What do you mean with "direction"? Local and global cues to biological motion perception in pigeons

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ABSTRACT

Biological motion point-light displays are a rich and versatile instrument to study perceptual organization. Humans are able to retrieve information from biological motion through at least two different channels: The global articulated structure as revealed by the non-rigid, yet highly constrained deformation of the dot pattern, and the characteristics of local motion trajectories of individual dots. Here, we tested eight pigeons on a task in which they had to discriminate a left-facing from a right-facing biological motion point-light figure. Since the two stimuli were mirror-flipped versions of each other, we were not sure if the birds would be able to solve the task at all. However, all birds learned the discrimination quickly and performed at high accuracy. We then challenged them with a number of test trials introduced into the sequence of the normal training trials. Tested on backwards moving walkers, the majority of the birds indicated that they used local motion cues to solve the training task, while the remaining birds obviously used global, configural cues. Testing the pigeons on different versions of scrambled biological motion confirmed that each individual bird had made a clear decision for one of the two potentially available strategies. While we confirm a previously described local precedence in processing visual patterns, the fact that some birds used global features suggests that even the birds who relied on local cues probably dispose of the perceptual abilities to use global structure, but "chose" to not use them.

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1. Introduction

Biological motion point-light displays have become a versatile tool to study perceptual organization in the human visual system (e.g. Johansson, 1973). Human observers readily derive the articulated shape of a human or animal body from just a few dots moving as if attached to the major joints of the body. Even though the motion underlying moving dot displays is clearly non-rigid, it still supports a coherent, global interpretation based upon the "common fate" of the individual dots which all belong to the same body as it undergoes coordinated intrinsic deformation. The interpretation in terms of an articulated body reveals the shape of the body at any point in time which can then be interpreted with respect to the identity of the actor and the nature of the action (Troje, 2002, 2008; Troje & Chang, 2013). Specifically, the retrieval of motion-mediated shape provides a critical cue for one of the most popular tasks used to assess biological motion perception: Determining the direction into which a stationary walker (as if on a treadmill) shown in sagittal view is facing (Cutting, Moore, & Morrison, 1988).

However, point-light displays may also contain information that is independent of global motion-mediated shape. Working with scrambled walkers, Troje and Westhoff (2006) showed that observers can still assign the correct facing direction to "walkers" that are deprived of any sort of coherent shape, and it has further been shown that the critical cues by which this is accomplished are contained in specific characteristics of the local motion of the feet (Chang & Troje, 2009a, 2009b; Troje & Chang, 2013). The visual filters that respond to these cues seem to be already present at birth, at least to some degree (Simion, Regolin, & Bulf, 2008). Visually inexperienced chickens already show a preference for biological motion over random motion – independently of the particular shape of the point-light display (Vallortigara, Regolin, & Marconato, 2005), but specific to its orientation (Vallortigara & Regolin, 2006) – findings that point to an evolutionarily old origin and a functional significance that goes beyond simply determining facing direction of a stationary walker (Johnson, 2006). It has been suggested that the invariants that signal facing direction in biological motion are more generally used to detect the presence of an articulated, terrestrial animal and it has been shown that they do in fact predict perceived animacy of a point-light stimulus (Chang & Troje, 2008; Troje & Chang, 2013).

The degree to which these local motion cues are used by the human visual system depends on additional properties which in

themselves are not direction specific. One of these validating properties is the vertical acceleration pattern of the foot trajectory and whether or not it is compatible with gravitational acceleration (Chang & Troje, 2009a). A second validating cue is the vertical location of the dots representing the feet and whether or not they are at their expected location below the rest of the display (e.g. Hirai, Saunders, & Troje, 2011b; Troje & Chang, 2013).

Studies on the ability of non-human species to learn and discriminate moving point-light patterns are sparse, despite the important implications they may have for the evolution of visual processing as well as for current theories of both animal and human cognition. One example was provided by Blake (1993), who reported that cats could discriminate between biological and non-biological motion in point light displays of cats. In a different study, rats were shown to be able to discriminate between a left-facing and a right-facing point-light walker at moderate rates, but were not able to generalize from a human walker to a point-light cat. Confronted with backwards moving walkers, they also responded randomly (MacKinnon, Troje, & Dringenberg, 2010). Dittrich et al. (1998) showed that pigeons could be trained to discriminate between two different pigeon movement categories (pecking and walking) presented as point-light displays, and (Ryan et al., 2001) extended this result to chickens. The same authors also found transfer from normally rendered video scenes to point-light displays of the same movement categories and vice versa. This result suggests that the information preserved in point-light displays – either motion-mediated shape, or asymmetries contained in the local motion of individual parts of the body – must have played a role even in the discrimination of the video displays (see also Dittrich & Lea, 2001). Evidence of whether pigeons are also able to determine the facing direction of a stationary walking point-light figure, as has been shown for humans, is still missing. However, recent work employing three-dimensionally rendered computer graphics models of animals as stimuli shows that pigeons can discriminate actions (in this case walking from running) and that this ability generalizes not only to new animals but also to new facing directions (Asen & Cook, 2012).

