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Head and Foot Coordination in Head Scratching and Food Manipulation by Purple Swamp Hens (*Porphyrio porphyrio*): Rules for Minimizing the Computational Costs of Combining Movements from Multiple Parts of the Body

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Complex movements, such as placing food into the mouth, involve coordinating multiple limb segments. Given the degrees of freedom for one limb segment, the computational costs of such complex movements can be high. One way to reduce such costs is to limit the adjusting movements needed to achieve coordination of distal body parts to only one part of the body. For example, for scratching the head, the hand or foot needs to make contact with the head and this involves movements of the head, neck and torso, as well as those of the foot and leg, or hand and arm. In this situation, the foot or hand is raised to a specific location in space and then makes oscillatory movements, but it is movements by the head and neck that ensure appropriate contact is made with the head (Pellis, 2010). In this paper, whether such cost-saving rules apply across functional contexts is tested in the purple swamp hen by comparing head and foot coordination during head scratching and during food reaching and handling. This species uses its foot to grasp and hold a wide range of food items that are picked up in its bill. Comparison of hundreds of videotaped sequences revealed that, in both cases, the bird uses the same rule: that of making the accommodating movements with only one of those body parts, even when coordination requires movements of disparate parts of the body. These data show that there are likely common computational cost-saving rules that widely apply to movements occurring in many different functional contexts.

In many life and death situations, such as when evading a predator's attack, taking in all the relevant information and evaluating the costs and benefits of all behavioral options would lead to an early death. Actions in such cases require the minimum computational time possible (Ellis, 1982). But even in non-dire circumstances, the range of possible actions can mire an organism in an endless evaluation of what is the best solution. In the 1990s, a revolution in robotics solved this problem: robots were designed to operate using simple rules, such as 'keep the intensity of light on the left and right light receptors balanced' and 'turn right when encountering an obstacle', instead of the traditional design of computing options based on the evaluation of multiple sources of incoming information (Pfeifer & Bongard, 2007). Similarly, such simple rules have been shown to be the most common ways by which organisms of varying neural complexity achieve action in real-world situations (Gigerenzer, 2002). They also capitalize on regularities in their bodies and environments to minimize the computational efforts required (i.e., embodied cognition; Clark, 1998). A consequence of these changes in thinking about robots and cognition is the recognition that complex behavioral outcomes can arise from relatively simple rules (Barrett, 2011).

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Viewed from this modern perspective, the fixed action pattern (FAP) of classical ethology can be thought of as a way of simplifying action patterns performed by composing those actions out of simpler subunits (Llinas, 2001). Simpler actions lower the costs of computing the organization of the constituent movements, where those costs can combine one or more of the following: time, energy and levels of control (i.e., number of contributing elements). The debate about how fixed the FAP may be, and whether statistical approaches are more appropriate than geometric ones in defining them (Barlow, 1968), is not relevant with regard to this proposed function. What is critical is that there are organizing principles by which constancy in the overall form of the behavior can be reconciled with the variability in the motor output (e.g., Bell & Pellis, 2011; Finley, Ireton, Schleidt, & Thompson, 1983; Marken, 2002; Pellis, 1985; Pellis, Gray, & Cade, 2009). The issue dealt with in this paper is whether each FAP is uniquely organized as a computational cost-saving device or whether there are meta-rules that apply across FAPs. Evidence from both vertebrates and invertebrates suggests that, in the same animals, some of the features of movement across different FAPs do indeed involve the use of some of the same movement modules (i.e., motor primitives) (Flash & Hochner, 2005; Mather, Griebel, & Byrne, 2010). That is, while some features of movement construction are FAP-specific, others are seemingly independent modules that can be inserted in many different FAPs (Jing, Cropper, Hurwitz, & Weiss, 2004). Similarly, principles of organization, rather than specific movement modules, may be common across FAPs (Field & Pellis, 2008).

Scratching the head with a limb is common across tetrapods, including reptiles, birds and mammals, and has the basic properties of a FAP, in that there is a high degree of form constancy across scratches and individuals (Llinas, 2001). However, there is variation: a scratch may start at one location on the head and then move to another (Pellis, 1983). Given that itches are unpredictable, neither the starting location nor the change to a new location can be pre-computed. Rather, with each scratch, the starting position, end position and trajectory in between needs to be created anew. Two rules appear to be used to lessen the computational costs of dealing with these unpredictable elements, and these are well illustrated in birds when using their hind feet (Pellis, 1983, 2010). First, the bird lifts its foot to a location in space past its torso, at about the level of the upper part of its wing. Once there, the bird begins to make up and down oscillatory movements with its foot (i.e., the scratching action), and then, by a combination of head, neck and torso movements, it lowers its head to the appropriate location to meet its foot. Second, when changing the location on its head contacted by its foot, the bird keeps its foot in the same spatial location while it is oscillating, and then, by further movements of the head and neck, the bird can change the location on the head that is contacted by the foot. Mammals that use their hind feet or their hands to scratch their heads follow the same rules (Pellis, 2010). The principle here appears to be something like: when more than one set of body parts can contribute to a coordinated movement, do not move both sets of body parts simultaneously (Whishaw et al., 1994). Computing the coordination of body parts distal to one another is likely more costly than keeping one body part fixed and only moving the other.

