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RESEARCH ARTICLE

An Experimental Study of Nettle Feeding in Captive Gorillas

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Mountain gorillas (*Gorilla beringei beringei*) in Karisoke, Rwanda, feed on the stinging nettle *Laportea alatipes* by means of elaborate processing skills. Byrne [e.g. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences 358:529–536, 2003] has claimed that individuals acquire these skills by means of the so-called program-level imitation, in which the overall sequence of problem-solving steps (not the precise actions) is reproduced. In this study we present western lowland gorillas (*Gorilla gorilla gorilla*) with highly similar nettles. Twelve gorillas in three different groups (including also one nettle-naïve gorilla) used the same program-level technique as wild mountain gorillas (with differences mainly on the action level). Chimpanzees, orangutans, and bonobos did not show these program-level patterns, nor did the gorillas when presented with a plant similar in structural design but lacking stinging defenses. We conclude that although certain aspects (i.e. single actions) of this complex skill may be owing to social learning, at the program level gorilla nettle feeding derives mostly from genetic predispositions and individual learning of plant affordances. Am. J. Primatol. 70:584–593, 2008.

Key words: program-level imitation; affordances; individual learning; traditions; gorillas; nettle feeding

INTRODUCTION

Mountain gorillas (*Gorilla beringei beringei*) of Karisoke, Rwanda (hereafter ''MGs''), feed mainly on leaves and the stem-piths of various herbs [Watts, 1984]. Some of these plants possess defenses such as thorns, spines, and irritant hairs that individuals have to overcome before ingestion. MGs tackle plant defenses using complex manipulative sequences that render the defenses ineffective. Moreover, MG individuals show a high degree of concordance in the steps that they use to tackle the different plant species, though they differ both within and between individuals in the specific actions that are used to accomplish each step [Byrne & Byrne, 1993].

Byrne [2003; see also Byrne & Russon, 1998] has argued that the complex manipulative sequences applied to each plant species are acquired by what he calls program-level imitation. Program-level imitation involves the reproduction at a coarse, structural level of the behavior of a model without reproducing the specific actions observed. Thus, all individuals may pull and then fold a plant before eating it, but the actions used to pull or fold may vary within and between individuals. Hence, on this view, the steps and the order of those steps are socially learned, whereas the underlying actions of the program (also named ''skill elements'') are acquired via trial-and-error learning [Byrne & Byrne, 1993]—or they may have already formed part of the species' natural behavioral repertoire.

Several authors have offered alternative explanations for the acquisition of food-processing skills in MG. They have proposed that the combination of trial-and-error learning, plant affordances, genetic predispositions, and motivational factors may produce the observed feeding pattern [e.g. De Waal, 1998; Matheson & Fragaszy, 1998; Tomasello, 1998; Vereijken & Whiting, 1998]. Bauer [1998] has questioned ''whether the target behavior is inevitable, given the organism, its goals, its environment and the constraints imposed thereby'' [see also Midford, 1998; Miklosi, 1998; Tomasello, 1998]. Several authors have proposed that the case for program-level imitation would be much stronger if another population of MGs living in the same environment and also eating the same plants had

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developed a group technique that is different from the one described [e.g. Bauer, 1998; De Waal, 1998; Tomasello, 1998; Vereijken & Whiting, 1998]. Although Byrne [2005] acknowledged this point, he has predicted that even naïve human subjects would not discover the precise method of nettle feeding used by MGs. He has also argued that chance discoveries are unlikely, especially given that plants with defenses ''discourage playful exploration by the pain they induce'' [Byrne, 2005]. Moreover, Byrne and Russon [1998] argued that it is unlikely that environmental pressures would lead all gorillas to converge mostly on one technique, while still allowing for diverse small-scale actions. Thus, the distilled argument in favor of social learning for MG complex-feeding techniques appears to be one based on its improbability and complexity—especially given that gorillas are yet to show skills of program-level imitation in experiments [Stoinski et al., 2001].

One of the staple foods of the Karisoke MG population is the nettle *Laportea alatipes* [Watts, 1984]. According to the work by Byrne and colleagues, MGs follow six basic steps to process this plant before ingestion: (1) pull the nettle into range, (2) strip up the nettle stem(s) to produce a whorl of leaves, (3) hold the resulting whorl and rip off the small stems of the leaves (petioles), (4) clean the whorl of debris (if it exists), (5) fold the mass of blades over the thumb ''with the powerful stings of the leaf margin enclosed within a parcel that presents to the outside only the less sting-infested undersurface of the leaf'' [Byrne & Russon, 1998], and (6) introduce the resulting parcel in the mouth [Byrne & Byrne, 2003; Byrne et al., 2001a]. The standardization of the six-step nettle-feeding process reaches 88% concordance in the MG population [i.e. when lateralization is left out; Byrne & Byrne, 1993]. Byrne and Byrne [1993] and also Byrne and Russon [1998] have claimed, again, that such high levels of correspondence are most parsimoniously explained by program-level imitation.