In the experiment reported here, we tested the ability of pigeons to distinguish between two stationary point-light walkers shown in sagittal view and facing either to the left or to the right. The main questions we investigated were: (1) Would pigeons learn the discrimination at all, and, if so, (2) would their decision be based on local or global information? Both issues require closer consideration.

(1) A number of studies have reported that when tested on visual form discrimination pigeons are highly invariant with respect to the orientation of an object in the image plane (e.g. Delius & Hollard, 1987, 1995; Hollard & Delius, 1982; Lombardi, 1986). This good generalization performance, however, seems to come at the expense of a poor ability to discriminate between objects that differ only in orientation. Although not undisputed in the literature (e.g. Hamm, Matheson, & Honig, 1997), there are ample reports that pigeons have difficulties discriminating between forms that differ only in their handedness, that is, forms that are mirror images of each other (Lohmann et al., 1988; Mello, 1965; Mello, 1966a, 1966b; Thomas, Klipec, & Lyons, 1976; Todrin & Blough, 1983). For instance, in the study by Lohmann et al. (1988) pigeons found forms that were mirror images of each other more difficult to distinguish than otherwise similar forms, and mirror images were also shown to be less discriminable than upside-down versions of the stimuli. Confusion of mirror images has also been documented in other species, including humans (for a review, see Corballis &

Beale, 1976), but generally, discriminating mirror images seems to be a more difficult task for pigeons than for humans. This difference has often been interpreted in terms of different bioevolutionary adaptations to the primary planes on which the two species operate visually (vertical in humans vs horizontal in pigeons, Delius & Hollard, 1995; Hollard & Delius, 1982).

(2) The second aspect of pigeon vision that was examined in the present experiment concerned local versus global processing. Should pigeons indeed be able to discriminate facing direction in a point-light walker, would their decision be based on global, dynamic, motion-mediated shape, or on the local motion of individual dots? Since Cerella (1980) demonstrated in his seminal study that pigeons focused on local elements of line drawings showing cartoon characters rather than on the overall configuration, it has become a widely accepted assumption that pigeons' visual processing is primarily based on local features while global properties are less important. Indeed, such a "local precedence effect" has subsequently been shown for pigeons in a number of studies (e.g. Cavoto & Cook, 2001; Gibson et al., 2005). However, solid evidence has also emerged that pigeons attend to configural (i.e., global) cues, and that the latter can be critical under appropriate experimental conditions (e.g. Aust & Huber, 2003; Wasserman et al., 1993) (for reviews, see Cook, 2001; Vallortigara, 2004). It seems that in pigeons both local and global information can guide response behavior and that they are able to flexibly switch attention between these levels of processing (Cook, 2001; Fremouw, Herbranson, & Shimp, 1998, 2002; Shimp et al., 2006). Which level will eventually come to control responding in a specific task seems to depend on a number of factors, including attentional factors controlled by the history of reinforcement, and stimulus factors such as feature salience, configural organization, and viewing distance (Cook, 2001; Goto, Wills, & Lea, 2004; Watanabe, 2011). The part of the visual field within which a stimulus is projected might also play a role. The retina of the pigeon contains two foveae (Binggeli & Paule, 1969). The so-called red field of the area dorsalis points into the frontal, binocular field of view and the yellow field of the area centralis into the lateral field of view (Nye, 1973). The projections of these areas into the visual brain diverge strongly and their processing properties are probably quite different. It has been suggested that information from the lateral field of view undergoes more global processing than information from the frontal field of view (Martinoya, Rivaud, & Bloch, 1983).

An interesting yet widely unexplored question concerns the relation between global versus local attention modes in the context of motion perception. Motion is likely to be a factor that influences the type of control—local or global—exhibited in complex stimulus discrimination tasks. First, as put forward by the Gestalt principle of Common Fate, common motion serves the important function of binding features together (Johansson, 1973). Second, it has been suggested that stimuli shown in motion will offer more opportunities for encoding information than static presentation (Pike et al., 1997). Therefore, it is not implausible to expect that the coherent motion of separate stimulus properties may lead to the perception of larger, more object-like units (Cook, 2001). In short, motion may facilitate global processing.

In the present experiment we confronted the birds with tasks that could be either solved by means of recovering motion-mediated global structure, or by means of differentiating local motion patterns. Testing pigeons with walkers that were temporally

reversed (that is, walkers that walked backwards) introduces a condition in which the two cues are in conflict with each other as they point into opposite directions (Test 1).

Next, we tested the pigeons with scrambled biological motion (Test 2). If they used local motion rather than the global shape of the point-light walker to discriminate its walking direction, they should be able to do that with scrambled motion, too. On the other hand, if they relied on motion-mediated shape, they should not be able to determine the walking direction in scrambled point-light displays.

