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Abstract

Recognizing and categorizing behavior is essential for animals (e.g., during mate selection, courtship, and avoidance of predators). In a study examining if and how animals classify different actions, a go/no-go procedure was used to train 4 pigeons to discriminate among "walking" and "running" digital animal models (each portrayed from I2 different viewpoints). Action discrimination acquired for two models significantly transferred to six novel animal models moving in novel and biomechanically characteristic ways. Randomization of frame order in the animated sequences, stimulus inversion, and static presentation all disrupted this discrimination, whereas changes in the direction and speed (both increases and decreases) of the actions did not. These results suggest that the pigeons discriminated the behaviors on the basis of generalized recognition of the models' sequence of poses across time and provide the best evidence yet that animals use action categories to identify contrasting behavioral units.

Keywords

comparative psychology, categorization, motion perception, learning

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Detection, recognition, categorization, and interpretation of behavior are vital skills for complex animals in the natural world. Recognizing and interpreting behavior is an essential social skill in humans, who have well-developed capacities for this function (Blake & Shiffrar, 2007). The study of action recognition by humans has grown rapidly in the past decade. Studies have shown, for example, that humans are able to accurately and rapidly detect a rich collection of human actions and physical characteristics on the basis of as few as 10 strategically placed points of light on a human figure (e.g., Johansson, 1973), and there is evidence that specific neural pathways are involved in this capacity (e.g., Rizzolatti, Fogassi, & Gallese, 2001).

Being able to recognize and classify behavior would be equally valuable for nonhuman animals during courtship, mate selection, agonistic situations, social foraging, learning by imitation, and predator-prey interactions (e.g., Byrne & Russon, 1998; Fernández-Juricic, Erichsen, & Kacelnik, 2004). Using behaviors as discriminative stimuli has been theoretically challenging, however, because they are complex, temporally extended, dynamic, and organized sequences of semirigid, articulated motions (Aggarwal & Cai, 1999; Blake & Shiffrar, 2007; Shipley & Zacks, 2008; Zacks & Tversky, 2001). Although there is substantial evidence that animals can tell different behaviors apart in the wild, the origins, boundaries,

and mental representation of such dynamic stimulus discrimination have been neglected in the study of animal cognition and behavior (Cook & Murphy, 2012). Here, we report a novel approach to investigating how pigeons, *Columba livia*, visually recognize and potentially classify different complex behaviors into action categories.

Whereas noun categories allow the grouping of items with similar appearance (e.g., Bhatt, Wasserman, Reynolds, & Knauss, 1988; Herrnstein, Loveland, & Cable, 1976), action categories would be equally useful for classifying common types of motions, actions, and behaviors. Dittrich and Lea were the first to consider this important possibility—with mixed experimental success (Dittrich & Lea, 1993; Dittrich, Lea, Barrett, & Gurr, 1998). More recently, several studies have suggested that pigeons might be able to form such motion-based categories. Mui et al. (2007) looked at the discrimination of natural movements by budgerigars (*Melopsittacus undulates*) and pigeons. They found that both species could discriminate between forward and backward videos of a human walking a dog. This discrimination then transferred to the forward and backward

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motions of these figures facing a new direction. This study suggests that birds can detect the direction of actions on the basis of the sequencing of identical postures (see also Koban & Cook, 2009). Cook, Shaw, and Blaisdell (2001) tested pigeons to see if they could classify different types of object-based motions. Using dynamic video displays in which a camera's perspective went either around or through an approaching hollow object over the final few frames, they found that pigeons could learn and transfer this discrimination between "around" and "through" actions. Finally, Cook, Beale, and Koban (2011) found that pigeons could learn to categorize the "fast" and "slow" velocity of different kinds of object motion. Their evidence suggested that this fast/slow discrimination was specific to rotational or translational motions of the objects, as the pigeons could not discriminate the velocity of changes in the color, size, or shape of objects.