Not only do these studies on head scratching show that there is a computational cost-saving means with which to organize some features of the movement, but also, that this cost saving device applies to *both* birds and mammals. These findings suggest that the same FAP uses at least some aspects of the same rule structure across very different animals. From an evolutionary perspective, it would be of interest to know whether reptiles, that scratch their heads (e.g., turtles, Morton & Stein, 1989), also follow the same rule. If so, it would suggest that birds and mammals inherited this organizing rule from their reptilian ancestors rather than inventing it independently. Another question that arises is whether the same rule applies across different FAPs in the same species, rather than it being an inherited feature of head scratching in all or some tetrapods. A study of object grasping requiring foot and head coordination in the Australian magpie (*Gymnorhina tibicen*) suggests so. When manipulating objects held in its bill, a magpie will lift its foot to a fixed location, and then lower its head, in order to meet its foot (Pellis, 1983). Because of the sporadic occurrence of such foot-bill object manipulation, the wide diversity of objects involved, the opportunistic nature of the filming and also because most of the cases involved immature birds (and hence, possibly reflecting incomplete development of the motor system), it was not possible, in that study, to determine whether changes in object size and shape were dealt with by modifying the movement of the head, by changes in spatial location of the foot, or by some combination of both. If head and foot coordination during food handling follows the same rules as during head scratching, then the compensatory movements should be made by the head, not the foot.

In the present study, videotaped sequences from purple swamp hens (*Porphyrio porphyrio*), a bird renowned for the use of its feet for food manipulation (e.g., Balasubramaniam & Guay, 2008; Washington, Paterson, Sixtus, & Ross, 2008), were used to determine whether the same organizing rule for head-foot coordination occurred in both head scratching and food grasping. Specifically, based on previous studies (Pellis, 1983, 2010), six predictions, derived from the hypothesis that when the foot and the head need to coordinate their movements the coordination is achieved by adjusting movements by the head, not the foot, were tested. The data suggest that this is a conservative rule with widespread applicability across different FAPs.

Method

Over the course of four weeks in August 2002, 4 hours of videotaped sequences of food handling and head scratching were collected from a flock of six adult purple swamp hens (1 male, 5 female), maintained at the Barcelona Zoological Gardens in Spain. They were housed in a large outdoor aviary, containing flocks of water birds (e.g., ibis, spoon bills), with open areas, shrubs and a small, shallow pond (of wading depth for the swamp hens). Each bird had a distinct color band on its legs. The birds were filmed during feeding sessions, with food ranging from small fish fry (2 cm long, 0.5 cm wide), pieces of fruit and vegetables (e.g., cubes of melon about 4-6 cm in length), to leaves of romaine lettuce (up to 30 cm long and 11 cm wide at the widest end).

Video Analysis

Video sequences were collected with a Sony 8mm Camcorder and then were converted to VHS format. When dubbed, a time code (1/30th of a second) was added using a Horita TRG-50 time encoder (Horita, Mission Viejo, CA). As done previously (Pellis, 1983, 2010), sequences of head scratching and grasping were analyzed using Eshkol Wachman Movement Notation (EWMN) (Eshkol & Wachmann, 1958).

In brief, EWMN is designed to express relations and changes of relation between parts of the body, with the body treated as a system of articulated axes (i.e., body and limb segments). A limb is any part of a body that either lies between two joints or has a joint and an extremity. These are imagined as straight lines (axes), of constant length, which move with one end fixed to the center of a sphere. The body is represented on a horizontally ruled page into columns that denote units of time (e.g., frames of a video). The signs for movement are read from left to right and from bottom to top (e.g., see Fig. 2). An important feature of EWMN is that the same movements can be notated in several polar coordinate systems, for example, with reference to the environment or to the next proximal or distal limb or body segment. By transforming the description of the same behavior from one coordinate system to the next, invariance in the behavior may emerge in some coordinates but not others (e.g., Eilam & Golani, 1988; Golani, 1976; Pellis, 1983, 2010; Whishaw & Pellis, 1990).

Behavioral and Statistical Analyses

A total of 33 instances of swamp hen head scratching and 556 instances of them grasping a food item held in their bills were available. Once held in the bird's foot, any given food item could be pecked at repeatedly, yielding over a thousand instances of such food pecking. All instances of these behaviors were watched once, and those cases in which the entire sequence could be viewed without obstruction, and beginning with the video frame that preceded the swamp hen raising its foot and ending with the frame in which it returned its foot to a standing position on the ground, were used for further analysis. For head scratching, the first example per bird that met the criteria was subjected to analysis using EWMN, and for food grasping, the first two examples, one with small food items (≤ 2 cm) and one with relatively large food items (≥ 8 cm), were so analyzed. The size of food items was judged relative to the size of the bird's bill (2-3 cm long). Once the pattern of organization was determined using EWMN, the remaining cases of head scratching and food grasping were used to test specific predictions about foot and head coordination quantitatively. As different analyses were conducted to test different predictions, the manner of scoring data and their analysis will be described as needed in the Results. Due to the small number of birds filmed and because most measurements for the movements performed used nominal or ordinal scales for the ratings, non-parametric tests were used for most statistical comparisons (Siegel & Castellan, 1988). However, as measurements of duration were in an interval scale, these data were analyzed using parametric statistics (Lehner, 1996).