In a recent study, Huffman and Hirata [2004] gave medicinal leaves—whose use was thought to be socially transmitted in the wild—to naïve chimpanzees in captivity. The result was that some individuals used them in ways similar to wild chimpanzees straightaway, whereas others took some time to acquire the behavior. This suggests that although socially facilitated learning may play some role in the use of medicinal leaves, it is not necessary for all individuals. In this study we followed a similar strategy by providing three different groups of captive lowland gorillas (CGs) with nettles very similar to *L. alatipes* (European nettles, *Urtica dioica*). Most of these individuals had previously had some opportunities to process nettles in their outdoor enclosures, but there was one completely nettle-naïve gorilla. For additional relevant information, we also presented these nettles to bonobos, chimpanzees, and orangutans, and we also presented the CGs with a plant without any stinging hairs (i.e. ''willow''—suited as controls, because they are similar in structural design to nettles insofar as they are long, straight, and unbranched). We looked at the individuals' food-processing technique both at the action level and at the program level. Together, these analyses enabled us to examine with experimental data the various mechanisms that have been postulated to explain the acquisition of nettle processing: genetic predispositions, individual learning taking account of plant affordances, and social learning (particularly program-level imitation).

METHODS

Subjects

We tested 12 western lowland gorillas housed in three different zoos (Leipzig, Arnhem, and Stuttgart: Table I) ranging from 4 to 27 years of age. Whereas four of the five Leipzig gorillas had origins in Arnhem Zoo, there was no connection between these two zoos and the naïve Stuttgart gorilla. Additionally

TABLE I. Study Subjects, Gorillas

Name	Sex	Age	Zoo	Arrived at zoo	Transferred from	Rearing	Nettle experience
Gorgo	M	24	Leipzig	5.3.2001	Arnhem	Hand	Yes
Bebe	F	26	Leipzig	5.3.2001	Arnhem	Wild	Yes
Ruby	F	8	Leipzig	5.3.2001	Arnhem	Parent	Yes
N'diki	F	27	Leipzig	12.10.2001	Arnhem	Wild	Yes
Viringika	F	10	Leipzig	23.1.2001	Zurich	Parent	Yes
Bauwi	M	17	Arnhem	29.3.1995	Apeldoorn	Parent	Yes
N'gayla	F	13	Arnhem	9.5.1993	Apeldoorn	Parent	Yes
Shatilla	F	9	Arnhem	17.4.1997	Apeldoorn	Parent	Yes
Shinda	F	5	Arnhem	9.10.2001	Apeldoorn	Parent	Yes
N'yaounda	F	5	Arnhem	5.2.2001	Apeldoorn	Parent	Yes
Likale	M	4	Arnhem	14.12.2001	Apeldoorn	Parent	Yes
Mutasi	F	12	Stuttgart	12.6.1994	No transfer	Parent	No

we also included five bonobos, five orangutans, and five chimpanzees from the Leipzig Zoo.

All study subjects were fed a diet of fruit and vegetables and were regularly supplied with leafy twigs of various tree and shrub species. The apes at both Leipzig and Arnhem Zoos had outdoor enclosures where they had access to nettles (*U. dioica*) in the past; indeed, they were previously known to feed on them. Two gorillas in Leipzig were born in the wild (Cameroon); however, wild western lowland gorillas are not known to feed on nettle [Rogers et al., 2004]. The gorillas in Stuttgart only had access to tiled indoor and outdoor enclosures. Despite the regular supply of leafy shrubs and herbaceous plants, Stuttgart gorillas were never provided with nettles. In Stuttgart, we focused on the gorilla ''Mutasi'' because she was born in Stuttgart Zoo and never transferred—so that any previous nettle experience could be completely excluded.

All subjects had access to large outdoor enclosures and smaller indoor ones. All Leipzig subjects were housed in the Wolfgang Köhler Center (group size: gorillas, six; chimpanzees, 17; bonobos, six; orangutans, eight). Group size for the gorillas at Stuttgart was nine, and at Arnhem it was eight. There were various climbing structures and various enrichment devices such as food that required processing or tool use (e.g. puzzle boxes) and ropes for all apes in all zoos. Except for the Stuttgart gorillas all apes also had access to natural vegetation.

Materials

Although the European nettle species used in this study, *U. dioica*, show general structural similarity to the African nettle *L. alatipes*, the two species show differences in distribution and quality of stinging hairs (Table II). The Leipzig apes were also supplied with willow *Salix* sp., which lacks the defensive features of nettles while sharing the general structural design features. Fresh plant stems were collected within 15 min before tests and if not provided immediately placed in water to maintain freshness. Stinginess of the nettles was controlled before tests by E (D. Hedwig) applying a sample to her own skin.

Procedure

The study was conducted between July 2005 and June 2006. The apes in all zoos were provided with plant material and their subsequent behavior was videotaped. The detailed procedure differed slightly between the zoos owing to differences in local conditions.

Leipzig Zoo

For observations on feeding behavior, the study individuals received plant material under controlled conditions in special observation rooms. Tests were conducted under two different conditions, in which the apes were offered either *U. dioica* or willow *Salix* sp. A minimum of three experimental sessions in either condition were set for all study animals. Each session consisted of three testing trials in which the individual had access to two equal-sized plant stems for 10 min.