One persistent problem in the study of natural animal behavior has been the difficulty of creating highly controlled stimuli to study the discrimination and recognition of behavioral action. To investigate how pigeons detect, recognize, and categorize different behaviors, we took a novel approach of using animation software to generate two classes of lifelike biomechanical models of locomotion in three-dimensional figures. Walking and running appeared to be good categories to start with because modes of locomotion are likely to be salient natural categories (Malt et al., 2008), and their periodic and repetitive nature makes them more tractable to analysis than complex sequences of nonrepetitive actions.

The pigeons were tested with a variety of digital animal models that either walked or ran in place on a textured ground. To encourage categorization and investigate viewpoint invariance, we rendered the animal models from combinations of different camera perspectives: high and low camera angles; ³/₄ front, 3/4 back, and side views; and close and far camera placements (see Fig. 1). In a go/no-go procedure, half the pigeons were reinforced for pecking at exemplars of the "running" category, and the remaining half for pecking at exemplars of the "walking" category. We found that the pigeons learned this action discrimination and transferred it across a variety of digital animal models in which species walked or ran with novel, species-appropriate kinematic sequences of limb movements. Tests designed to isolate the controlling feature of this movement discrimination suggested that the pigeons likely recognized the coordinated actions of the model animals and grouped them into contrasting action classes.

Method Animals

Four male pigeons were trained and tested. They were maintained at 80 to 85% of their free-feeding weights and had free access to grit and water. Three of these birds had experience in discriminations involving static color or shape stimuli. After analogous training, a 5th pigeon substituted for 1 bird that

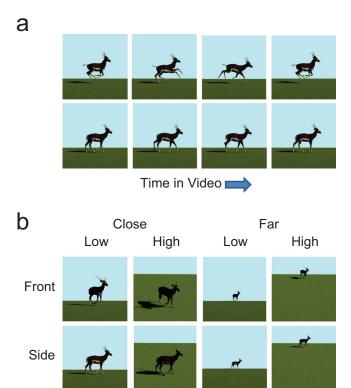


Fig. 1. Example frames from the running and walking conditions used in this experiment. In (a), the top row shows frames selected from the running condition for the buck model; the bottom row shows analogous frames from the walking condition for the same model. The frames in (b) illustrate the different combinations of camera distance, elevation, and perspective that were used. All these combinations were used in both the walking and the running conditions for each digital model animal.

became ill prior to the randomization test (described in the Procedure section).

Apparatus and stimuli

Back

Testing was conducted in a computer-controlled chamber. Stimuli were presented on an LCD monitor (NEC Accusync 51VM, resolution of 1024×768 pixels) that was recessed 8 cm behind a $33-\times 22$ -cm infrared touch screen. A ceiling light was illuminated at all times, except during time-outs. A central food hopper under the touch screen delivered mixed grain.

Three-dimensionally rendered animal models of walking and running were presented in a 11.5- × 11.5-cm display area using looped AVI videos (using Microsoft Video1 compression). The animated digital model animals were created with animation software (Poser 7, www.smithmicro.com) using third-source models of the animals' actions (Daz 3D, www.daz3d.com; Eclipse Studios, www.es3d.com/index2.html). The digital model within each video followed biomechanical

action models characteristic of the depicted species and moved in a fixed central position so as to minimize confounds with translated spatial position. Each model was rendered on a receding green-textured flat surface below a pale blue "sky" and illuminated from a fixed overhead light source. The number of composite frames in each video and the rate of presentation (frames per second) depended on the digital model and action. Across the eight model animals tested, the total sequence of action before repetition (i.e., a behavioral cycle) occurred more frequently for the run actions (M = 1.7 behavioral cycles per second, or cps) than for the walk action (M =0.82 cps). To promote the generalized recognition of each behavior, we rendered the models from all 12 combinations of three camera perspectives (side: 0°; front: -45°; back: +45°), two camera distances (near: ~8°-16° of visual angle, depending on the modeled species' body size; far: ~26°-40°), and two camera elevations (low: ~0.5° relative to the surface, high: $\sim 26.3^{\circ}$).