In humans, as discussed above, the ability to use local motion for direction discrimination depends strongly on two validating cues which in themselves do not provide directional information (Hirai et al., 2011b): Whether or not the vertical acceleration pattern con-forms with the orientation specificity of gravity, and whether or not the location of the dots carrying directional information below the rest of the display (that is, at a location where the feet are expected to be). If pigeons respond to the same cues, the orientation (upright or inverted) of the scrambled point-light displays should affect their performance, and the location of the dots representing the feet should have an effect, too (Tests 2 and 3).

2. Materials and methods

2.1. Subjects

Eight homing pigeons (*Columba livia*) were used. All animals had been acquired from local pigeon breeders who kept racing pi-geons. At the outset of the experiment most of the animals had al-ready lived in our pigeon colony for more than 2 years but had not participated in other experiments during this time. Pigeons were housed individually during the duration of the experiment. We restricted food such that all pigeons maintained 90% of their free-feeding weight. Pigeon participated in experiments in the mornings, were then weighted, and received food in the afternoon if they had not eaten enough during the experimental session. Water and grid were provided *ad libitum* at all times. All proce-dures had been approved by the local Animal Care Committee.

2.2. Apparatus

The pigeons were trained and tested in custom made Skinner boxes with a length of 51 cm, a width of 31 cm, and a height of 42 cm. Each box was equipped with a 15″ IR touch screen, a food hopper right in front of it, a house light, and a loudspeaker. The screens were LCD screen with a refresh rate of 80 Hz. All stimuli were generated and presented using Matlab in conjunction with the Psychophysics Toolbox (Brainard, 1997). This system allowed us to synchronize stimulus generation with the screen refresh rate for accurate timing and smooth, frame-accurate motion.

2.3. Stimuli

For autoshaping and the initial discrimination training simple shapes (disk, square, triangle, cross, arrow, diamond), shown as white silhouettes on a black background, were used as stimuli. The diameter of each of the shapes was about 2.5 cm (see Fig. 1).

Point-light displays used in the main experiment were based on two different sequences: A walking human and a walking pigeon (Fig. 1). The human walker was created by averaging motion cap-ture data obtained from 100 individuals and represents a generic, average walking pattern (Troje, 2002, 2008). It was rendered with 11 dots representing the major joints of the body (two ankles, two knees, one hip, one shoulder, two elbows, two wrists) and the cen-tre of the head and was always shown in profile view (either facing to the left or to the right). The pigeon also consisted of 11 dots (three on the head, four on the body, and two on each foot). Trans-lation was subtracted such that the walkers (human and pigeon) remained stationary, as if they were moving on a treadmill. Dots were white on a black background and each had a diameter of 1 mm (3 × 3 pixels). The whole point-light displays were about 6 cm high. The human walker had a width of 2.5 cm, the pigeon was 4 cm wide. Both human and pigeon were played back at their veridical walking speeds, which was 0.94 Hz for the human and 1.56 Hz for the pigeon.

A number of point-light stimuli were derived from these two sequences. For the backwards sequences used as test trials in Test 1, we simply played them backwards. For the scrambled walkers used in Test 2, we displaced each dot's trajectory to a randomly chosen location within the area covered by the original display. The trajectories themselves where not changed for the upright scrambled displays, but were mirror-flipped about a horizontal axis for the inverted versions. The stimuli for Test 3 were identical to the ones for Test 2 except that the dots representing the feet re-tained their original location at the bottom of the display. For the inverted version, the individual trajectories of all dots (including
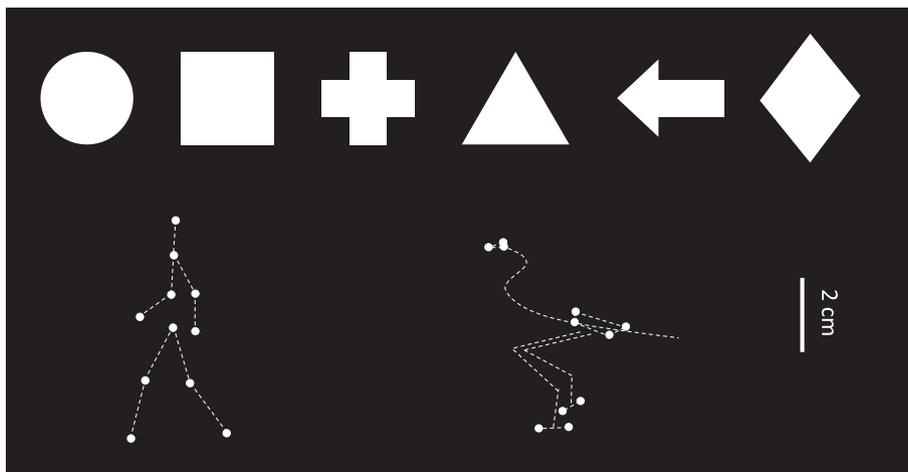

Fig. 1. *Stimuli.* The upper row shows the static shapes used for the initial training procedure. The lower row shows the two different point-light stimuli (human and pigeon) used for training and also as a basis for all test stimuli. Only the left-facing versions are shown. The dotted lines were not shown to the pigeons and are provided here only to illustrate the articulated shape of the two displays. The scale on the right (not a part of the stimuli) applies to both static shapes and point-light displays.

the ones representing the feet) were inverted, but the location of the dots representing the feet remained at the bottom of the display (Fig. 2).