Intra- and Inter-observer Reliability

Two methods were used to verify consistency in the measurements. First, for intra-observer consistency, the quantitative measures were repeated with videotaped sequences that had not been previously scored. In all cases, there were no significant differences in the scores from the two analyses ($p > 0.05$). Second, for inter-observer consistency, a second independent observer was asked to rescore the same sequences scored by the author. Again, there were no significant differences between the scores from the two observers ($p > 0.05$).

Results

Head Scratching

Prediction 1: *As is the case in other birds, when a swamp hen uses its foot to scratch its head, it was predicted that foot-head contact, and change in the location of that contact, would be achieved by movements of its head and neck, rather than by movements of its foot and leg.*

EWMN analysis showed that the swamp hen scratched its head in the same way described for other birds (see description in the Introduction). In all 6 cases analyzed, the initial contact and change in the location of contact was achieved by head and neck movements and not by movements of the leg and foot or by a combination of head and neck and foot and leg movements (sign test: X (6) = 0, $p < 0.05$). Of the remaining 27 head scratches not used for EWMN analysis, 18 involved a change in location from the initial site of foot-head contact. Assuming an equal likelihood for the three alternative combinations of movement (i.e., head alone, foot alone, head and foot combined), a Chi-square analysis showed that there was a significant bias for only one combination (χ^2 (2, 18) = 24, $p < 0.001$), that of altering the location by head and neck movements.

Food Manipulation

There were two distinct phases to food grasping and holding in the swamp hen. First, the swamp hen picked up the object in its bill and then grasped the object with its foot while it was held in its bill. Second, the swamp hen then held the object securely with its foot as it pecked off pieces using its bill. In both cases, any combination of head and neck and foot and leg movements could theoretically achieve the coordination needed for handling the food object (Fig. 1).

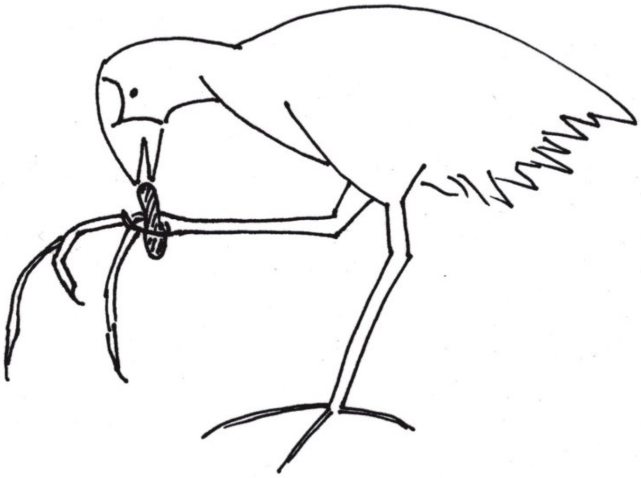
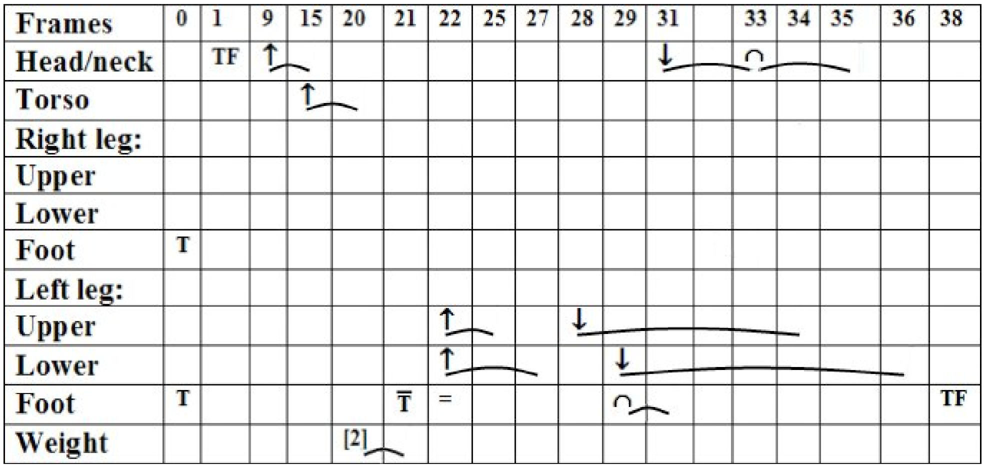


Figure 1. Drawing derived from a video image showing a swamp hen holding a food item in its foot while the item is being manipulated with its bill. The swamp hen holds the food item in its foot in this elevated position as it maneuvers its head around so that it can peck, from any orientation, at the pieces of food protruding from its digits.