Procedure

Acquisition. Each training trial (and later, all test trials) started with a peck to a centrally presented 2.5-cm, white ready signal. This signal was replaced by a looped video of the digital model, which was presented for 20 s (starting from a randomly selected frame). Two pigeons were reinforced for pecking at running models, and the other 2 were reinforced for pecking at walking models. Pecks to these correct (S+) actions were reinforced with 2.9 s of access to mixed grain on a variableinterval schedule (VI 10), and an additional 2.9 s at the end of the presentation. Pecks to the incorrect (S-) action resulted in no reinforcement and a variable dark time-out (1 s per peck) at the end of the presentation. During acquisition, 25% of S+ trials were randomly selected to be probe trials during which no reinforcement occurred. These trials allowed for the uncontaminated measurement of peck rate without the presence of food. All S+ dependent measures were calculated from these probe trials.

Acquisition sessions consisted of 64 trials (32 in the walking condition and 32 in the running condition) portrayed by two right-facing model animals (dog 1 and buck). The two model animals, two camera distances, and two actions were presented equally often within a session; camera perspective and elevation varied randomly across trials. Thus, 48 different videos were used during training (2 models × 12 perspectives × 2 actions). Learning was measured by the discrimination ratio (DR), calculated as follows: DR = peck rate on S+ probe trials/(peck rate on S+ probe trials + peck rate on S- trials). Each pigeon continued training until it reached the learning criterion of a discrimination ratio greater than or equal to .7 in two sessions.

An important question concerned the nature of the psychological control mediating any action discrimination learned by the pigeons. Theories of action representation are split between those hypothesizing a higher-level global, or configural, organization of movements and those suggesting that low-level,

nonparametric representations are sufficient. To examine such issues, we conducted the following analytical tests.

Novel animals. If the pigeons' recognition of actions was based on global representations, it would be independent of the model animals' appearance and biologically characteristic manner of running and walking. Over 2 months, we successively tested transfer of learning to six new models and incorporated these model animals into the pigeons' repertoire (see the illustrations in Fig. 2). The first two novel models (dog 2 and gazelle) used the same biomechanical actions as the baseline models (i.e., the two models presented during acquisition) but did not have the same external appearance as those models. The next four models-cat, camel, elephant, and human (tested in this order)—were different from the baseline models in both external appearance and kinematics. To get an unbiased estimate of transfer, we tested each novel model in 4 randomly inserted, nonreinforced probe trials in each of six consecutive sessions. These 24 probe trials (12 walking trials and 12 running trials) tested the 12 camera perspectives used during training. After the completion of its transfer testing, each model was added to the differentially reinforced repertoire of baseline actions. In this way, the number of different kinds of motions experienced for each action increased gradually.

Reversal and inversion. We expected that the pigeons' categorization of behavior would be independent of the facing direction of the motion, but would likely be disrupted by its inversion, as has been found with humans (Sumi, 1984). To test this prediction, we presented both reversed (leftwardfacing) and 180° inverted versions of the two baseline models (dog 1 and buck). Over 12 test sessions, each viewpoint, except those from the far camera distance, was tested with each combination of model, action, and orientation (total of 48 tests per pigeon). Each session tested four different combination of these factors on 4 nonreinforced probe test trials that were randomly mixed into 80 baseline trials. After this test, leftward-facing models were incorporated into the pigeons' training repertoire.

Action randomization. If the sequential motion of the models carried the information important for discrimination, then the coherent appearance of the different poses for each action would have been critical. To examine this possibility, we randomized the order of the frames on selected test trials. Over four sessions, all camera viewpoints, except those from the far camera distance, were tested with two models (dog 1 and buck), for both actions (total of 24 tests per pigeon). Each session tested six different combinations of these factors as 6 nonreinforced probe test trials that were randomly mixed into 72 baseline trials.

