach the training criterion. Thereafter they resumed testing.

Data analysis

To analyze the data, we calculated the percent correct for each coherence level, for each motion pattern. Participants' coherence threshold for each motion pattern was estimated using a four-parameter cumulative Weibull function (Weibull 1951) of the following form:

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

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 chosen as it provides a good approximation to the psychometric function (May and Solomon 2013; Quick 1974). The Weibull function was fit to data for each pattern, for each participant, 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 1,000 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 Sigma-Plot (Systat Software Inc., Chicago, IL) and MATLAB (The MathWorks Inc., Natick, MA). Effects were considered significant based on an alpha level of 0.05. One-way repeated-measures ANOVAs and post hoc pairwise analyses, using Holm-Sidak method, were conducted on the threshold coherence levels of the different motion patterns.

Results and discussion for Experiment 1

Humans

Accuracy for each pattern is plotted as a function of coherence level in Fig. 3a. Figure 3b shows the mean detection threshold of each motion pattern. A one-way repeated-measures ANOVA yielded a significant main effect of motion pattern, $F(2, 10) = 103.08$, $p < .001$. Holm-Sidak post hoc pairwise comparisons demonstrated that the thresholds for rotation and radial patterns were significantly lower than the threshold for spiral motion [$t(5)_{\text{rotation vs spiral}} = 12.88$; $t(5)_{\text{radial vs spiral}} = 11.94$; all ps $< .001$] but did not differ from each other [$t(5)_{\text{rotation vs radial}} = 0.94$; $p = .37$]. Paired t test revealed that there were no differences between clockwise and counterclockwise rotational motion [$t(5) = 2.37$; $p = .06$]. However, the threshold for
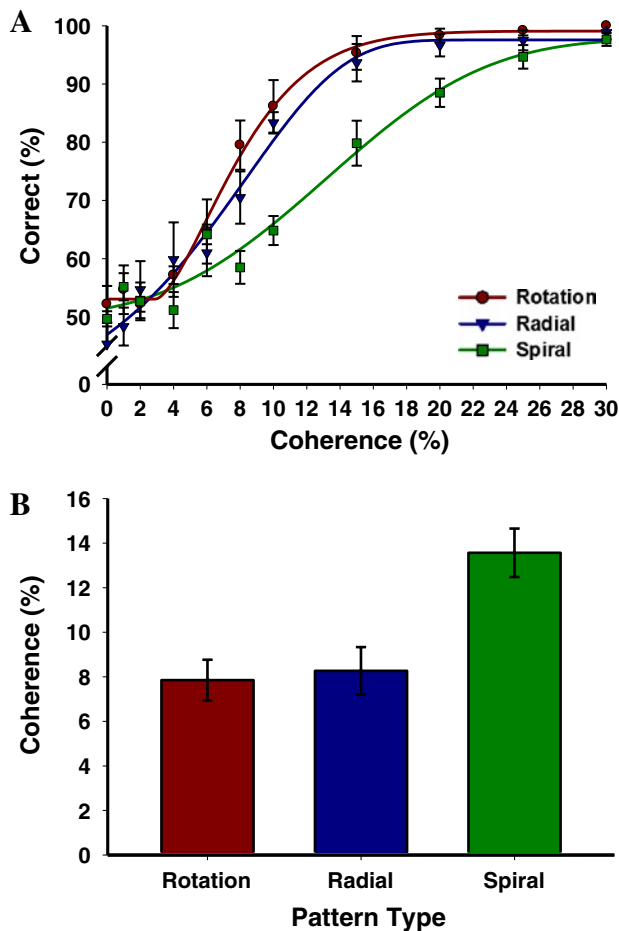
Fig. 3 a Represents the percent correct as a function of coherence level for each motion pattern type for the human participants. *Lines* represent the Weibull function fit for each pattern type; *markers* represent the observed mean percentage correct. **b** Represents the estimated threshold (coherence level corresponding to 75 % correct) for each motion pattern for the human participants. *Error bars* represent the standard error of the mean

Fig. 4 a Represents the percent correct as a function of coherence level for each motion pattern type for the pigeons. *Lines* represent the Weibull function fit for each pattern type; *markers* represent the observed mean percentage correct. **b** Represents the estimated threshold (coherence level corresponding to 75 % correct) for each motion pattern for the pigeons. *Error bars* represent the standard error of the mean

contraction in the radial motion condition was significantly lower than the threshold for expansion [$t(5) = 4.62$; $p = .006$], as was the threshold for clockwise contraction spiral motion compared to counter-clockwise expansion spiral motion [$t(5) = 2.73, p = .04$; Fig. 5].