All stimuli (the static shapes employed during pretraining as well as the point-light displays shown in the main experiment) were presented such that their centers were at a height of 6 cm above the floor of the Skinner box. If two displays were shown, then the lateral center-to-center distance between them was 6 cm.

2.4. Procedure

2.4.1. Pretraining
2.4.1.1. Autoshaping. Training started with a standard autoshaping procedure which was used to train pigeons to peck at a single disk that appeared on the screen. During this phase of the training, the stimulus remained on the screen a maximum time of 15 s. Then it disappeared and food was presented. If the pigeon pecked on the screen, the stimulus disappeared immediately and food became available. At this stage, the exact time of food presentation and the duration of the following inter-trial-interval varied depending on the behavior and progress of the individual pigeons. Eventually, all pigeons learned that pecking at the disk initiated the presentation of food (mixed grain). Once pigeons started to peck at the disk the control program was switched to a mode in which the stimulus disappeared and the pigeons received food only if they pecked at the disk. During this phase we also fixed feeding time to 4 s and adopted a constant inter-trial-interval of 3 s.

2.4.1.2. Discrimination of two static shapes. Once a pigeon pecked reliably at the single disk, training was switched to a two-choice discrimination task. The same disk was now shown along with a square. The two shapes were displayed side by side with their positions (left or right) varying randomly from trial to trial. Pigeons gained food accesses only after pecking the disk. When they pecked at the square, the screen turned red for a second and a sound was played by the speaker. The following inter-trial-interval was extended by an additional 3 s, and the display was then repeated in the same configuration as before – if necessary, more than once. These "correction trials" were also used in all subsequent training steps and during the final test sessions. Once a pigeon had developed a "routine" and was reliably working, we adopted a schedule with individual sessions containing exactly 40 trials (not counting the correction trials). Initially, birds participated in only one session per day. Later in the experiment, we tested them twice a day with a break of at least on hour between sessions. Training proceeded to the next level after pigeons had learned to peck correctly in 28 out of 40 times in three consecutive sessions.

2.4.1.3. Generalization to other shapes. During this stage, the circle and square were replaced with two other shapes: a cross (rewarded) and a triangle (unrewarded). Once they had succeeded to peck at the correct shape 28 out of 40 trials in three consecutive sessions, stimuli changed again. This time, we showed them the shapes of an arrow and a diamond, with the arrow being the rewarded stimulus. Training proceeded to the final phase once a bird had pecked correctly in 28 out of the 40 trials in three consecutive sessions.

2.4.1.4. Biological motion direction discrimination. Next, pigeons were simultaneously presented with a left-facing and a right-facing point-light display. For four of the birds, the point-light display showed a human walker and for the other four we used a walking pigeon. In each group half of the birds were rewarded for pecking on a right-facing walker and the other half was rewarded for pecking on a left-facing walker. This last training task was applied until pigeons were able to respond correctly in 34 out of 40 trials for three consecutive sessions. All eight birds eventually reached this stage and testing began forthwith.

2.4.2. Main experiment
Test sessions during the main experiment were identical to the previous biological motion discrimination training sessions except that six test trials were added to each session. These were inserted in a randomized fashion into the sequence of training stimuli, avoiding, however, the first trial, and with at least one training trial appearing between two test trials. Test trials were not reinforced. A peck on either of the two simultaneously presented stimuli immediately terminated the trial without being followed by a correction trial or by reward. If pigeons performed worse than 34/40 correct first choices on the training trials, the session was repeated. For each of the five test stimuli and for each bird, we collected data from 20 sessions. In total, each bird was given 600 test trials in 100 sessions. The whole experiment lasted about 6 months. We ran the following test sessions:

Test 1: Each test trial contained a pair of backwards moving walkers. One of them was facing left (but moving as if going to the right), and the other one was facing right (but moving as if going to the left).
Test 2: Here, we tested pigeons with fully scrambled walkers. Each test trial contained scrambled point-light displays created
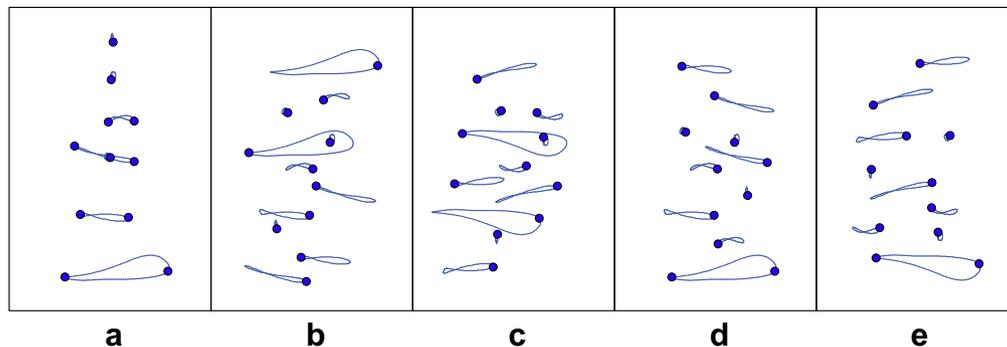