Prediction 2: *It was predicted that, just as that which occurs in another bird, the Australian magpie (Pellis, 1983), when a swamp hen uses its foot to grasp food items that are held in its bill, contact would be achieved by adjusting movements of its head and neck, and not by adjusting movements of its foot and leg.*

Based on the EWMN analysis of the twelve examples from the six birds, the swamp hen's initial foot contact with the food item held in its bill was achieved by movements of its head and neck. A notated score of this action illustrates the core features of the grasp sequence as seen from the side (Fig. 2). The swamp hen stood with its body weight distributed equally between its two feet and lowered its head by a combination of head, neck and body movements. This led to it grasping the food item in its bill - in this case, a piece of a romaine lettuce leaf (about 6-8 cm long and 2-3 cm wide). Once the swamp hen had grasped the food item, it raised its head by a combination of head, neck and body movements, until its head was sitting horizontal relative to the ground and held in alignment with the midline of its torso. The swamp hen then shifted its body weight to the right, unloading its left foot. Once it was free to move, the swamp hen raised its left foot by flexion around the ankle joint and an upward movement of the lower leg, and, while it was being raised, it partially flexed the digits of its foot. The swamp hen then thrust its foot forward as it lowered its lower leg and extended its ankle, and, as its foot approached the level of its head, it extended its digits and partially rotated its foot, so that the inner surface obliquely faced the side of its head. As it thrust its foot further forward, the swamp hen moved its head so that its bill went from facing forward to facing downward, and there was also a slight rotation of its head, which lead to the tip of its bill moving towards the path of the oncoming foot. Thus, as the swamp hen's foot swept along the side of its head, the foot contacted the food item.



Frames	0	1	9	15	20	21	22	25	27	28	29	31		33	34	35	36	38
Head/neck		TF	↑									↓		∩				
Torso				↑														
Right leg:																		
Upper																		
Lower																		
Foot	T																	
Left leg:																		
Upper							↑			↓								
Lower							↑				↓							
Foot	T					T̄	=				∩							TF
Weight					[2]													

Figure 2. A sequence showing a swamp hen grasping at a food item that is being held in its bill by its foot as a simplified EWMN score, with body elements on the left hand side and movements depicted over time on the right (vertical columns represent video frames). This particular sequence was observed from the side, and, for simplicity, the magnitudes of the movement are not shown. The notation begins with the frame when the food item is picked up with the bill. The various symbols represent movements, with up and down facing arrows indicating vertical movements, and the inverted U indicating rotation of the foot and head, respectively. The T and = signs indicate weight bearing contact and loss of that contact, respectively, while the T with a bar on top indicates non-weight bearing contact on the ground. TF indicates contact with the food item by the bill and foot, respectively. The row indicating weight denotes shifts of body weight, in this case [2], it indicates that the bird shifted its body weight to the right and in doing so, shifted weight away from its left foot. The arcs connecting frames denote the duration of movement.

Close inspection of the notated sequences, some of which were observed from the side (as in Fig. 2) and some from oblique frontal angles, confirmed the pattern: the movement used by the swamp hen to achieve foot-food (bill) contact was produced by its head and neck. The two critical movements made by its head and neck included a vertical movement, between 45-90°, as it positioned its bill to point downwards, and a small head rotation, about $\leq$ 10°. Together, these head movements by the swamp hen brought its bill into the spatial location where it intercepted the movement of its foot. Figure 3 shows the position of the swamp hen's head when it first begins to raise its foot and when its foot sweeps across its bill. By superimposing the positions, the amount of combined reorientation of the head and bill are evident.

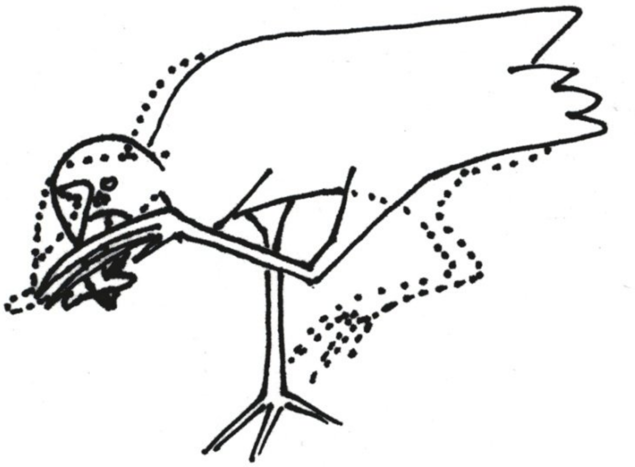


Figure 3. Drawing of a swamp hen reaching to grasp a foot item, held in its bill, with its foot. The solid line drawing shows the position of its head and torso when its foot contacts the food item held in its bill. The dotted line represents the position of the swamp hen's head and neck, and the left leg when it is being raised off the ground. Note that the swamp hen rotates its head to point downwards, tucks its neck inward, and partly tilts its head so that the tip of its bill is pointing towards its foot. The body and right limb do not change between the two points in the reaching sequence.