Pigeons

Accuracy for each motion pattern is plotted as a function of coherence level in Fig. 4a. Figure 4b shows the mean detection threshold of each motion pattern. A one-way repeated-measures ANOVA yielded a significant main effect of motion pattern, $F(2, 10) = 13.51, p < .001$. The results of Holm-Sidak post hoc pairwise comparisons revealed that the thresholds for each motion pattern differed significantly from each other. The threshold for rotational motion was significantly lower than those of radial
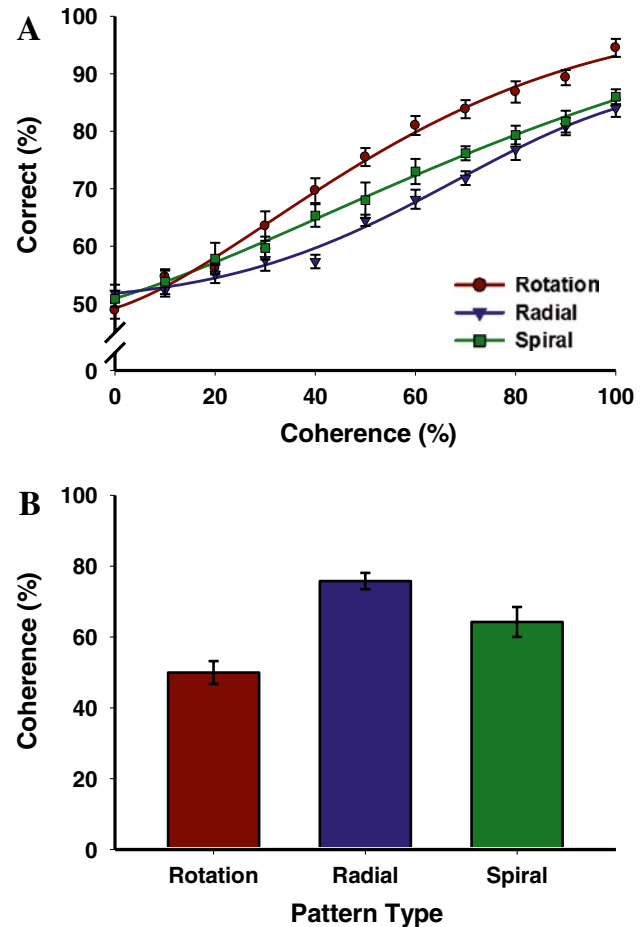
[$t(5) = 5.19$; $p < .001$] and spiral motion [$t(5) = 2.87$; $p = .01$]. The threshold for spiral motion was also found to be significantly lower than the threshold for radial motion [$t(5) = 2.32$; $p = .04$]. Paired t tests revealed that there were no differences between clockwise and counterclockwise rotational motion [$t(5) = 0.42$; $p = .70$], clockwise contraction and counter-clockwise expansion spiral motion [$t(5) = 0.23$; $p = .83$], or expansion and contraction radial motion [$t(5) = 1.18$; $p = .29$] (Fig. 5).

The number of training sessions required to reach criterion varied among motion patterns and individual birds. In particular, the pigeons reached criterion on rotational motion faster than for the other two patterns ($M \pm SD = 9.83 \pm 8.33$ sessions). Both radial ($M = 35.33 \pm 20.61$ sessions) and spiral motion ($M = 34.18 \pm 16.14$ sessions) required similar number of sessions to reach criterion. Shown in Table 1, four out of the
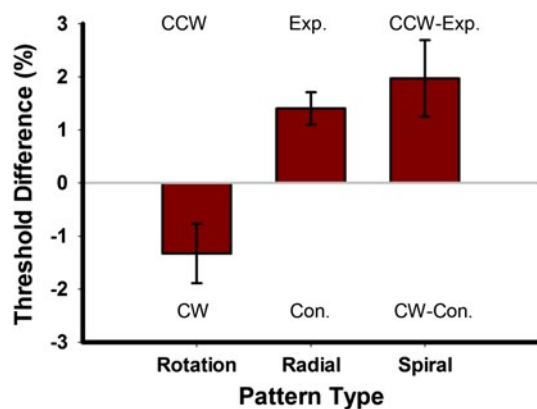
Fig. 5 Shows the difference in estimated threshold (coherence level corresponding to 75 % correct) between the direction of motion in each of the three conditions for the human participants. For the rotation condition, the *bar* represents the difference between counterclockwise and clockwise motion. For the radial condition, the *bar* represents the difference between expansion and contraction motion. For the spiral condition, the *bar* represents the difference between counter-clockwise expansion and clockwise contraction motion. *Error bars* represent the standard error of the mean

six birds learned the task in the rotational motion condition within 6 days, providing further evidence that birds were much more sensitive to rotational motion. The differences, however, were not significant ($F(2, 10) = 3.60$, $p = .07$).

The results from the human data are congruent with the reported literature (e.g., Nankoo et al. 2012) in that we found that our participants were more sensitive to rotation and radial motion compared to spiral motion. With respect to the direction of radial motion, we found that our participants were more sensitive to contraction as opposed to expansion. This result is consistent with previous studies on radial motion detection (Edwards and Badcock 1993; Edwards and Ibbotson 2007; Shirai et al. 2006). We also noted lower thresholds for clockwise contraction spiral motion compared to counter-clockwise expansion spiral motion. In contrast, pigeons were most sensitive to rotational motion but least sensitive to radial motion, with detection of spiral motion at an intermediate level. The higher sensitivity to rotational motion in pigeons was corroborated by the smaller number of sessions required to reach criterion in the rotation condition relative to both spiral and radial conditions. No differences due to the direction of motion were found.