Tests were carried out in the morning (starting at 8:30) and the animals were fed their regular small breakfast consisting of a few pieces of fruit or vegetables beforehand. Before each trial an individual waited in a cage beside the testing cage. From there the apes could observe the experimenter attaching the plant stems to a mesh with a short burlap ribbon. Subsequently a sliding door was opened whereby the subject gained access to the plants. If subjects did not show interest in the provided plants, the experimenter tried to

TABLE II. Characteristic Features of African Nettle (*Laportea alatipes*), European Nettle (*Urtica dioica*), and willow (*Salix* sp.)

	Laportea alatipes	*Urtica dioica*	*Salix* sp.
Growth form	Herb	Herb	Shrub
Leaf arrangement	Alternate	Opposite	Alternate
Distribution of stinging hairs	Most stings on stem and petioles[a] Least on leaf underside[a]	Equal on either side of leaves[b]	n.a.: no stinging hairs
Quality of stinging hairs	Readily burned through two layers of clothing (…)[c] My knees were swollen and red welts covered my face[c] Is extremely painful[d]	Does not burn through two layers of clothing[d] Causes tiny swellings[d] Produces an endurable pain that disappears quickly[d]	n.a.: no stinging hairs

[a]Byrne and Russon [1998] and Byrne [2005].
[b]Maximilian Weigend [personal communication].
[c]Schaller [1963].
[d]Personal observation of the authors.

encourage them through pointing and calling the subject. After each trial the ape was led back into the adjacent cage and received a grape. During those breaks, plants in the testing cage were replaced with fresh ones and the remains of processed plants were removed. Subjects were tested individually, except females with dependent offspring. To avoid distress for some individuals, a conspecific was placed in a non-adjacent cage nearby the testing cage, from where it could not observe or, as far as could be assessed, influence the activity of the focus animal.

Burger's Zoo (Arnhem)

Owing to local restrictions, the gorillas were supplied with nettles in a social setting in their outdoor enclosure. That is, the gorillas received 20 nettle stems on 12 consecutive days twice a day after they received their regular food at 13:30 and 15:00. Nettles were thrown into the enclosure from an observation platform, and to avoid monopolization, the plants were scattered throughout the enclosure. Focal subject video recordings (with one camera) were conducted until all nettles were consumed. We aimed to record as many feeding sequences from as many individuals as possible, while also collecting equal sample sizes from the individuals.

Wilhelma Zoo (Stuttgart)

Owing to local restrictions, the one naïve subject was supplied with nettles in a social setting in its indoor enclosure on 15 subsequent days. Nettles were supplied alongside with regular food. The number of daily sessions and provided nettle stems was increased over the study period, according to increasing nettle intake of the study subject. Initially, nine nettles were provided once a day, but from session ten onward 18 nettles were provided twice a day at 8:00 and 11:00 in the morning. Video recordings were conducted for a maximum of 2.5 hr after the nettles were first provided. Video recordings ended once all nettles were consumed.

We obtained 68 hr of video recordings containing 296 behavioral sequences of nettle feeding from 12 subjects and 176 behavioral sequences of willow feeding from 11 subjects (Table III).

Data Scoring and Analysis

We videotaped the plant processing of each subject and subsequently scored the manual actions (action level) as well as the sequential structure (program level) that constituted the behavioral sequences [see Table IV for the study ethogram, slightly modified from Byrne & Byrne, 1993]. Like Byrne and Byrne [1993] we also defined an action as a manipulation that led to an observable change of state of the plant material. Unlike Byrne and Byrne [1993] we did not score information about laterality and manual dexterity on the level of finger movements because they are not socially transmitted [Byrne, 2003; Byrne & Byrne, 1991], nor did we include levels of bimanual coordination, as this constitutes a natural predisposition of ape object manipulation in general [compare Torigoe, 1985]. Also, because of the way we presented the nettles to our gorillas (a few clean nettles), we could not investigate any potentially ''iterative loops'' to accomplish ''sub-goals'' (e.g. cleaning the nettles) within the main goal. We also ignored some plant procuring actions because our plants were never rooted to the ground. Thus, we focus here on the two most central characterizations of the task from a social learning point of view: the repertoires of action elements (action level) and the ''ordering'' of them (program level).