The first 6 successful grasps by each bird that were not notated were scored for the presence of these head movements. All of the birds incorporated these movements in their grasping sequence (X (6) = 0, $p < 0.05$) and did so in every single case (χ^2 (1, 36) = 18, $p < 0.001$).

Prediction 3: *It was predicted that, when a swamp hen grasps food items of different sizes, head and neck movements, rather than foot and leg movements, would compensate for the problems posed by changes in size and shape.*

Six complete and successful grasps each for three categories of food sizes (small ($\leq$ 2cm), moderate (3-6 cm) and large ($\geq$ 8 cm) were scored for each of the six birds. All sequences of grasping that met the criteria were scored as they appeared in the videotapes to avoid any bias in the selection process. In each case, the foot’s trajectory was scored as to whether the foot was in near proximity to the swamp hen’s bill or further away when it made contact with the food item. For example, a small fish (2 cm) only protruded about a centimeter from the side of a swamp hen's bill, whereas a 30-cm-long piece of romaine lettuce could protrude 20 cm or more from the side of its bill. Thus, with larger food items, it was possible for the bird to grasp them further away from the edge of its bill. In each case, the grasp was scored for whether the base of the digits of the foot was next to the bill when the grasping occurred ($\leq$ 1cm) (1), or was greater than half a bill length away ($\geq$ 2cm) (2). A mean score of 6 meant that all trials were a category 1 and a mean score of 12 meant that all trials were a category 2. The mean score for the three sizes of food item was 6, 6 and 6.5, respectively. Only for the largest food size were there grasps further away from the side of the bill and this was the case for only three trials. Combining all trials for all birds for each size category showed that, for all sizes, there was a significant bias for grasping near the bill (χ^2 1, 36) = 18, $p < 0.001$; χ^2 (1, 36) = 18, $p < 0.001$; χ^2 (1, 36) = 25, $p < 0.001$). That is, irrespective of the length of the food item, the foot grasped the item with the nearest digit, just as it protruded from the bill, supporting the view that it was the head movements, not the foot movements, that provided the adjustment for the swamp hen to bring differently sized food items to the foot.

Prediction 4: *Based on the results from an earlier study (Pellis, 1983), it was predicted that any failure by the swamp hen to grasp a food item being held in its bill would be due to delayed or atypical movements made by its head, not its foot.*

About 10% of the swamp hens’ attempts to grasp a food item held in the bill failed. Comparison of successful with unsuccessful grasps, using EWMN, indicated that a failed contact was associated with atypical movements of the bird’s head, rather than atypical movements of its foot. The role of head movements in achieving a successful grasp is well illustrated when the swamp hens had to compensate for differently sized or oddly shaped food items. For example, one bird picked up a large, pyramidal shaped wedge of watermelon (about 4 cm length at the base and about 5 cm from base to apex). The base was the green skin and the fleshy part of the fruit was the apex. The bird picked up the wedge near the apex of the pyramid; this resulted in the large base of the fruit facing the swamp hen's approaching foot. As the bird rotated its head, its foot made contact with the fruit, but the contact was made on the slippery green skin of the fruit and it failed in its grasp. The swamp hen then retracted its foot and began to reach again, but this time, the magnitude of the rotation by its head was larger, so that as its foot struck the watermelon, it hit nearer to the fleshy red part of the fruit. This example, like many others, shows that it is the amount of head rotation that accommodates for the size and shape of the food, allowing for the correct placement of the digits on the food as it protrudes from the bill.

To test the relative contribution of head and foot movements in the failure to achieve a grasp quantitatively, 3-6 cases each of successful and unsuccessful grasps were scored. The first failed grasps that could be observed for each bird were used. The next successful grasp by the same bird occurring on the videotape was scored for comparison. In each case, head movements (vertically down plus rotation) were scored as being absent or present. If present, they were scored for whether they temporally preceded the foot reaching the level of the tip of the bill (within 2-3 video frames as indicated in Fig. 2), or were out of phase with the foot's movement (i.e., occurring as or after the foot reached the level of the tip of the bill). Grasps with head movements present and correctly timed were given a score of 0 and grasps with such movements absent or inappropriately timed were given a score of 1. The values for all grasps for each bird were added together with the total value per bird having a possible range from 0 to 6. A Wilcoxon paired ranks test was used to compare the scores for successful grasps with unsuccessful grasps, revealing a significant difference (T (6) = 0, $p < 0.05$). In all successful trials, the movements of the head were present and correctly timed, whereas, in all cases of failure, the head movements were either absent or delayed.