Fig. 2. *Scrambled biological motion.* The figure illustrates how the different scrambled point-light displays were derived (shown only for the human figure). (a) Unscrambled walker. The dots indicate the same posture depicted in Fig. 3, lower left. The lines trace their trajectories. Note that the trajectories of dots representing symmetric locations of the body (e.g. left and right foot) coincide in the lateral projection. (b) Upright scrambled version of the same point-light display. The individual trajectories were randomly displaced within the area covered by the whole display. (c) Inverted scrambled point-light display. Each individual trajectory was mirror-flipped about a horizontal axis before being randomly displaced within the display area. (d) Upright scrambled with feet in place. Same as (b) but the trajectories representing the feet remained at their original location. (e) Inverted scrambled with feet in place. Same as (c) but the trajectories of the feet, even though locally inverted, retained their location.

from a left and a right-facing walker. We also tested birds on the inverted versions of the scrambled walker with upright and inverted versions appearing on alternate sessions. Test 2 therefore consisted of 40 sessions.

Test 3: Same as Experiment 2, but here we kept the location of the feet intact while scrambling the location of all other dots. Again, upright and inverted versions were shown for a total of 40 sessions.

2.5. Data analysis

With only eight birds and interesting inter-individual differences between them, and a substantial number of data collected from each of them, it appeared reasonable to conduct data evaluation and both descriptive and inferential statistics for individual birds rather than on a group level. Thereby, the random factor was the session and the independent variable was the percentage of correct first responses either for the training trials or for the test trials. Correction trials did not enter analyses. We conducted t-tests to test for significant difference from random pecking across sessions, and a two-factor ANOVA for a combined analysis of Tests 2 and 3.

In order to estimate significance in performance within individual sessions, we conducted binomial tests. For performances at and above 26/40 correct responses the Type I error probability becomes smaller than 5%. For performances at and above 28/40 correct responses the Type 1 error gets smaller than 1%.

3. Results

3.1. Discrimination of static shapes and biological motion direction discrimination

All pigeon succeeded in learning the static shape discrimination task. The fastest bird (Ducky) required 28 sessions of different shape discriminations until it reached the criterion required to proceed to presenting point-light displays. The slowest bird (Maria) required 41 sessions.

Transition from the last pair of static shapes to the pair of point-light figures (one facing left and the other facing right) did not seem to pose any additional problem to the birds. Indeed, it did not take them more than a few sessions to discriminate the two point-light patterns at above chance level (binomial test, $p(26/40) < 0.05$, $p(28/40) < 0.01$)) (Fig. 3). However, the birds needed additional training to achieve criterion performance required as a prerequisite for the introduction of test trials (34/40 correct responses in three consecutive sessions). The fastest bird (Claudia) reached criterion performance after 36 sessions and the slowest bird (Juliet) after 65 sessions.

No systematic differences were apparent between the birds that were trained to discriminate human walkers and the birds that had been trained to discriminate point-light displays of pigeons. Even though striking inter-individual differences were revealed, these could not be attributed to the use of the two different point-light walkers (pigeons and humans).

The horizontal lines in the diagrams of Fig. 4 show the performance in the training trials for each bird averaged over all 100 sessions that constituted Tests 1–3. The bird with the worst performance was Maria with 87% correct responses, the best one was Ophelia who pecked correctly in 98.5% of all 4000 training trials contained in the 100 test session.

In summary, all birds mastered the task to discriminate between left and right-facing point-light walkers at exceptionally high performance levels. Recall that the only difference between the two point-light displays is a mirror-flip about the vertical axis. Clearly, the pigeons were able to discriminate between them.
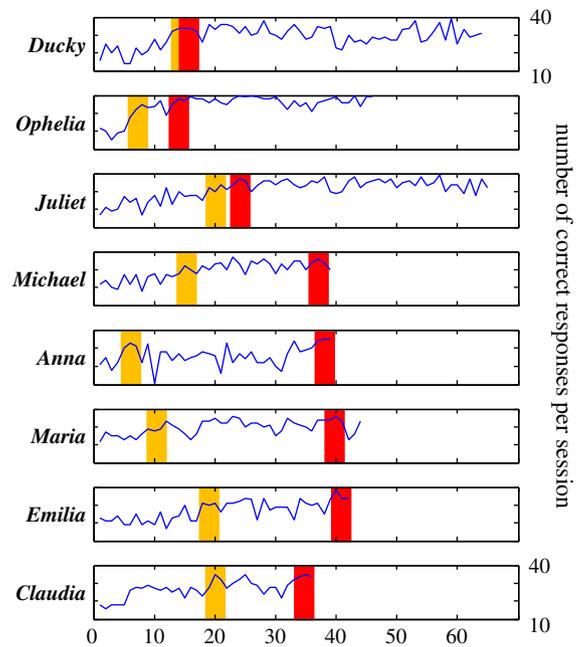