Static presentation. To examine whether motion was critical to the pigeons' action discrimination and whether a single view of a model's pose was sufficient for discrimination, we

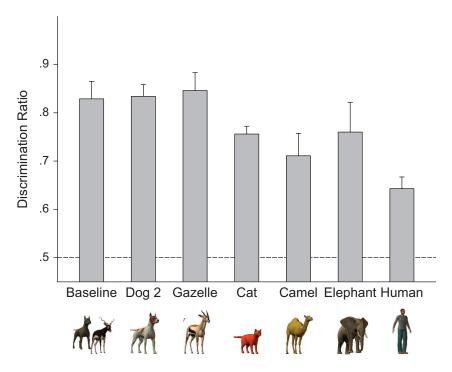


Fig. 2. Mean discrimination ratios for the transfer tests with the six different novel animal models. Also shown is the combined mean performance with all nontransfer models from the expanding baseline set across the different transfer tests. (For the baseline results, the original training set of models is illustrated.) Error bars show I SEM for each model. The dashed line indicates the level of chance discrimination.

conducted tests with static frames. On static trials, a randomly selected frame of the video was presented for the entire 20-s presentation. Over four sessions, all camera viewpoints, except those from the far camera distance, were tested with two models (dog 1 and buck), for both actions (total of 24 tests per pigeon). Each session tested six different combinations of these factors as 6 nonreinforced probe trials randomly mixed into 72 baseline trials.

Manipulation of action rate. This test examined how the speed of the actions influenced discrimination. The presentation time for the individual frames was manipulated, such that the digital model (buck) moved through its actions either quickly or in slow motion. All camera viewpoints, except those from the far camera position, were tested within each six-session block. Each session tested one combination of elevation and perspective, with six nonreinforced probe trials for each action (2 trials at normal speed, 2 trials at a faster speed, and 2 trials at a slower speed) randomly mixed into the baseline trials. Over three different test blocks, the faster and slower presentation speeds were progressively increased and decreased. Across these three blocks, the presentation rate for the running condition (baseline = 1.75 cps) was varied between 0.92 and 17.5 cps, and the presentation rate for the walking condition (baseline = 1.01 cps) was varied between 0.53 and 10.1 cps.

Analysis

The dependent variables were DR and mean number of pecks per 20-s presentation interval. Statistical tests were conducted with the SPSS software package (v. 15). An alpha level of \leq .05 was used to judge significance for all statistical tests. Repeated measures analyses of variance (ANOVAs) were evaluated with and without Greenhouse-Geisser and Huynh-Feldt corrections. The results for the two-tailed t tests were confirmed by additional nonparametric tests. As these procedures did not produce different outcomes, only the uncorrected test values are reported.

Results

The pigeons learned the discrimination relatively quickly and easily. It took a mean of 10.25 sessions to reach the learning criterion, although clear evidence of discriminative behavior was present within 5 sessions. The particular assignment of the two actions to the S+ and S- categories made no noticeable difference in the rate of learning. Examination of the 10 sessions immediately following acquisition confirmed that all the pigeons discriminated the two actions at above-chance levels (mean DR = .81), all ts(9) > 2.3 (single-mean two-tailed t tests). Comparisons revealed that discrimination (mean DR) was not significantly influenced by differences in the digital

model (dog: .82; buck: .80), camera perspective (front: .82; side: .81; back: .80), or camera elevation (low: .81; high: .81). Larger apparent distance (smaller size) of the model reduced mean DR for 1 pigeon (near: .85; far: .60), but not for the other 3 (near: .85; far: .85). The failure of these variables to have any influence on performance was confirmed by a repeated measures ANOVA (Action Category \times Perspective \times Distance \times Elevation) conducted on peck rate. Although action category (S+ vs. S-) had a highly significant main effect, F(1, 3) = 142.5, none of its interactions with the other variables were significant.