Prediction 5: *Studies have shown that, for a wide range of FAPs encompassing diverse species, there is more variability in the movements performed (kinematics) than in the trajectories described in space or the velocity or duration of those FAPs (e.g., Dane, Wakott, & Drury, 1959; Dixon, Duncan, & Mason, 2008; Davies, 1978; Finley et al., 1983; Mather, 1986; Pellis, 1985; Pellis et al., 2009; Stamps & Barlow, 1973; Wiley, 1973). Therefore, it was predicted that there should be low variability in the duration of the reaching to grasp movement, or, at least, there should be no systematic variation with food size or shape and movements of the head.*

The duration of the first 10 sequences of reaching for each bird were scored. A reach was defined as starting from the frame in which the swamp hen lifted its foot (base of the metatarsals) off the ground to the frame in which its digit closest to the food–contacted the food item. A one-way ANOVA showed no significant differences among the birds ($p > 0.05$), and so the data from all birds were combined. Reaches lasted just under half a second and were relatively invariant, as indicated by a coefficient of variation close to 20% (Table 1). Moreover, there were two phases in the reach, a forward and upward movement that brought the bird's foot to the level of the junction between the upper edge of the wing and the neck, and a forward and downward movement that brought its foot to the side of its bill (see Fig. 2). The first phase was significantly longer than the second phase (2-tailed matched pairs t-test: t (59) = 3.09, $p < 0.01$), but there was no significant difference in the variance (comparison of the coefficients of variation: C-statistic, $p > 0.05$) (Table 1). However, four of the reaches differed from the others. In these instances, once the forward movement of the bird's foot reached the apex of its upward movement, its foot remained stationary for several frames before commencing the forward and downward movement. Even though these reaches with pauses were rare (6.7% of reaches), they tended to be among the longest lasting sequences.

All the videotapes were re-examined to locate additional sequences with pauses. A total of 12 reaches were identified with at least one each per bird. However, given that different birds contributed differing numbers of cases (1-4), for comparison with sequences without pauses, the next sequence from the same bird that did not contain a pause was scored. This provided a matched control sequence for each sequence with a pause. The total duration of sequences were scored as were the duration of the first and second phases of the reach. The total duration of sequences with pauses were significantly longer than those without (t (11) = 3.30, $p < 0.01$), but the duration of both the first and second phases were not ($p > 0.05$) (Table 1). That is, the main reason for the longer duration of the sequences with pauses was the intervening length of the pause.

Table 1

Duration of reaching calculated in msec is shown as means and standard deviations with values for the coefficient of variation given beneath in parentheses.

Phase of reach	Complete reach	Phase 1	Phase 2
Overall sample (N = 60)	486.67 ± 113.67 (23.4%)	286.67 ± 60.0 (20.9%)	186.67 ± 42.0 (22.5%)
Sample with pause (after phase 1) (N = 12)	673.33 ± 130.00 (19.2%)	313.33 ± 66.33 (21.2%)	191.67 ± 44.67 (23.3%)
Matched sample without pause (N = 12)	496.67 ± 80.00 (16.1%)	306.67 ± 56.67 (18.5%)	191.67 ± 36.67 (19.1%)

A common feature of the sequences with the pauses was that the swamp hen's head was at an orientation away from its midline (in line between the two wings and in a horizontal position). For example, in one sequence, as the swamp hen lifted its foot, it moved its head upward, and by the time its foot reached its peak height, the bird had turned to face the opposite direction. At that moment, the swamp hen's foot paused in its movement and then remained in that position until the bird turned its head and moved to align it to its midline, at which point it began to move its foot in a downward stroke as its head was lowered and rotated. This resulted in the food item being positioned to intercept the foot. To test whether such head misalignment accounted for the pauses in the foot's reaching movement quantitatively, all the cases of reaches with pauses were scored for the position of the bird's head at the frame when it stopped its foot moving. In all but one case, the swamp hen raised its head above the horizontal orientation and/or turned it to the opposite side of its body (X (12) = 1, $p < 0.01$). In the remaining case, the bird was lifting a large leaf of romaine lettuce, which seemed to be stuck to the substrate, and even though its head was in the midline position, it stalled it in its upward movement to approximately the horizontal starting position, and it was at this moment that it paused its foot's movement. The swamp hen did not move its foot towards the position of its head in any of these cases - rather, its foot followed its typical upward trajectory, paused, and then resumed the typical downward trajectory. That the pauses are functionally related to the position of the head is also supported by the greater variation in the length of pauses (CV = 53.9%), which was significantly greater than the variation in the other two phases of the reach (phase 1: C (11) = 2.77, $p < 0.05$; phase 2: C (11) = 2.57, $p < 0.05$) (Table 1). That is, the foot 'waits' until the head moves into the correct position, and the duration of this pause can vary from case to case.

Prediction 6: *When a swamp hen is eating food items, they are often held in the air with its foot. It was predicted that, when so held, it would be movements of the head and neck that the swamp hen would use to access the food item so as to* *break pieces off, rather than it being foot and leg movements by which it would bring the food item to its bill.*

The first 10 cases in each bird of pecking at food that was held in its foot were scored. Three possible combinations of movement were recorded: the head and neck made all the movements necessary to access the food, the foot and leg was raised upwards to bring the food to the bill, or contact between the bill and the food arose from a combination of both head and neck, and foot and leg movements. For all the birds (X (6) = 0, $p < 0.05$) and in all cases (χ^2 (2, 60) = 80, $p < 0.001$), contact with the food item involved the birds moving their head and neck, not their foot and leg. When the swamp hen held an item with its foot, especially large items that took 10 s or more to consume, its foot, likely due to fatigue, was gradually lowered before being partially lifted again. However, in each case, if the swamp hen kept its foot at a new location, it moved its head to compensate for the position of the foot; its foot was never raised fully to the location of its bill.