In the global form literature, an aperture artifact has been suggested to facilitate perception of concentric form, shown with Glass patterns (Dakin and Bex 2002; Glass 1969). Glass patterns are stimuli considered to be equivalent to random-dot motion for studying global form perception given that the local signals in these patterns consist of dots pairs whose orientations are summated to identify the global structure. Wilson and Wilkinson (1998) have

reported that human adults were better at detecting concentric form from noise compared to translation form from noise. However, Wilson and Wilkinson (1998) used a circular stimulus window. Dakin and Bex (2002) have shown that windowing Glass patterns in a square window abolish the advantage of concentric patterns relative to translation. They note that translation and noise patterns windowed in a circular aperture cause the pattern to be less dense at the edge because the dot pairs are perpendicular to the edge. This artifact is not found in concentric Glass patterns because the dot pairs align with the edge orientation (which makes the edge more defined than in translation or random). Dakin and Bex (2002) suggest that the more defined edge of concentric form relative to noise is what explains the concentric advantage found in the literature. Similarly, because both translation and noise have less defined edges, participants cannot use edge integrity to identify the pattern from the noise as easily as in the concentric condition. Given the effect of shape aperture in Glass patterns, it is unclear whether the lower thresholds for rotational motion found with the pigeons were also an artifact of the shape of the stimulus display. Because we used a circular display aperture, no dots would cross the edge of the display compared to radial and spiral motion, but also compared to the random motion. Thus, the rotation patterns had fewer flickers as fewer dots disappeared at the edges. This may have facilitated discrimination of rotational motion from random motion. To address this concern, we carried out Experiment 2, in which we compared the thresholds of the pigeons for rotational motion within a circular display aperture to rotational motion within a square aperture.
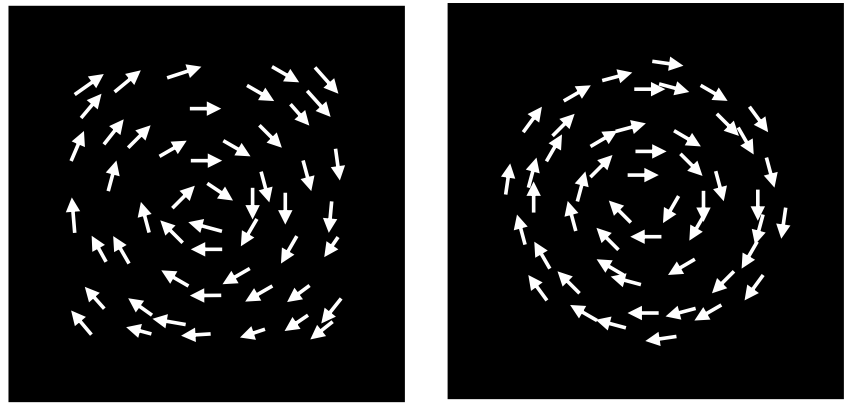
Experiment 2

Method

Four pigeons with previous unrelated touch screen experience served as subjects for Experiment 2. Housing and feeding protocols were the same as in Experiment 1.

Apparatus, stimuli, and design

The apparatus was the same as in Experiment 1. In the circular aperture condition, the stimuli consisted of dots in a circular aperture with a diameter of 39.81°. In the square aperture condition, the dots (white dots on black background) were placed in a square aperture that subtended 36.62° × 36.62° (see electronic supplemental material 5). The areas of both apertures were identical. Both stimuli contained 326 dots. The dots in the square and circular aperture moved on average 0.72° per frame, which means that the average speed was 42.93°/s, similar to the stimuli

Fig. 6 Illustration of the stimulus used in Experiment 2. **a** Shows the square display aperture and **b** shows the circular display aperture. The areas of both apertures in the actual experiment were identical. Note that this is not an exact reproduction (see electronic supplemental material 5)

in Experiment 1. The stimuli and design were similar to Experiment 1 in every other aspect.

Procedure

The procedure for the pigeons was identical to Experiment 1 except that we only used rotational motion, and the manipulated variable was the shape of the aperture: circular or square (Fig. 6). The order of the two conditions was counterbalanced across birds.

Results and discussion for Experiment 2

Figure 7a shows the mean percentage correct for each aperture shape plotted as a function of coherence level. Figure 7b shows the mean detection threshold of each motion pattern. A paired t test revealed that the difference in performance between the two aperture shapes did not differ significantly [$t(3) = 1.48$, $p = .23$].