Second, following Byrne and Byrne's [1993] procedure, we collapsed the actions into functional categories to create the program level (see Table V). The program level consisted of a sequence of actions grouped into categories leading from plant procurement to the ingestion of leaves. We distinguished the following four categories, strictly according to functions [see Byrne & Russon, 1998]: (1) procurement (2) gathering a whorl of leaf blades, (3) processing the whorl, and (4) insertion into mouth. Although we did not consider actions for cleaning (as explained

TABLE III. Overview of Data Set

		Nettle		Willow	
	Tested subjects	Consuming subjects	Leaf-feeding sequences	Consuming subjects	Leaf-feeding sequences
Leipzig gorilla	5	3	61	4	62
Arnhem gorilla	6	6	203	n.a.	n.a.
Stuttgart gorilla	1	1	22	n.a.	n.a.
Leipzig orangutan	5	1	9	4	96
Leipzig bonobo	5	1	1	3	18
Leipzig chimpanzee	5	0	0	0	0

TABLE IV. Ethogram of Actions Used for Feeding on Leaves by the Apes in Leipzig Zoo and the Captive Western Lowland Gorillas in Arnhem and Stuttgart Zoos

Gather	
Pick out	Pinch grip on small item that is pulled off an object or out from among a mass of items
Strip	Half-open grip around leafy stem to slide up stem against force of detachment or the other hand's supporting grip, ending up with holding a bundle of leaves in the hand
Process	
Manipulate	Form and position of a bundle of items held in one hand is changed by using the fingers of the same hand. Often the leaves held in the hand are folded over in that way
Adjust	Delicately changing the position of an item held in one hand with fingers or knuckles of the other hand
Pinch	Bundle of leaves held in one hand is passed to the other hand, mostly grasped with a pinch grip and taken back to first hand with pinch grip
Rumple	Loose bundle held in one hand is compressed by pushing it with the knuckles or palm of the other hand
Roll	Untidy bundle is rubbed with hand on parts of the body to produce a roll-shaped bundle
Fold	Bundle held in one hand is loosened and then pulled out by the other hand. Next, the bundle is folded over by the latter hand (often, not always, using the thumb of the first hand as fulcrum). Lastly, the thumb of the first hand re-grasps the bundle
Folding	Leaves held loosely in one hand are folded over with thumb or index finger of the other hand and grasped again with the holding hand
Unplug	Part of leaf, mostly petiole, is teared off the leaf with pinch grip
Palm squeeze	Altering the form of an untidy bundle of leaves held in one hand by pushing it repeatedly against the palm with the fingers of the other hand (mostly thumb), thus often folding it up into a compact bundle
Squeeze up	Bundle of leaves held in the hand is compressed by the closure of the hand, then handed over and compressed again
Pull apart	Bundle of leaves held in two hands, applying force to it in opposite direction, to tearing the bundle apart
Twist apart	Object held in both hands, then twisting of each hand vs. the other used to tear the object
Lever apart	Object held in both hands, then leverage of rocking the hands or knuckles against each other used to tear the object
Insert	
Put into mouth	Food item is put into the mouth as a whole
Bite off	Teeth used to cut off a part of a handful of leaves to ingest it
Sausage feed	Repeated loosening and grasping lower down a food item to feed it into the mouth as a whole
Two-hand feed	Leaf is inserted into the mouth while being held with two hands
Tooth strip	Partial closure of teeth around stem, pulling against support of hand ending up with leaves inserted in the mouth
Leaf strip	Single leaf is stripped with teeth along the midrib, ending up with material inserted into the mouth
Mouth pick	Single or several small items are picked off the stem with grip of teeth or lips
Put in	Food item held in the hand is inserted into the mouth as a whole

above), we nevertheless scored removing debris as another functional category. These are the same categories (in the same order) used by Byrne and Russon [1998], except that here two processing parts (steps 3 and 5) of Byrne and Russon [1998] were combined into one category to accommodate the fact that they both serve the same function (i.e. to process the whorl of leaves to make it palatable).

We compared the relative frequency of the various actions and programs for nettle processing within all CGs. We depicted the program that was performed by all individuals with a flowchart. Second, we compared CGs with MGs and other ape species including their respective flowcharts. Finally, we assessed the impact of plant defenses on the processing behavior by captive apes by contrasting processing technique for nettles and willows. High interobserver reliability was achieved for nettle-feeding actions (see Table IV) by an independent coder (C. Tennie), who randomly selected and coded 15% of feeding sequences available for every zoo (Pearson's: Stuttgart $r = 0.968$; Arnhem $r = 0.977$; Leipzig $r = 0.971$).

RESULTS

Captive Gorillas

Most CGs in all tested groups fed on nettles, including the naïve individual from Stuttgart. The only two CGs that were never motivated to feed on nettles were Gorgo and Viringika, both in Leipzig. Table VI gives the repertoires of actions for gathering, processing, and ingesting plant material in each of the three groups. The overall size of the repertoire was 13 and 11 actions for the Leipzig and Arnhem nettle-experienced gorillas, respectively. The nettle-naïve individual at Stuttgart Zoo performed eight actions for gathering, processing, and ingesting nettles.

Focusing on the program-level analysis, all gorillas sorted actions into sequences in similar ways. In particular, all gorillas in Leipzig and Arnhem most frequently performed the sequence ''procure–gather–process–insert'' (Fig. 1a, Table VII). In Leipzig and Stuttgart divergences occurred in the form of removing debris off the plant stem (Table VII, ''other''). In Arnhem the individual ''Shinda'' once performed the sequence ''procure–process–gather–insert'' (Table VII, ''other''). The naïve gorilla also performed the program ''procure–gather–process–ingest'' for feeding on nettle leaves. However, she did so less frequently than experienced gorillas and mostly left out the processing step (Fig. 1d).