Discussion

Foot-head contact during head scratching can theoretically be achieved by one of three patterns of movement: head and neck movements alone, foot and leg movements alone, or by some combination of foot and head movements. As with other birds (Pellis, 1983, 2010), when a purple swamp hen scratches its head, foot-head contact arises from movements of the head, neck and body. Thus, the first prediction made, that head scratching in this species follows the same rule for foot-head coordination as in other species, was upheld. The main hypothesis tested in this paper was whether the same constraint on foot and leg movement applies in another functional context involving head-foot coordination. In the case of the purple swamp hen grasping a food item in its bill, it was expected that, if this rule applied, it would be the head that made the adjusting movements necessary to achieve a successful grasp, not the foot. Four of the predictions on foot-head coordination during food manipulation concerned the kinematics of the movements, and, in all cases, the data supported the hypothesis. The fifth prediction concerned the duration of reaches, and while generally consistent with the view that the foot made a relatively invariant motion, these data also revealed one possible way in which the movement of the foot could be modified to accommodate the position of the head.

If the swamp hen's head was not in the midline, the bird could pause the movement of its foot once it reached its maximum height, and only resume the downward part of the reach once it returned its head to the midline. Under some conditions, then, the swamp hen could interrupt the movement of its foot to facilitate head-foot coordination. However, in no case were such pauses associated with a change in the path that the foot traveled. That is, while the swamp hen can modify some aspects of the timing of movement to coordinate with the position of its head, the coordination needed for bill-foot contact still depends on head and neck movements.

Avoiding Making two Movements at Once

Conceptualized as a FAP (Llinas, 2001), head scratching is organized around the principle that when different parts of the body that are distally connected move simultaneously to achieve a coordinated outcome, that coordination arises from the movements of only one component of the body. That is, in head scratching, the rule of not moving multiple body parts, and so minimizing computational costs, is used (Pellis, 2010). This rule is followed in the head scratching of purple swamp hens, and as indicated above, they also follow this rule when grasping and manipulating food items.

When the swamp hen's foot grasps the food item that is held in its bill, the movements of its head and neck intercept the trajectory of its foot. Failure to achieve a grasp occurs when the swamp hen makes inadequate or delayed movements of its head and neck. In Australian magpies, when grasping with the foot first emerges early in post-fledging development, this type of failure is common, and arises from delayed or inadequate head and neck movements (Pellis, 1983). Although such a failure was rare in the adult purple swamp hens observed in this study, when it did occur, it was for the same reason as for the immature magpies – due to not making an appropriate movement of the head.

In humans, hands are used to reach for food items and then bring them to the mouth and the coordination between the head and hand appears to follow a similar rule structure (Whishaw, Pellis, & Gorny, 1992) to that described for birds (Pellis, 1983; this study). The dissociation of the two independent actions by the hand and head are most evident in people with Parkinson’s disease (PD) (Whishaw et al., 2002). In control subjects, the trajectory of the hand and the head converge together in what appears to be a combined movement, which results in the food being placed in the mouth. In PD patients, however, the independence of these two movements is clear. The patients pick up a food item with one of their hands, and then bring that item towards a location in space where, in control subjects, their mouths would be, but in this case, due to a delay in their head movements, their hands reach the location before their heads. As in the case of the Australian magpie and the purple swamp hen, the hand does not move to where the head is really situated, but rather, makes a relatively stereotyped movement to where the head ‘should be’. What these actions of the PD patients show is that successful contact between the limb extremity (in this case, the hand) and the mouth depends on appropriate compensatory movements by the head and neck to meet the hand.

In a manner similar to humans, a rat uses its forepaws to grasp food items and bring them to its mouth, with apparently coordinated movements of the paw and head (Whishaw & Pellis, 1990). As with PD patients, rats with experimental brain damage to both cortical and subcortical areas, which can include damage to areas that are dysfunctional in PD, also show that the retrieval of the food item and bringing the mouth into position to meet the paw can be dissociated (e.g., Whishaw, Pellis, Gorny, & Pellis, 1991; Whishaw, Pellis, & Pellis, 1992). In such a case, the paw typically moves back to a position where, in a control rat, the head is normally, but due to a delay in the movement of its head, its mouth does not arrive at the correct spatial location to receive the food item.