Fig. 3. *Time course of performance of the individual birds during training.* Starting with the first and ending with the last session of the point-light direction discrimination training we plotted the number of correct pecks in response to the first appearance of the stimulus within a trial (i.e., correction trials are not counted). The orange bar indicates when they first pecked correctly in three consecutive sessions at least 28/40 (binomial test, $p < 0.01$) times. The red bar indicates when they first reached the required criterion of 34/40 correct in three consecutive sessions. The first four birds were presented with human point-light walkers, and the following four birds with point-light displays of walking pigeons. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Putting local and global cues into conflict (Test 1)

In the first set of 20 test sessions, all test trials showed walkers that were walking backwards. One of the two walkers was facing left but was walking right, while the other one was facing right while walking to the left. Recall that walking was stationary, that is, there was no translation of the walkers across the screen.

The first bar of each panel in Fig. 4 shows the rate of correct responses for each bird. "Correct" was defined in terms of the direction into which the walker was facing. Two sided t-tests showed that all birds responded significantly different from chance level ($p < 0.01$ for Emilia, and $p < 0.001$ for all other birds).

Six out of the eight birds responded to local motion rather than to global shape. Only Emilia and Claudia had "correct" response rates larger than 50% – indicating that they were responding to the global, motion-mediated shape of the point-light display.

3.3. Upright and inverted scrambled biological motion (Test 2)

The six birds that had demonstrated in Test 1 that they had based their direction discrimination responses in the training on local rather than global information were all able to discriminate direction both in the upright (second bar) and in the inverted (third bar) scrambled condition (t-test, $p < 0.05$) – with one exception: Ducky's performance in the scrambled, inverted condition did not reach significance (Table 1 and Fig. 4). Inversion effects measured in terms of the difference in performance between upright and inverted stimuli were relatively weak. In only two of the six birds (Ducky and Juliet) did we observe significantly higher performance in the upright condition. In one bird (Maria), the inverted stimulus seemed to be easier to process.
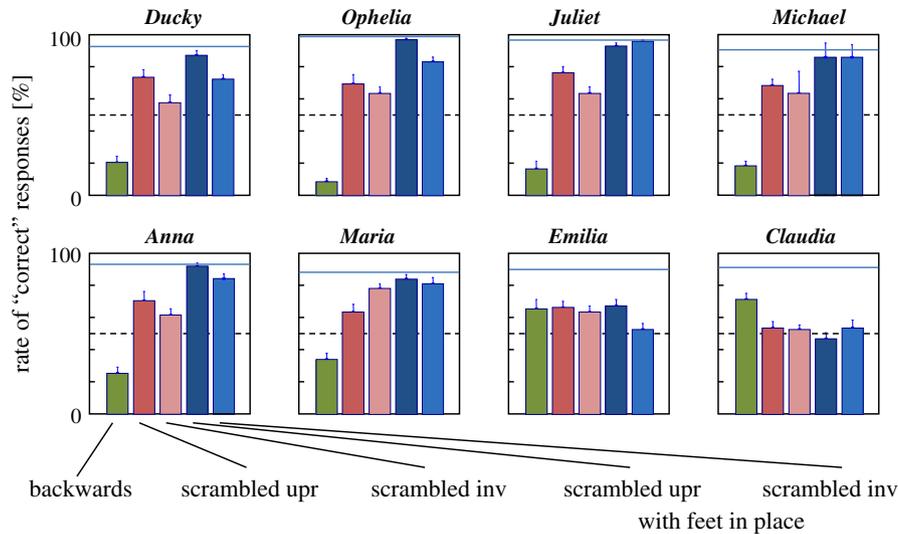
Fig. 4. *Performance during testing.* The solid horizontal lines indicate performance in the training trials in terms of the percentage of correct responses to the first presentation of each trial (not counting correction trials) for each bird averaged over all 100 sessions that constituted Tests 1–3. Bars indicate performance on the various types of test stimuli, again shown as percentage of correct first choices. *Test 1:* Backwards. *Test 2:* Scrambled upright and scrambled inverted. *Test 3:* Same as Test 2, but with the feet kept in place. Error bars indicate standard error of the mean ($n = 20$). The four birds whose results are shown in the upper row had been presented with human point-light walkers, and the four birds in the lower row with point-light displays of walking pigeons.

Table 1
Descriptive and inferencial statistics for individual birds. The upper part lists the rates of correct first answers (in percent) during the three tests as well as the differences in the rates for upright and inverted displays in Tests 2 and 3. The number of sessions in Test 1 was 20 per bird. Tests 2 and 3 consisted of 40 sessions each. The lower part lists F-values obtained from a 2-factor ANOVA for the two main effects and the interaction. Degrees of freedom are always 1 for the numerator and 76 for the denominator of the F-fraction. Colours encode Type I error probabilities. For the upper part of the table they are based on two-tailed, unpaired t-tests, testing either for differences from chance level, or for the difference between the two conditions in Tests 2 and 3. For the lower part of the table the colours are based on the Type I error computed by the ANOVA. Yellow: $p < 0.05$; orange: $p < 0.01$; red: $p < 0.001$.