TABLE V. Ethogram of Functional Behavioral Categories Used for Feeding on Leaves by the Apes in Leipzig Zoo and the Captive Western Lowland Gorillas in Arnhem and Stuttgart Zoos [Largely Based on Byrne & Byrne, 1993]

Functional category	Description
Procurement	Initial procurement of nettles that were provided
Gather	Leaves are manually collected ending up with a bundle of leaves held in the hand
Process	Bundle of leaves held in the hand is treated manually to change the position and shape of single leaves or the whole bundle
Insert	Handful of leaves is put into the mouth to ingest

Captive Gorillas and MGs

Table VI also gives the repertoires of actions for gathering, processing, and ingesting plant material in MGs. CGs and MGs showed a substantial overlap in the actions used to process nettles. Seven out of the 11 actions used by MGs were also observed in lowland gorilla nettle feeding. MGs and CGs use the same actions for gathering leaves with their hands (''pick out'' and ''strip'') and showed large overlap in the repertoire of actions for manually processing leaves (''adjust'', ''manipulate'', ''squeeze up'', ''pull apart''). However only the MGs twist or lever apart

TABLE VI. Actions Performed by the CG Groups in Comparison With the MGs

	Mountain gorilla *L. alatipes*	Stuttgart *U. dioica*	Arnhem *U. dioica*	Leipzig *U. dioica*	*Salix* sp.
Gather					
Pick out	×	1	6	3	4
Strip	×	1	6	3	4
Process					
Manipulate	×	1	6	1	–
Adjust	×	1	1	1	–
Pinch[a]	–	–	1	–	–
Rumple[a]	–	–	1	2	–
Roll	–	–	5	3	–
Fold	×	–	–	–	–
Folding[a]	–	–	1	1	–
Unplug[a]	–	1	–	–	–
Palm squeeze[a]	–	–	–	1	–
Squeeze up	×	–	–	1	–
Pull apart	×	–	–	1	–
Twist apart	×	–	–	–	–
Lever apart	×	–	–	–	–
Insert					
Put in[a]	–	1	6	3	4
Bite off	×	–	3	1	–
Sausage	–	1	6	1	1
Two-hand feed[a]	–	1	–	–	–
Tooth strip[a]	–	–	–	–	4
Mouth pick	×	–	–	–	4
Sequences	> 4/individual	22	203	61	62
Individuals	39	1	6	3	4

CG, captive lowland gorilla; MG, mountain gorilla. For CGs number of individuals performing the action are indicated. Crosses indicate unknown number of individuals. See Methods section for descriptions of actions and further details on the construction of the here presented ethogram.
[a]These actions were not coded in Byrne and Byrne [1993].

TABLE VII. Feeding Sequences for European Nettle *Urtica dioica* of Captive Western Lowland Gorillas in Leipzig and Arnhem and the Naïve Gorilla in Stuttgart

Zoo	Subject	1–2–3–4	1–2–4	Other	Number of sequences
Leipzig	Ndiki	100	0	0	9
	Bebe	87.5	0	12.5	16
	Ruby	73	21.6	5.4	37
Arnhem	Bauwi	83.9	17.7	0	62
	Ngayla	87.5	12.5	0	24
	Shatilla	96	4	0	25
	Likale	77.8	22.2	0	18
	Nyaounda	100	0	0	15
	Shinda	86.4	11.9	1.7	59
Stuttgart	Mutasi	31.8	59.1	10.1	22

Numbers indicate frequency of performance of a sequence. 1, procurement; 2, gather leaves; 3, process leaves; 4, insert leaves; other, divergence from most common sequence.

the bundle of nettle leaves to remove the petioles—but, in a different context, they also conduct the actions ‘‘roll’’ and ‘‘sausage feed’’, namely for feeding on a plant called bedstraw *Galium ruwenzori* [Byrne & Byrne, 1993]. Interestingly the naïve CG also removed petioles, however, with a seemingly different method (‘‘unplug’’). Similar to the MGs, CGs also performed standardized actions with idiosyncratic means. For the Leipzig gorillas we recorded for every rolling action the body part on which the leaves were rubbed and found that each subject at Leipzig Zoo had a preferred way of rolling leaves.

Focusing on the program-level analysis revealed great overlap between CGs and MGs. When pooling the actions that constitute the modal technique for nettle feeding in MGs [Byrne & Byrne, 1993] according to the functional categories applied in this study, there remain no differences between the sequential organization of nettle feeding of MGs and the gorillas at Arnhem and Leipzig Zoos. All gorillas regardless of the species or population followed the sequence: (1) procure plant, (2) gather leaves, (3) process handful of leaves, and (4) insert leaves (Fig. 1a and b). The naïve gorilla we tested followed this common structure also often—in a third of all cases (Fig. 1d).

Other Apes

In contrast to the gorillas’ propensity for consuming nettles, only two out of the 15 non-gorilla apes ingested nettles at least once. Whereas one orangutan ingested nettle leaves repeatedly, the one nettle-eating bonobo tried a leaf only once. He picked this leaf off and inserted it in his mouth—slightly coughing afterward. He did not repeat this behavior. When the orangutan fed on nettles she preferably ingested nettle leaves directly from the stem, but sometimes gathered leaves manually for insertion. Neither the bonobo nor the orangutan engaged in any processing actions.