The six novel digital models supported significant discrimination transfer, as indicated by the difference in the number of pecks recorded for the S+ and S- action categories for each bird (mean number of pecks across all six models = 24.9 for the S+ category and 8.4 for the S- category). This difference is comparable to that between the S+ and S- means on the baseline trials during the transfer sessions (S+: 28.5; S-: 6.3; adjusted for the expanding repertoire across tests). ANOVAs conducted on the transfer-test results separately for each new model (Action Category × Perspective × Distance × Elevation) revealed a signification main effect of action category for each model—dog 2: F(1, 3) = 525.7; gazelle: F(1, 3) = 171.2; cat: F(1, 3) = 166.8; camel: F(1, 3) = 36.4; elephant: F(1, 3) = 24.7; human: F(1, 3) = 18.2. There were no higher-order interactions with any of the camera-viewpoint variables.

Figure 2 shows the mean DRs for the training (baseline) and novel models in the transfer tests. Paired two-tailed t tests (df = 3) on the DRs revealed that the cat and human models supported significantly lower discrimination than the baseline models did, but discrimination for the dog 2, gazelle, and elephant models was not significantly different from discrimination for the baseline models. The difference between the camel and baseline models was marginally nonsignificant (p = .08). Performance with the novel models when they were subsequently integrated into the baseline repertoire was consistent with this pattern. The mean number of sessions required for the pigeons to reach the learning criterion (two sessions of $DR \ge .7$) indicated that four of the novel models immediately supported good performance—dog 2: 2.0; gazelle: 2.0; camel: 3.0; elephant: 2.75. Discrimination performance with the cat and human models was lower at first and improved over subsequent sessions. The pigeons required a mean of 7.25 sessions to reach the learning criterion with the cat model and 18.3 sessions to reach the criterion with the human model; these results are consistent with the significantly lower level of transfer performance for these models.

Reversing the direction of the models had no impact on discrimination. Mean peck rates on reversal trials (S+: 29.3; S-: 4.9) were not significantly different from mean peck rates on baseline trials (S+: 31.5; S-: 4.7). A repeated measures ANOVA (Action Category × Reversal × Perspective × Elevation) on peck rate confirmed that there were no significant interactions involving action category and the reversal variable. An analogous ANOVA (Action Category × Perspective × Elevation) on

just the reversal trials confirmed the presence of a significant main effect of action category in these trials, F(1, 3) = 71.5. Inverting the displays significantly reduced, and in fact eliminated, the action discrimination in all 4 pigeons (mean peck rate = 9.8 for S+ trials and 4.9 for S- trials). Consistent with the absence of any discrimination, an ANOVA examining just the inversion trials no longer found a significant main effect of action category.

Randomizing the sequence of the frames also significantly reduced action discrimination for all 4 pigeons (randomized trials: mean peck rate = 26.9 for S+ trials and 19.7 for Strials; baseline trials with the identical models: mean peck rate = 39.8 for S+ trials and 5.2 for S- trials). The birds treated the randomized presentations as if the models appeared to be moving quickly. The 2 birds for which running was the Saction (walk+/run- group) showed reduced numbers of pecks (8.6) to these stimuli, whereas the 2 birds for which running was the S+ action (run+/walk- group) showed higher numbers of pecks (38.1). An ANOVA (Action Category × Perspective × Elevation) on just the results from the randomization trials revealed no significant main effect of action category and no interactions between action category and the other factors. These results indicate that frame randomization reduced or eliminated the pigeons' capacity to discriminate the two actions, and suggest that coherent motion is required for action discrimination.

Removing motion from the animations by presenting static frames also reduced or eliminated the action discrimination (static trials: mean peck rate = 22.1 for S+ trials and 18.4 for S- trials; baseline trials with the identical models: mean peck rate = 37.3 for S+ trials and 4.6 for S- trials). An ANOVA (Action Category × Perspective × Elevation) on peck rate in the static trials only did not reveal any significant main effect of action category or interactions between action category and the other factors, indicating that sequenced motion involving different postures is needed for action discrimination.