Some Anatomical Caveats

Before concluding that the pattern of head and foot coordination is best explained by a neural rule, it is important to consider whether a simple constraint created by body morphology provides a more parsimonious explanation (e.g., Barrett, 2011; Chiel & Beer, 1997; Coghill, 1929). In both the data presented and the interpretations from the literature, two cases where a neural rule cannot be assumed until the role of peripheral anatomy can be discounted are most evident. First, PD patients suffer from muscular rigidity and this may constrain the movements of the hand and arm and so impose the limits on hand-mouth coordination. This explanation for the dissociation between the coordination of the head and hand movements in such patients is unlikely for two reasons. The same dissociation was present in patients treated with medications and brain stimulation that by standard neurological measurement largely normalizes muscular rigidity (Melvin et al., 2005), and for rats with some versions of brain damage mimicking that of PD patients, the dissociation in the coordination of the head and paw occurs in the absence of symptoms of muscular rigidity (Whishaw et al., 1994). Thus, it would seem that the lack of coordination between the head and the hand (paw) arises from some neural disturbance to a brain-derived rule rather than to a peripheral problem with the muscles.

Second, the leg and foot joints of birds have very limited mobility in the lateral plane, and virtually no capacity for rotation around the longitudinal axis, leaving most of the movement available to vertical movements in the anterior-posterior plane. As a consequence, it could be argued that the foot would have little option but to be limited to the vertical plane, requiring the head to make the necessary compensatory movements for coordination of head and foot contact. If so, then the ‘not making two movements at once rule’ would be an artifact of body anatomy, not a cost-saving neural rule. There are several reasons that suggest that such morphological constraint is insufficient to account for the entire pattern described in this paper for head and foot coordination.

First, the lack of lateral and rotational movements may be explained by the anatomical constraints on the joints of the leg segments, but not why the foot fails to move vertically so as to meet the head. Rather, the foot is raised to a relatively stereotyped location in front of the body, with head and neck movements required to lower the bill to intercept the foot. It is anatomically feasible that the vertical elevation of the foot could vary from reach to reach, but this was not the case. The same is true when head movements are used to peck at a food item held in the foot. As noted in the Results, on occasion, the foot gradually sinks downward during a protracted bout of feeding, but it is the head that moves down to meet the foot after an interruption where, say, the head is raised to scan the terrain. There is no anatomical reason as to why the foot is not raised to the vertical location of the head, or for both the head and foot to move and so converge on a common spatial location. In all cases, the head has to converge on the position of the foot. Second, given the freedom of movement of the leg in the vertical plane, the limited lateral and rotational movements of the leg cannot account for the relative invariance in the duration of the vertical movements comprising the reaching to grasp action. Third, there is an inward component to the reaching to grasp movement, indicating that there is some, if limited, movement in the lateral domain, yet when grasping food items that are large or oddly shaped and so protrude far from the bill, the foot does not move as far laterally as it is capable of, but rather, maintains the same trajectory, leaving the head to make the compensatory lateral and rotational movements. Finally, from a comparative perspective, a similar morphological constraint may apply to both the hind limbs of birds and to some mammals in restricting the amount of lateral and rotational movements when the foot is used to scratch the head (Pellis, 1983, 2010, this study), but this does not account for spider monkeys restricting themselves to the same rule of coordination when using the hand to scratch the head (Pellis, 2010). Spider monkeys brachiate as their main form of arboreal locomotion, and to accommodate this type of locomotion, they have an enormous amount of rotational freedom in the shoulder, elbow and wrist, and hence, there is no anatomical constraint for them to moving their hands and arms to contact their head. Thus, while the constraints imposed by body morphology may be important to account for some of features of head and foot coordination, they do not account for the limitation in the contribution of the foot (or hand). Rather, there does appear to be a neural constraint that accounts for at least part of this phenomenon.

Keeping Computational Costs Down

The data on head scratching (Pellis, 1983, 2010) and food grasping (Pellis, 1983; Whishaw & Pellis, 1990; Whishaw, Pellis, & Gorny, 1992, Whishaw, Pellis, & Pellis, 1992, Whishaw et al., 1994, 2002) show that, within these tasks, the rule of limiting the computational costs of coordinating multiple parts of the body applies to many species (e.g., Australian magpies, flamingos, deer, rats, spider monkeys, humans). The data on purple swamp hens show that this rule applies across tasks in the same species. That is, in two different FAPs involving head-foot coordination, head scratching and food grasping, the same organizing principle for head-foot movement is used. These data are consistent with findings that some of the same distinctive components of movement can be used across different FAPs (e.g., Flash & Hochner, 2005; Jing et al., 2004; Mather et al., 2010), except that in the case of head-foot coordination, that component is a rule for coordinating different body parts across different FAPs. The use of such modular construction, either in the particular movements used (Llinas, 2001), or in the rules by which multiple parts of the body are coordinated (Field & Pellis, 2008; Pellis, 2010), provides ways by which the computational costs of constructing complex and functionally varied movements are curtailed. Using the same modules of movement repeatedly, and applying the same organizing rules across contexts, could be fairly general ways by which relatively simple rules can generate complex and varied behavior (e.g., Alberts, 2002; Barrett, 2011; Gigerenzer, 2002; Powers, 2009; Schank, May, Tran, & Joshi, 2004).

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