Nettle vs. Willow Techniques

Four out of the five tested gorillas and seven out of the 15 non-gorilla apes consumed willow. The technique CGs used for feeding on willow can be best described as the same technique used for feeding on nettles but skipping all processing actions and sometimes gathering leaves directly with their mouths to ingest them (Table VI, Fig. 1c). Other apes followed a similar technique for willow; however, in contrast to the gorillas they preferred gathering leaves directly from the stem for ingestion.

DISCUSSION

All CGs including the naïve gorilla processed and ate nettles in very similar ways at the program level and also to a considerable extent at the action level. The program-level sequences used by all the CGs were very comparable to those used by MGs, and there was also considerable overlap in the actions they used as well. In contrast, none of the non-gorilla apes except one orangutan ate nettles regularly despite the fact that nettles were available in their outdoor enclosures. Finally, CGs used the processing step (needed to neutralize the plant defenses) only for the nettles but not for the willows.

These findings do not rule out social learning as one part of the process of nettle feeding in MGs, but they do suggest that it may play a somewhat limited role. At the program level, our data provide strong evidence for the view that the similarities in action sequences used by all MGs in the wild—and by the CGs in this study including the naïve gorilla—are derived mainly from a mixture of genetic predispositions and individual learning driven by the problem space presented by the nettled plant. The sequence ‘‘procure–gather–process–insert’’ is practically inevitable given: (a) gorillas’ natural tendency to eat these plants (not shared with other apes, as shown in the current data); and (b) the problem space presented by the overall structure of the plant and its stinging nettles for gorilla skills (not shared by the willow, and so a different sequence was used for this plant).

One could argue that wild-born CGs may have learned the technique by program-level imitation in the wild, and when they were brought into zoos, they carried the technique with them. Later on, the technique spread through the captive population by program-level imitation. One problem with this explanation—in addition to the performance of the naïve gorilla—is that CGs belong to the western lowland gorilla species that are not known to eat nettles in the wild [Rogers et al., 2004]. Therefore, it is most likely that the technique was invented in captivity—much like the case of the naïve gorilla in