Finally, the pigeons' action discrimination was robust to changes in the rate of presentation of the animations. Figure 3 shows peck rate as a function of presentation rate for the running and walking animations, separately for the run+/walk—and walk+/run—groups. Across a wide range of rates, the pigeons continued to recognize the different actions despite changes in the speed at which the actions were performed. The implication of this finding is that the pigeons had learned to recognize and classify the configural sequences of poses that characterize running and walking and were not using a low-level feature, such as the speed of leg movement or head bobbing, as their main discriminative cue. If the latter had been the case, then animations of the slow runners and fast walkers tested here should have been systematically misclassified.

Discussion

These experiments reveal for the first time that pigeons can learn and discriminate action classes (walking and running) in

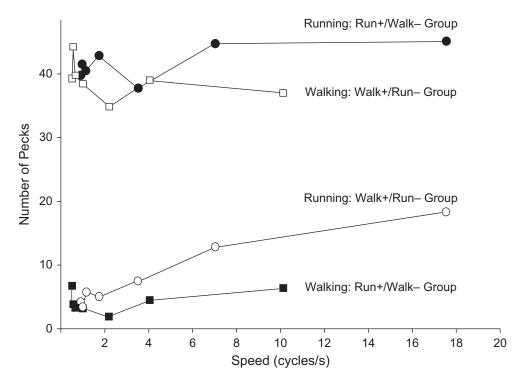


Fig. 3. Mean peck rate (number of pecks per presentation) to the running (circles) and walking (squares) models as a function of speed of the action. Results are presented separately for pigeons that were reinforced for pecking the walking models (walk+/run- group; unfilled symbols) and those that were reinforced for pecking the running models (run+/walk- group; filled symbols).

digital animal models moving in biomechanically appropriate ways and then transfer this learning to a large set of novel digital animal models. This generalized discrimination appeared to be viewpoint invariant, as discrimination of the actions was generally equivalent for all 12 combinations of camera perspective, distance, and elevation. This discrimination was disrupted by stimulus inversion, randomization of the frame sequences, and the absence of motion, but not by reversal of the models' direction of movement. Further, this discrimination was maintained over a wide variety of presentation speeds. These results seem most consistent with a hypothesis that the pigeons learned action categories by grouping together the varying exemplars of each behavior as performed by the different models. If our interpretation is correct, this study provides the best evidence yet that pigeons can discriminate and categorize motion-based behavioral actions. The evidence further suggests that the sequencing of the configural postures of the models was the primary cue for discrimination.

Researchers in computer vision have tested a number of algorithms for recognition of behaviors (e.g., human gait and facial expressions) across a number of applications (e.g., human-computer interfaces, surveillance, video searching). One major approach has focused on using model-based configural representations involving hierarchical global relations, such as two-dimensional stick models or three-dimensional volumetric models (see the review by Aggarwal & Cai, 1999).

Another approach has focused on using non-model-based features such as local contours or other repetitive features of the displays (e.g., Polana & Nelson, 1997). A biologically inspired hybrid model postulates that low-level motion and shape units are formed into higher-level sequences of postures (Giese & Poggio, 2003).

Given this context, a highly relevant question concerns how the pigeons might have represented and discriminated the actions. Did the pigeons recognize the global, or configural, organization of the two different behaviors, or did they instead learn to distinguish a set of repetitive local features correlated with these behaviors (e.g., the differences in leg speed, positioning, or head bobbing)? The evidence here seems to more strongly favor the former possibility. First, the discrimination generalized across a wide variety of walking and running gaits in the different models. The kinematics and timing of each model's gaits simulated the natural appearance of running and walking for that species. Thus, the heavy elephant and awkward camel ran quite differently from the loping cat, yet these actions supported similar levels of classification. Nevertheless, the fact that the pigeons were able to perform the action discrimination across so many different animals and gaits suggests that the representation mediating the discrimination was relatively invariant to the different kinematics and physical appearances of the models. Second, stimulus inversion disrupted the discrimination, even though the inverted stimuli retained the same low-level motion features that were in the upright versions.