	Ducky	Ophelia	Juliet	Michael	Anna	Maria	Emilia	Claudia
Test								
training	88	96	90	88	87	85	87	86
backward	21	09	17	19	26	35	67	73
Test 2								
training	94	99	96	92	91	84	89	88
scrambled up	75	71	78	70	72	65	68	55
scrambled inv	59	65	65	65	63	80	65	54
up - inv	16	06	13	05	09	-15	03	01
Test 3								
training	93	99	97	90	94	91	90	92
up, feet down	89	99	95	88	94	86	69	48
inv , feet down	74	85	98	88	86	83	54	55
up - inv	15	14	-03	01	08	03	15	-08
ANOVA								
Inversion	13.35	7.37	2.68	0.675	5.05	2.2	5	0.67
Feet	11.94	43.01	66.93	33.081	34.6	8.814	1.489	0.67
IxF	0.01	1.28	6.023	0.34	0.011	5.441	2.026	1.05

From the two birds that had indicated to use structural cues to direction in Test 1, one bird (Claudia) failed entirely in Test 2. The other bird (Emilia) performed at 67% correct responses – worse than the other birds, but still statistically different from chance level. Neither Emilia nor Claudia showed an inversion effect.

3.4. Upright and inverted scrambled biological motion with the feet kept in place (Test 3)

While all the birds that had indicated to use local motion cues in Test 1 were able to discriminate the direction of scrambled point-

light walkers, their performance was much lower than for the coherent stimuli used in the training trials. We therefore wondered if the location of the feet within the display—which seems to affect their usage as a cue to direction in humans—would also modify the pigeons' behavior.

The results of Test 3 seem to indicate that this was indeed the case (Fig. 4). Of the six birds that had indicated using local cues in Test 1, all reached performances above 80% correct on average over upright (forth bar) and inverted versions (fifth bar) of the displays. Juliet showed the highest performance with 96%. An inversion effect was manifest in three of the six birds, though it was very weak in one of them (Anna).

Claudia who had indicated in Test 1 to use configural cues and failed to discriminate the stimuli of Test 2, also performed at chance level in Test 3. Emilia, who had also chosen the configural cue in the conflict situation of Test 1, showed weak, yet statistically significant performance in the upright condition, but fell back to chance level in the inverted condition. In this case the inversion effect was significant.

3.5. Combined analysis of Tests 2 and 3

In order to compare the results of Tests 2 and 3 more directly we conducted an ANOVA with factors "inversion" and "foot location" separately for each bird. Again, we first look at the data from the six birds that had indicated the use of local cues in Test 1.

Consistent with the above analyses a significant main effect of "inversion" was found only in three of the six birds (Table 1). These birds performed better for upright than for inverted stimuli.

The main effect of factor "foot location" came out highly significant in all six birds. All of them performed much better when the feet were located at the bottom of the display as compared to a random location of the fully scrambled condition.

Moderate interactions between the two factors were observed in two cases (Juliet and Maria). In both cases, they were due to the absence of inversion effects in the condition in which the feet maintained their location – a tendency that can also be seen in some of the other birds (Anna and Michael).

By contrast the two birds that had indicated in Test 1 that they responded to the global shape of the point-light stimuli did not show any effect of the location of the feet. Emilia showed a moderate inversion effect driven mainly by the results of Test 3. No such effect was observed for Claudia who remained at chance level in all four condition.

4. Discussion

The present study investigated whether pigeons were able to discriminate the direction into which a biological motion point-light walker was facing and whether they would solve this task by relying rather on local or on global information. The main findings can be summarized as follows: (1) The pigeons could indeed distinguish between the mirror-flipped versions of the presented motion patterns, with all birds readily acquiring the initial discrimination. (2) Most, though not all, birds relied on local motion rather than on global motion-mediated shape as a cue to direction, with each single bird making a clear decision for one or the other strategy. (3) Inversion effects were seen in some of the birds but remained relatively weak. (4) The pigeons that used local information seemed to rely on the motion of the feet and expected them to be located in the lower part of the display.

The fact that the birds learned the present direction discrimination task at all, that they learned it quickly, and eventually reached very high performance levels seems to stand in contrast to the difficulty reported to train pigeons to distinguish between mirror-

flipped versions of static shapes (Lohmann et al., 1988). Our study was not designed to compare discrimination between static and dynamic mirror-flipped stimuli directly, but it was evident that the transition from the discrimination of the static shapes to the point-light walker discrimination was no harder for our birds than the transition from one set of static shapes to a new one.