The result from Experiment 2 suggests that the greater sensitivity of pigeons to rotational motion was not due to an artifact of the shape of the aperture. While Experiment 2 controlled the shape of the aperture to address the higher sensitivity of rotational motion, it is unclear whether the lower sensitivity of pigeons to radial motion, relative to rotation, is due to the characteristics of the rotational and radial motion patterns. The rotational motion used in Experiment 1 is a motion pattern that can be generated by rotational optic flow from self-motion or by object motion in the environment. However, the radial motion from Experiment 1 (i.e., radial motion with constant linear velocity) cannot be generated by self-motion or object motion. To control for this difference, we conducted Experiment 3 to investigate whether the lower sensitivity of the pigeons for radial motion in Experiment 1 was not due to the fact that the animal never encounters radial motion with constant linear velocity. The radial motion from Experiment 3 used an increasing linear velocity (in expansion; decreasing in contraction), akin to what an animal would encounter in nature (Gibson 1954).
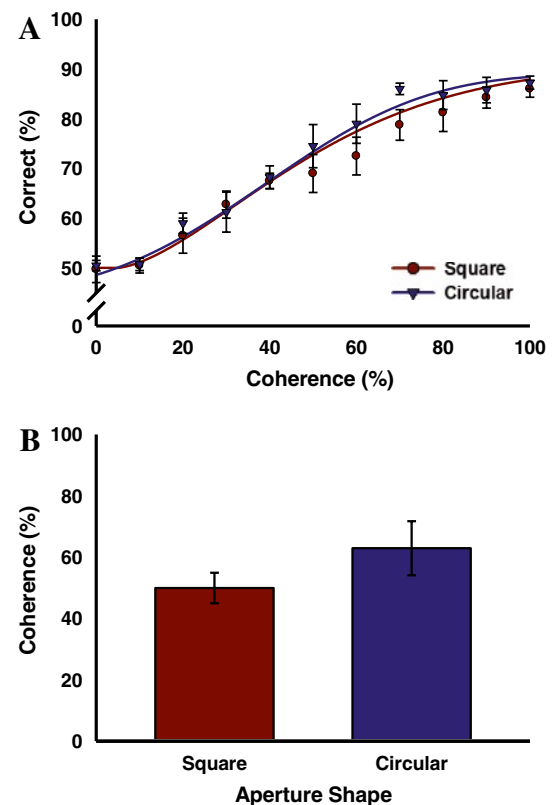

Fig. 7 a Represents the percent correct as a function of coherence level for each aperture shape. *Lines* represent the Weibull function fit for each pattern type; *markers* represent the observed mean percentage correct. **b** Represents the estimated threshold (coherence level corresponding to 75 % correct) for each aperture shape. *Error bars* represent the standard error of the mean

Experiment 3

Method

Four pigeons with previous unrelated touch screen experience served as subjects for Experiment 3. Housing and feeding protocols were the same as in Experiments 1 and 2.

Apparatus, stimuli, and design

The apparatus was the same as in Experiment 1. In one condition, the stimuli consisted of radial motion with dots moving at a constant linear velocity of 42.93°/s. In the second condition, we used radial motion with dots increasing speed with eccentricity (see electronic supplemental material 6). Here dots moved at a curvilinear speed such that as dots moved further from the origin, speed increased. Importantly, the average speed of the dots was equal that of the constant linear velocity condition.

Results and discussion for Experiment 3

Figure 7a shows the accuracy for each condition plotted as a function of coherence level. Figure 7b shows the mean detection threshold of each radial motion condition. A paired *t* test found that the pigeons performed better on the radial motion with accelerating dots as opposed to radial motion with constant linear velocity, $t(3) = 3.28$, $p = 0.046$ (Fig. 8).

The result of Experiment 3 shows that the pigeons are more sensitive to radial motion when there is a nonlinear acceleration as opposed to a constant velocity. This may be because optic flow consists of elements that move with a nonlinear acceleration as the animals move in the environment (Gibson 1954). Thus, the pigeon visual system may be more sensitive to this naturalistic motion pattern. However, it should be noted that Edwards and Ibbotson (2007) showed that humans have lower thresholds for radial motion when there is a constant velocity. Nonetheless, even with the accelerating dots, the thresholds of the pigeons did not match those found for rotational motion. As shown in Fig. 9, they instead were comparable to those of spiral motion in Experiment 1.