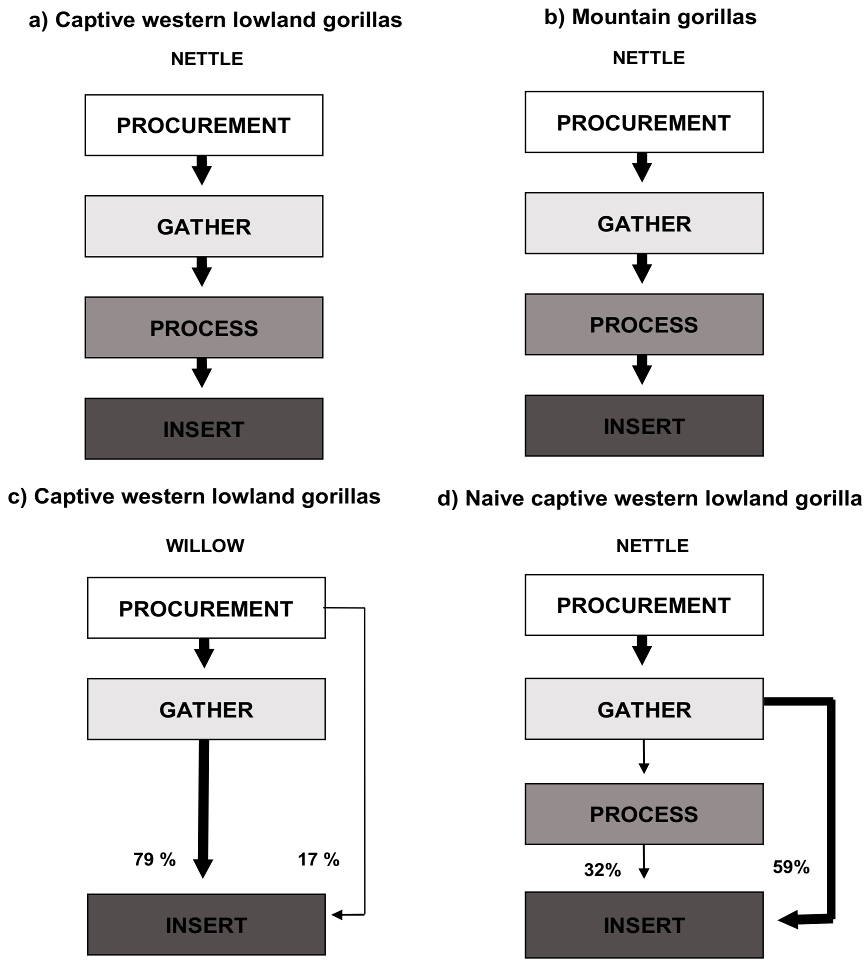

Fig. 1. Leaf-feeding skills of captive western lowland gorillas and mountain gorillas. Thick arrows illustrate the behavioral sequence most frequently performed by all consuming gorillas. Thin arrows indicate divergences from the most frequent sequence performed by all gorillas. Percentage indicates the relative frequency of use of a sequence. Boxes represent functional categories. (**a**) Nettle (*Urtica dioica*)-feeding technique of captive western lowland gorillas in Leipzig and Arnhem Zoos. Comprises 88% of observed feeding sequences of nine study subjects. (**b**) Nettle (*Laportea alatipes*)-feeding skill of wild mountain gorillas. Number of subjects = 39. Comprises 88% of observed feeding sequences of 39 study subjects. (**c**) Willow-feeding skill of captive western lowland gorillas at Leipzig Zoo. Comprises 96 % of observed feeding sequences of four study subjects. (**d**) Nettle-feeding skill of the naïve captive western lowland gorilla at ''Wilhelma'' Stuttgart Zoo (100% of observed feeding sequences of one study subject).

this study. The existence of multiple re-inventions does not support the view of Byrne [2005] that spontaneous invention is unlikely because of the complexity and open-endedness of the problem.

At the level of single actions, also Byrne himself does not believe that social learning plays a decisive role in the ontogeny of nettle feeding in MGs [Byrne & Byrne, 1993]. In the current data, there are some similarities across almost all individuals in the specific actions used; but, as in the case of the program level, most of these are probably based on a mixture of genetic predispositions and individual learning. The existence of individual differences in action techniques (e.g. the exact way in which each Leipzig gorilla used the ''rolling'' action) also supports this view. The pattern of results that would best support a social learning view would be group differences.

Relevant to this possibility, we found some actions that MGs regularly use to eat nettles missing from the repertoires of the CGs (see Table VI). Most of these actions were within the processing part of the program—in particular, in the actions applied to the whorl of leaves. Although all gathering actions were used by both CGs and MGs, there was one insertion action that was missing in the nettle-feeding repertoire of CGs: ''mouth pick''. However, mouth pick occurred during feeding on willows in the Leipzig CGs; hence, this action is clearly in the CGs' repertoire. As for the processing actions, there were some MG-processing actions that were never found in any CG: ''fold'', ''twist apart'', and ''lever apart''. The slight differences between the fold-producing action used by MGs (i.e. ''fold'') and the corresponding actions used by CGs (''folding'' and some of the actions subsumed under ''manipulate'') open the possibility that these behaviors are socially transmitted. Alternatively, they may be a result of the slight differences in affordances of the two different nettle types—specifically the different distribution of nettle stings (see Table II).

We also found some actions performed by CGs but not by MGs. Some of these actions were restricted to single individuals, and others cannot be compared with the MG repertoire as they were not coded by Byrne and Byrne [1993]. Hence, the two actions that are the best candidates for social learning in CG are ''roll'' and ''sausage feed''. However, neither of these were group specific: ''rolling'' was a common action at both Leipzig and Arnhem (and each gorilla in Leipzig used her own idiosyncratic way of rolling). Interestingly, rolling is a very frequent processing technique for another type of plant in MGs, Karisoke: *G. ruwenzori* [''bedstraw'', Byrne & Byrne, 1993], which may possess some of the same affordances of *U. dioica* (although bedstraw does not possess stinging hairs, it is covered also in small extensions that can be a nuisance). ''Sausage feed'' was the predominant technique in Arnhem but not in Leipzig, which presents the best candidate for social learning. However, it was also used by at least one gorilla in Leipzig and, critically, by the naïve gorilla.

Differences of action usage between MGs and CGs were thus very likely owing to the fact that in our study we used the European nettle *U. dioica*, which resembles the African nettle *L. alatipes* in most, but not all, respects. Hence, the observed actions used for nettle feeding of *L. alatipes* will be adapted to the affordances of *L. alatipes* just as the observed actions used for nettle feeding of *U. dioica* will be adapted to the affordances of *U. dioica*. There were no systematic differences between the different groups of CGs on the action level—just as there are no such systematic differences among MG groups in the wild—and so the current data provide no support for social learning as a major factor in gorilla nettle feeding.

Hence, in terms of the general classes of factors that might account for the way gorillas feed upon nettles, the current experimental data, in combination with facts about natural behavior of great apes, suggest the following account. First, genetic predispositions clearly play an important role—perhaps especially in terms of attraction to nettles as edible items. The other species of captive apes were generally not interested in eating the nettles, despite the fact that their individual backgrounds and housing conditions were similar to those of the CGs. Second, individual learning almost certainly plays an important role as well. The CGs processed the defenseless willows in a very different manner to the nettles, apparently adapting to the affordances of the particular plant. Although in theory it is possible that they have separate genetically based programs for the two plants, the different particular actions used by individuals—as documented both by Byrne and Byrne [1993] in the wild and in the current experiment—suggest that some form of individual learning plays a critical role, especially at the action level. Finally, it is conceivable that social learning plays some role in the acquisition of the food-processing techniques described here, but we think that it is a minor one. Most telling in this respect was that the totally naïve gorilla tackled the nettles in a way that was very similar—especially at the program level—to the way the more experienced individuals (including wild MGs) did. There were differences as well, as the naïve individual engaged in less processing. However, this individual was naïve both to social demonstrations of nettle processing and also to nettles themselves, and so these differences could either be owing to lack of social experience or lack of experience with nettles in general. At the level of individual actions, we agree with Byrne [2005] that social learning probably does not play an important role, and in general it looks to us like most of the particular actions exist in the behavioral repertoire of gorillas, or else are easily learned individually when an appropriate situation presents itself. Our overall conclusion may not be totally surprising, as gorillas are yet to be observed using program-level imitation in controlled experiments [Stoinski et al., 2001].