When confronted with the conflicting cues provided by the backwards walking figures in Test 1, all birds demonstrated a clear strategy regarding how to deal with them, and all of them then confirmed the use of their preferred choice strategy in the following Tests 2 and 3. Six of the eight birds indicated that they relied on the local motion of individual dots while two preferred global shape.

In five of the six "local precedence" birds the percentage of responses indicating the use of local motion approached the one they showed in the (unambiguous) training trials of the same session. In one bird – Maria, who also clearly favoured local motion over global shape – performance dropped from 85% in the training trials to a preference of 65% for the local motion direction in the ambiguous test trials of Test 1. The two "global precedence" birds were not using the global shape with the same precision with which they had mastered the unambiguous training trials. From the tests with scrambled biological motion patterns (Tests 2 and 3) it was obvious that one of them (Emilia) retained low but significant performance, indicating that this bird was able to use local motion at least to some degree.

Even though we tested only a relatively small number of birds we saw the full spectrum of possible strategies. Most birds relied exclusively on local motion to solve the task, but others seemed to be influenced by the fact that global information pointed in the opposite direction (Maria), preferred global over local information (Emilia) or ignored local information altogether and relied only on global information (Claudia).

I should be noted that all three birds were trained and later tested with point-light displays of walking pigeons rather than humans. We did not see these differences during training, and the numbers of tested birds were too small to draw strong conclusions from this observation, but it seems possible that increased familiarity or behavioral significance of the appearance of conspecifics has facilitated the recognition of global shape.

We also want to mention that the pecking paradigm that we employed potentially favours the use of the frontal visual field with its red field fovea. Poorer configural processing as observed in our experiment may not generalize to other parts of the pigeon's visual field.

We conclude that pigeons are in principle able to use both, the local motion of individual dots and the motion-mediated shape of the global display, to derive directional information from the point-light displays. Nevertheless, at least within the limited population that we tested, the majority of the birds showed a clear precedence for local motion features. The fact that some birds used global features, though, suggests that the "local precedence" birds probably also dispose of the perceptual abilities to do so, but "chose" to not use them.

In that respect, pigeons behave similarly to humans. Our data show that pigeons' preference regarding processing mode is in fact more on the local than on the global side, but the observed differences seem incremental rather than qualitative in nature. Human observers are definitely able to use both local motion and global structure in a biological motion direction task (Hirai et al., 2011b), and presented with the backwards walker test, they would probably ask the experimenter for unambiguous instructions ("what do you mean with 'direction'?").

One observation that we made in the current experiment was different from what one may expect to see in humans, though. If humans are presented with scrambled biological motion in which

the feet retain their position at the bottom of the display, but local trajectories are inverted, they tend to see the display walking into the direction opposite to the original one (Hirai, Chang, Saunders, & Troje, 2011a). This finding provides a strong hint towards the cue that signals direction. Hirai and colleagues dubbed it the "rolling wheel" cue. If the dot representing the feet circumscribes a clockwise path, the walker is perceived to face to the right side – the direction into which a wheel would be rolling whose rim follows a clockwise rotation. Likewise, if the dot circumscribes a counterclockwise path, the walker is seen to face to the left. Inverting the trajectory by means of flipping it about a horizontal axis changes the direction of the "rolling wheel" and therefore perceived direction.

In pigeons, we found moderate inversion effects in some birds, but clearly no indication of reversal of the perceived direction upon flipping local trajectories upside down. For that reason, it is unlikely that they also used the "rolling wheel" cue. As discussed by Hirai et al. (2011a) another candidate cue that would not reverse upon inversion are the different movements of the foot during stance phase and swing phase. Relative to the rest of the body, during the stance phase the feet move in one direction at moderate, constant speed, and are accelerated to a faster speed in the opposite direction during the swing phase. The differences in the velocity profile (faster and shorter during swing, slower and longer during stance) could potentially identify the two phases and therefore the walking direction. Upon inversion, perceived direction would still be the same. Our study does not reveal whether this was indeed the cue that pigeons used. However, it may not be easy to come up with other candidate cues of similar explanatory power that would be in accordance with the present data.

A comparison with an experiment that tested rats on very similar stimuli as the ones used in the current experiment further corroborates how impressive performance of our birds actually was. MacKinnon, Troje, and Dringenberg (2010) trained rats in a water maze setup to visually discriminate between a left-facing and a right-facing human point-light walker. The rats eventually learned the task, but their performance remained at a rate of about 75% correct responses. When tested with the same backwards walking human figure used in the current experiment, they responded completely randomly. The same was the case when they were presented with point-light displays of a walking cat. It seems like the rats had managed to discriminate the two displays used during training but without deriving from them any kind of invariant that would have helped them to arrive at a consistent decision about the test displays.

The pigeons, in contrast, demonstrated with their behavior a remarkable ability to solve the initial task and to generalize consistently to new stimuli. How they did that varied among individual birds, demonstrating a rich spectrum of visual processing abilities which challenges attempts the simply characterize these birds' visual processing strategies in terms of local vs global precedence categories.

Acknowledgments

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