Discussion

Our results indicate that humans and pigeons differ in their ability to detect complex motion. Specifically, we found that pigeons were more sensitive to rotational motion than to radial or spiral motion. Humans, on the other hand, were more sensitive to both radial and rotational motion than to spiral motion. We also noted a higher sensitivity for contraction compared to expansion in the radial motion condition and to clockwise contraction compared to counter-clockwise expansion in the spiral motion. Experiment 2 demonstrated that the superior detection for rotational motion by pigeons was not an artifact of the shape of the display aperture. In Experiment 3, we found that pigeons were better at detecting radial motion that contained elements moving with a nonlinear acceleration, although the thresholds did not reach the levels found for rotational motion.
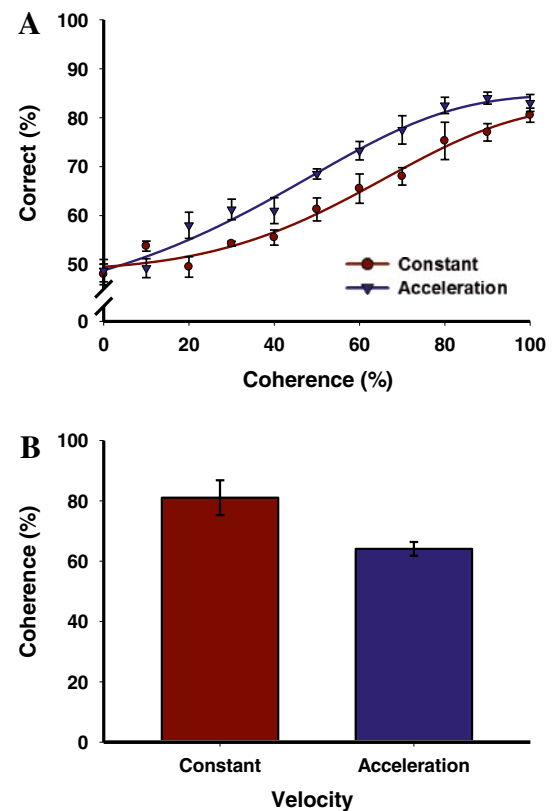
Fig. 8 **a** Represents the percent correct as a function of coherence level for each velocity types. *Lines* represent the Weibull function fit for each pattern type; *markers* represent the observed mean percentage correct. **b** Represents the estimated threshold (coherence level corresponding to 75 % correct) for each velocity types. *Error bars* represent the standard error of the mean
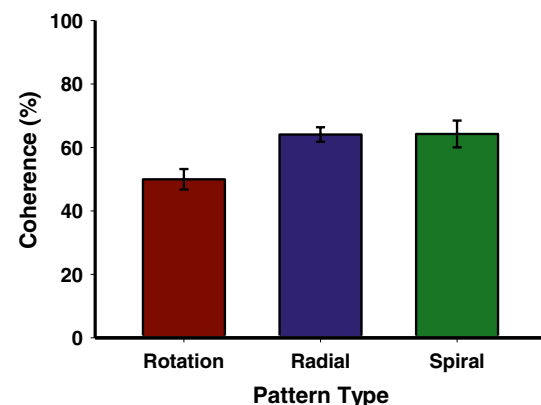
Fig. 9 The estimated threshold (coherence level corresponding to 75 % correct) for rotational and spiral motion from Experiment 1, and radial motion with accelerating velocity from Experiment 3 are shown. *Error bars* represent the standard error of the mean

Neuroimaging studies have shown that the human homologue of MT/MST, respond to complex motion (Huk et al. 2002; Morrone et al. 2000; Pitzalis et al. 2010).

Furthermore, Morrone et al. (1999) and Burr et al. (2001) demonstrated that humans are more sensitive to rotational and radial motion relative to spiral motion. These findings show that the primate visual system has the neural equipment to process complex motion, and it is most efficient at pooling signals along either a rotational or radial trajectory.

While there are many studies that probe the primate motion system, relatively little is known about the avian motion system, especially with respect to motion integration. Here, we provide evidence that the avian visual system is particularly sensitive to global rotation, but not radial and spiral motion. In other words, the pooling mechanism in the pigeon visual system is most efficient for motion along a rotational trajectory. This fundamental difference in global motion sensitivity is interesting as it raises the question as to why this difference exists. Global radial motion is generated during translational movement of the organism and is used to estimate heading (Gibson 1954; Warren 2004). Thus, radial pattern from optic flow is an important cue for visually dependent mobile animals. Optic flow components (i.e., radial, rotation, and translation) are processed in the AOS, a subcortical visual pathway found in all vertebrates (Simpson 1984). In the primate visual system, there are multiple connections between the AOS and MT/MST (Boussaoud et al. 1992; Distler and Hoffmann 2001), which suggests that the complex motion detectors in MST are involved in processing optic flow patterns. In the pigeon brain, cells in the AOS respond to radial optic flow as well as rotation optic flow (for recent reviews, see Wylie 2013, and Wylie and Iwaniuk 2012). Thus, it is surprising that the pigeon visual system is less sensitive to radial motion given the importance of radial motion as a self-motion cue and given that the mechanisms are in place for the pigeon visual system to process both radial and rotation global motion. However, one explanation for this is that our stimuli did not engage the AOS because our stimuli were of higher velocities to the preferred speed (i.e., 0.05–5°/s) of cells in the AOS. The AOS is specialized for large field slow moving motion resulting from self-motion (Frost 1985), although there are some cells responsive to higher velocities (Crowder and Wylie 2001; Wylie and Crowder 2000). Therefore, it is possible that our stimuli were interpreted as moving objects, as opposed to optic flow. The higher sensitivity for rotational motion may be specific to movement of objects in the environment as opposed to optic flow resulting from self-motion.