In all, then, our view is that gorilla nettle-feeding techniques at the program level most likely develop through a mixture of genetic predispositions, exposure, and stimulus enhancement to the plants, and individual learning channeled by the affordances of particular plants. At the action level, the particular actions involved are either part of gorillas' natural repertoires, or are (mostly) easily learned individually. Gorilla nettle feeding thus develops spontaneously, in the absence of social models, and is adjusted with time to the details of the environmental pressures and affordances attached to each nettle species—with social learning of some kind possibly playing some small role as well. In all likelihood this way of operating is not confined to the case of nettles alone but generalizes to gorillas' way of dealing with other defended plants [bedstraw: Byrne & Byrne, 1993; thistles: Byrne et al., 2001b] and even to other primate species' techniques for plant processing as well [e.g. in chimpanzees: Byrne & Stokes, 2002; but compare also a similar conclusion for stone-handling behavior in Japanese macaques: Nahallage & Huffman, 2007]. Each case must be examined separately in detail using both natural observations and experiments.

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REFERENCES

Bauer PJ. 1998. If it is inevitable, it need not be imitated. Behav Brain Sci 21:684–685.

Byrne RW. 2003. Imitation as behaviour parsing. Philos Trans R Soc Lond B Biol Sci 358:529–536.

Byrne RW. 2005. Detecting, understanding, and explaining animal imitation. In: Hurley S, Chater N, editors. Perspectives on imitation: from mirror neurons to memes. Cambridge, MA, USA: MIT Press. p 255–282.

Byrne RW, Byrne JM. 1991. Hand preferences in the skilled gathering tasks of mountain gorillas (*Gorilla g. beringei*). Cortex 27:521–546.

Byrne RW, Byrne JME. 1993. Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei*): variability and standardization. Am J Primatol 31:241–261.

Byrne RW, Russon AE. 1998. Learning by imitation: a hierarchical approach. Behav Brain Sci 21:667–721.

Byrne RW, Stokes EJ. 2002. Effects of manual disability on feeding skills in gorillas and chimpanzees. Int J Primatol 23:539–554.

Byrne RW, Corp N, Byrne JM. 2001a. Estimating the complexity of animal behaviour: how mountain gorillas eat thistles. Behaviour 138:525–557.

Byrne RW, Corp N, Byrne JM. 2001b. Manual dexterity in the gorilla: bimanual and digit role differentiation in a natural task. Anim Cogn 4:347–361.

De Waal FBM. 1998. No imitation without identification. Behav Brain Sci 21:689.

Huffman MA, Hirata S. 2004. An experimental study of leaf swallowing in captive chimpanzees: insights into the origin of a self-medicative behavior and the role of social learning. Primates 45:113–118.

Matheson MD, Fragaszy DM. 1998. Imitation is not the holy grail of comparative psychology. Behav Brain Sci 21:697–698.

Midford PE. 1998. High-level social learning in apes: imitation or observation-assisted planning? Behav Brain Sci 21: 698–699.

Miklosi A. 1998. In the search for the functional homology of human imitation: take play seriously! Behav Brain Sci 21:699–700.

Nahallage CAD, Huffman MA. 2007. Acquisition and development of stone handling behavior in infant Japanese macaques. Behaviour 144:1193–1215.

Rogers ME, Abernethy K, Bermejo M, Cipolletta C, Doran D, McFarland K, Nishihara T, Remis M, Tutin CEG. 2004. Western gorilla diet: a synthesis from six sites. Am J Primatol 64:173–192.

Schaller GB. 1963. The mountain gorilla: ecology and behavior. Chicago: Chicago University Press.

Stoinski TS, Wrate JL, Ure N, Whiten A. 2001. Imitative learning by captive western lowland gorillas (*Gorilla gorilla gorilla*) in a simulated food-processing task. J Comp Psychol 115:272–281.

Tomasello M. 1998. Emulation learning and cultural learning. Behav Brain Sci 21:703–704.

Torigoe T. 1985. Comparison of object manipulation among 74 species of non-human primates. Primates 26:182–194.

Vereijken B, Whiting HTA. 1998. Host by their own petard: the constraints of hierarchical models. Behav Brain Sci 21:705.

Watts DP. 1984. Composition and variability of mountain gorilla diets in the central Virungas. Am J Primatol 7: 323–356.