Third, the birds performed well regardless of the perspective and left/right orientation of the models. Discrimination was good even in the case of the videos with the front and back perspectives, in which leg velocity and positioning were not as visible as from the side view. Fourth, both randomization of the frame sequences and static presentations strongly disrupted discrimination. Thus, the presence of properly sequenced motion in the videos seemed necessary. Finally, varying the speed of the behaviors (i.e., fast walkers and slow runners) had little impact on performance, which suggests that the sequence of the walking and running postures was more important than low-level processing of the features of leg speed or position. Thus, it appears that it was the sequence of the models' postures across time that characterized the different behaviors for the pigeons.

Together, these different lines of evidence suggest that the pigeons recognized something about the higher-level configuration, or organization, of the sequenced actions and that their representations were general enough to support action discrimination. These results contrast with the highly mixed outcomes from testing animals with point-light displays that emphasize global configuration (Blake, 1993; Dittrich et al., 1998; Parron, Deruelle, & Fagot, 2007; Regolin, Tommasi, & Vallortigara, 2000; Tomonaga, 2001; Vallortigara, Regolin, & Marconato, 2005). It is possible that, compared with humans, animals have a harder time grouping such separated featural points into global configurations. The complete, contoured, and connected models employed in our study may have allowed the pigeons to overcome this limitation and more easily discern and use the global patterns of the actions.

Overall, our results provide some of the best evidence yet that pigeons, which are known to form noun-based concepts, can also form motion-based, or verblike, concepts. Just as noun categories allow the classification of objects, action categories would be useful for classifying similar-appearing motions and behaviors into larger units for encoding and representation. This would be especially valuable in recognizing the behaviors, and possibly intentions, of other animals across a wide variety of settings and perspectives. If birds and other animals can form and use such representations for recognizing different behaviors and actions, such verblike categorical representations could have formed the neural foundation for the later linguistic development of verbs and adverbs by humans to label and categorize classes of behaviors and motions (Arbib, 2005).

A large number of important questions remain to be answered. What other types of motions and behaviors can pigeons discriminate and classify? Would other kinds of natural behaviors, such as courtship or agonistic displays, be readily recognized and grouped by these animals? Do pigeons segment the semirigid actions of other animals within the structure of their own body plan? How is form and motion information integrated in such discriminations, and are such action discriminations mediated by neural pathways similar to

or different from those involved in humans (e.g., Decety & Grèzes, 1999) or monkeys (e.g., Singer & Sheinberg, 2010)? Can such action units allow long, complex sequences of behavior to be segmented and related hierarchically (Byrne & Russon, 1998; Zacks & Tversky, 2001)?

One recent hypothesis has suggested that humans understand actions by mapping visual representations onto motor representations of the same actions (Rizzolatti et al., 2001) and that the conjoint activation of these representations is critical. However, animals often need to recognize behaviors not only within, but also between, species. Some of these animals may share few motor programs for recognizing actions. Given that flying and bipedal pigeons likely do not have motor representations that have much in common with the different quadruped actions tested in this study, our results suggest that actions can sometimes be visually understood without necessarily being embodied in the observer.

Finally, increasing attention has been directed to the issue of animacy detection in humans and how people distinguish between living and inanimate objects (Gobbini et al., 2011; Rees, 2008). If the pigeons in our study did recognize the locomotive behaviors as the actions of creatures (albeit animated ones), our results potentially lay the foundation for exploring this intriguing question in other species. Thus, these digitally animated stimuli constitute an important advance over the static displays that have dominated the study of animal behavior and hold considerable promise for advancing understanding of animals' ability to identify, recognize, and classify behavior.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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