One interesting line of research has shown that circular trajectories of local motion are an important cue for identifying point-light walkers (see Troje and Chang 2013 for a review). Specifically, the research shows that humans may use the circular motion of the feet (termed rolling wheel), to identify biological movement, and provide facing direction. While Troje and Aust (2013) have noted that pigeons

do not appear to use this local rolling wheel cue, it does highlight the functional advantages of having specialized complex motion detectors that are independent from the optic flow system. Thus, one can hypothesize that the sensitivity to global circular motion in pigeons may serve critical functions such as identifying body direction of other flying animals with respect to gravity.

Object motion in pigeons is processed primarily in the tectofugal pathway, where information from the retina is sent to the optic tectum before reaching the nucleus rotundus (nRT) and finally the entopallium (see Hellmann et al. 2004; Wylie and Iwaniuk 2012, for review). Information in the nRT is segregated into regions containing neurons that are responsive to luminance, color, 2D motion, and motion in depth. Cells responsive for motion are found in the ventral, central, and caudal nRT (Wang et al. 1993). The projections from the nRT to entopallium, a telencephalic structure that some researchers have likened to the mammalian extrastriate cortices (Shimizu and Bowers 1999; Shimizu et al. 2010), are topographical. Neurons in the caudal entopallium respond to motion, and lesions to this area cause a deficit in the detection of global translation motion (Nguyen et al. 2004). Cells in the entopallium have a large receptive field and respond to stimuli moving at high velocities of 16–128°/s (Gu et al. 2002). In addition, the entopallium receives input from the visual Wulst, a telencephalic structure that is part of the thalamofugal pathway and that has been shown to respond to local components within plaid patterns but not to the global direction of the pattern (Baron et al. 2007). For these reasons, the entopallium appear to be a likely candidate for motion integration and processing of complex motion and where the rotation sensitivity stems from. Furthermore, the caudal entopallium contains cells that are responsive to looming stimuli (Xiao et al. 2006; Xiao and Frost 2009). Looming stimuli result from approaching objects, whether through movement of the object or through self-motion, as opposed to radial motion which is solely a result of self-motion. This again suggests the specialization of this system for object motion and may also explain the relatively low sensitivity to radial motion that we observed.

The thresholds of the pigeons for radial and spiral motion are also telling. If we assume that these motion patterns were activating the rotation global detectors, we should have observed a higher sensitivity for spiral motion relative to radial motion, as spiral motion is physically more closely related to rotational motion than the radial motion from Experiment 1. Although the results from Experiment 1 suggest that this is the case, it is likely that the reduced sensitivity was due to the fact that radial motion in Experiment 1 consisted of dots moving at a constant linear velocity. However, the radial motion in Experiment 3 contained accelerating dots and was therefore more

similar to spiral and rotational motion from Experiment 1 given that the speed of the dots within these patterns were also dependent on the distance from the center of the pattern. Thresholds for radial motion with accelerating dots in Experiment 3 remained higher than for rotation but were similar to the spiral motion. Therefore, we can surmise that there are other non-rotational detectors that are perhaps less efficient at pooling the local motion signals or fewer in numbers relative to rotation detectors.

Finally, our results also show that in general, pigeons perform poorly, relative to humans, on motion detection tasks. This is congruent with previous research on motion detection (e.g., Bischof et al. 1999). The validity of these results, however, is contentious given that the lack of psychophysical data on stimulus parameters necessary for optimal performance on motion tasks in pigeons. Furthermore, as shown by various researchers (Loidolt et al. 2006; Rubene et al. 2010), the apparatus used to present stimuli has a significant impact on birds' performance in tasks that rely on motion. Therefore, we should be cautious when interpreting the lower overall sensitivity of pigeons relative to humans in motion detection tasks.

It should be noted that Martinoya et al. (1983) reported behavioral data that suggest that there are differences in motion sensitivities when stimuli are presented in the lateral versus the frontal field in pigeons. These differences have been argued to reflect a difference in the anatomy of the pigeon retina (See Güntürkün 2000 for a review). The pigeon retina has two distinct areas: the red field and the yellow field. The red field is located dorsotemporal retina and contains an area of high ganglion cells density known as the area dorealis. The rest of the retina is part of the yellow field and contains the fovea. It has often been argued that the yellow field and the red field subserve different functions. The yellow field is often linked to the detection of motion (e.g., approaching predator), whereas the red field is associated with feeding behavior (e.g., pecking at the ground) (Maldonado et al. 1988; Nye 1973). In our study, the pigeons' movement was not restricted, and given the size of our stimuli, we argue that it is unlikely that the red field was specifically engaged during the task. In addition, the stimuli in our study were presented in the frontal plane, which means that the birds would need to tilt their head backwards to allow the image to project onto the red field. Based on video recordings of the birds, we did not observe any backward head tilts during the experiments.

Here, we have reported that the avian motion system is most sensitive to rotational motion, suggestive of a more efficient pooling mechanism. Furthermore, the bias for rotational motion suggests the presence of global detectors tuned to rotational motion in the pigeon visual system. In addition, based on the evidence, it appears that the rotation global detectors were not involved in processing radial and spiral global motion. Additionally, it is unlikely that these detectors are involved in processing optic flow as has been hypothesized for the detectors in the primate brain.

References

Baron J, Pinto L, Dias MO, Lima B, Neuenschwander S (2007) Directional responses of visual wulst neurones to grating and plaid patterns in the awake owl. Eur J Neurosci 26:1950–1968

Bischof WF, Reid SL, Wylie DR, Spetch ML (1999) Perception of coherent motion in random dot displays by pigeons and humans. Percept Psychophys 61:1089–1101

Boussaoud D, Desimone R, Ungerleider LG (1992) Subcortical connections of visual areas MST and FST in macaques. Vis Neurosci 9:291–302

Britten KJ, van Wezel RJ (1998) Electrical microstimulation of cortical area MST biases heading perception in monkeys. Nat Neurosci 1:59–63

Burr DC, Thompson P (2011) Motion psychophysics: 1985–2010. Vis Res 51:1431–1456

Burr DC, Badcock DR, Ross J (2001) Cardinal axes for radial and circular motion, revealed by summation and by masking. Vis Res 41:473–481

Butler AB, Hodos W (2005) Comparative vertebrate neuroanatomy: evolution and adaptation, 2nd edn. Wiley-Liss, New York

Chaves LM, Hodos W, Gunturkun O (1993) Color-reversal learning: effects after lesions of thalamic visual structures in pigeons. Vis Neurosci 10:1099–1107

Crowder NA, Wylie DR (2001) Fast and slow neurons in the nucleus of the basal optic root in pigeons. Neurosci Lett 304:133–136

Dakin SC, Bex PJ (2002) Summation of concentric orientation structure: seeing the Glass or the window? Vis Res 42:2013–2020

Distler C, Hoffmann K-P (2001) Cortical input to the nucleus of the optic tract and dorsal terminal nucleus (NOT-DTN) in macaques: a retrograde tracing study. Cereb Cortex 11:572–580

Duffy CJ, Wurtz RH (1991) Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. J Neurophysiol 65:1329–1345

Edwards M, Badcock DR (1993) Asymmetries in the sensitivity to motion in depth: a centripetal bias. Perception 22:1013–1023

Edwards M, Ibbotson MR (2007) Relative sensitivities to large-field optic-flow patterns varying in direction and speed. Perception 36:113–124

Frost BJ (1985) Neural mechanisms for detecting object motion and figure–ground boundaries contrasted with self-motion detecting systems. In: Ingle D, Jeannerod M, Lee D (eds) Brain mechanisms and spatial vision. Nijhoff, Dordrecht, pp 415–419

Geesaman BJ, Andersen RA (1996) The analysis of complex motion patterns by form/cue invariant MSTd neurons. J Neurosci 16:4716–4732

Gibson JJ (1954) The visual perception of objective motion and subjective movement. Psychol Rev 64:304–314

Glass L (1969) Moire effect from random dots. Nature 223:578–580

Graziano MS, Andersen RA, Snowden RJ (1994) Tuning of MST neurons to spiral motions. J Neurosci 14:54–67

Gu Y, Wang Y, Zhang T, Wang S-R (2002) Stimulus size selectivity and receptive field organization of ectostriatal neurons in the pigeon. J Comp Physiol A 188:173–178

Güntürkün O (2000) Sensory Physiology: Vision. In: Whittow GC (ed) Sturkie's avian physiology. Academic Press, Orlando, pp 1–19

Hellmann B, Güntürkün O, Manns M (2004) Tectal mosaic: organization of the descending tectal projections in comparison to the ascending tectofugal pathway in the pigeon. J Comp Neurol 472:395–410

Huk AC, Dougherty RF, Heeger DJ (2002) Retinotopy and functional subdivision of human areas MT and MST. J Neurosci 22:7195–7205

Husband S, Shimizu T (2001) Evolution of the avian visual system. In: Cook RG (ed) Avian visual cognition. www.pigeon.psy.tufts.edu/avc/husband/

Lazareva OF, Shimizu T, Wasserman EA (2012) How animals see the world: behavior, biology, and evolution of vision. Oxford University Press, London

Loidolt M, Aust U, Steurer M, Troje NF, Huber L (2006) Limits of dynamic object perception in pigeons: dynamic stimulus presentation does not enhance perception and discrimination of complex shape. Behaviour 34:71–85

Maldonado PE, Maturana H, Varela DJ (1988) Frontal and lateral visual system in birds. Frontal and lateral gaze. Brain Behav Evol 32:57–62

Martinoya C, Rivaud S, Bloch S (1983) Comparing frontal a n d lateral viewing in the pigeon. II. velocity thresholds for movement discrimination. Behav Brain Res 8:375–385

May KA, Solomon JA (2013) Four theorems on the psychometric function. PLoS One 8(10):e74815

Meese TS, Anderson SJ (2002) Spiral mechanisms are required to account for summation of complex motion components. Vis Res 42:1073–1080

Meese TS, Harris MG (2001) Independent detectors for expansion and rotation, and for orthogonal components of deformation. Perception 30:1189–1202

Milner AD, Goodale MA (1995) The visual brain in action. Oxford University Press, Oxford

Morrone MC, Burr DC, Di Pietro S, Stefanelli MA (1999) Cardinal directions for visual optic flow. Curr Biol 9:763–766

Morrone MC, Tosetti M, Montanaro D, Fiorentini A, Cioni G, Burr DC (2000) A cortical area that responds specifically to optic flow, revealed by fMRI. Nat Neurosci 3:1322–1328

Nakayama K (1985) Biological image motion processing: a review. Vis Res 25:625–660

Nankoo J-F, Madan CR, Spetch ML, Wylie DR (2012) Perception of dynamic Glass patterns. Vis Res 72:55–62

Nelder JA, Mead R (1965) A simplex method for function minimization. Comput J 7:308–313

Nguyen AP, Spetch ML, Crowder NA, Winship IR, Hurd PL, Wylie DRW (2004) A dissociation of motion and spatial-pattern vision in the avian telencephalon: implications for the evolution of "visual streams". J Neurosci 24:4962–4970

Nye PW (1973) On the functional differences between frontal and lateral visual fields of the pigeon. Vis Res 13:559–574

Pelli DG, Farell B (1999) Why use noise? J Opt Soc Am A 16:647–653

Pitzalis S, Sereno MI, Committeri G, Fattori P, Galati G, Patria F, Galletti C (2010) Human V6: the medial motion area. Cereb Cortex 20:411–424

Quick RF (1974) A vector-magnitude model of contrast detection. Kybernetik 16:65–67

Rubene D, Håstad O, Tauson R, Wall H, Odeen A (2010) The presence of UV wavelengths improves the temporal resolution of the avian visual system. J Exp Biol 213:3357–3363

Saito H, Yukie M, Tanaka K, Hikosaka K, Fukada Y, Iwai E (1986) Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. J Neurosci 6:145–157

Scase MO, Braddick OJ, Raymond JE (1996) What is noise for the motion system? Vis Res 36:2579–2586

Shimizu T, Bowers AN (1999) Visual pathways in the avian telencephalon: evolutionary implications. Behav Brain Res 98:183–191

Shimizu T, Patton TB, Husband S (2010) Avian visual behavior and the organization of the telencephalon. Brain Behav Evol 75:204–217

Shirai N, Kanazawa S, Yamaguchi MK (2006) Anisotropic motion coherence sensitivities to expansion/contraction motion in early infancy. Infant Child Dev 29:204–209

Simpson JI (1984) The accessory optic system. Annu Rev Neurosci 7:13–41

Snowden RJ, Milne AB (1996) The effects of adapting to complex motions: position invariance and tuning to spiral motions. J Cogn Neurosci 8:435–452

Tanaka K, Saito H (1989) Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. J Neurophysiol 62:626–641

Troje NF, Aust U (2013) What do you mean with "direction"? local and global cues to biological motion perception in pigeons. Vis Res 79:47–55

Troje NF, Chang DHF (2013) Shape-independent processes in biological motion perception. In: Johnson KL, Shiffrar M (eds) People watching: social, perceptual, and neurophysiological studies of body perception. Oxford University Press, Oxford, pp 82–100

Ungerleider LG, Mishkin M (1982) Two cortical visual systems. In: Ingle DJ, Goodale MA, Mansfield RJW (eds) Analysis of visual behavior. MIT, Cambridge, pp 549–586

Wall MB, Lingnau A, Ashida H, Smith AT (2008) Selective visual responses to expansion and rotation in the human MT complex revealed by functional magnetic resonance imaging adaptation. Eur J Neurosci 27:2747–2757

Wang YC, Jiang S, Frost BJ (1993) Visual processing in pigeon nucleus rotundus: luminance, color, motion, and looming subdivisions. Vis Neurosci 10:21–30

Warren W (2004) Optic flow. In: Chalupa L, Werner J (eds) The visual neurosciences. MIT Press, Boston, pp 1391–1401

Weibull W (1951) A statistical distribution function of wide applicability. J Appl Mech 18:292–297

Wilson HR, Wilkinson F (1998) Detection of global structure in Glass patterns: Implications for form vision. Vis Res 38:2933–2947

Wylie DR (2013) Processing of visual signals related to self-motion in the cerebellum of pigeons. Front Behav Neurosci 7:4

Wylie DRW, Crowder NA (2000) The spatiotemporal properties of fast and slow neurons in the pretectal lentiformis mesencephali in pigeons. J Neurophysiol 84:2529–2540

Wylie DR, Iwaniuk AN (2012) Neural mechanisms underlying visual motion detection in birds. In: Lazareva OF, Shimizu T, Wasserman EA (eds) How animals see the world: Behavior, biology, and evolution of vision. Oxford University Press, London, pp 289–318

Xiao Q, Frost BJ (2009) Looming responses of telencephalic neurons in the pigeon are modulated by optic flow. Brain Res 1035:40–46

Xiao Q, Li DP, Wang SR (2006) Looming-sensitive responses and receptive field organization of telencephalic neurons in the pigeon. Brain Res Bull 68:322–328