

Gestural Imitation by a Gorilla: Evidence and Nature of the Capacity

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ABSTRACT

We report the results of an opportunistic experiment on the capacity for gestural imitation in a zoo-housed, female western lowland gorilla (*Gorilla g. gorilla*). Taking advantage of her temporary disposition to copy humans, we presented 7 non-species-typical gestures, without training or rewards. The gorilla's behaviour was filmed and subsequently rated for gestural imitation by 20 naïve coders, controlling for general demeanour by comparing pre- and post-demonstration segments. For several gestures, behaviour that closely matched the demonstration was seen only or more often after demonstration: gestural imitation was therefore reliably detected. Nevertheless, as in previous studies of great ape gestural imitation, none of the gorilla copies was a perfect match. We suggest that gestural imitation in great apes is based on facilitation of rare behaviours in their extensive and often idiosyncratic gestural repertoire (e.g. by mirror neurons), rather than on acquiring novel behaviours by imitation.

Keywords: Gestural Imitation, Facilitation of Idiosyncratic Repertoire, Western Lowland Gorilla.

RESUMEN

Imitación gestual por un gorila: evidencia y naturaleza de la capacidad. Presentamos los resultados de un experimento oportunista sobre la capacidad para la imitación de gestos de una gorila de costa (*Gorilla gorilla gorilla*) alojada en un zoo. Aprovechando su disposición temporal a copiar a seres humanos, presentamos 7 gestos no específicos, sin entrenamiento ni recompensas. El comportamiento de la gorila fue filmado y puntuado en relación a la capacidad de imitación gestual por 20 codificadores que carecían de experiencia previa en observación de conducta animal y/o gorilas. Para ello, compararon los segmentos pre y post-demostración del modelo humano a imitar. Para varios gestos, la conducta que igualaba muy de cerca a la demostración, fue observada sólo o más a menudo después de presentada la demostración: la imitación gestual por lo tanto fue detectada de forma confiable. Sin embargo, como en estudios anteriores de la imitación de gestos en los grandes simios, ningunas de las imitaciones de la gorila fueron una copia perfecta. Sugerimos que la imitación de gestos por los grandes simios está basada más en la facilitación de comportamientos raros de su amplio y a menudo idiosincrásico repertorio de gestos (e.g., por las neuronas espejo) más que en la adquisición de nuevas conductas por imitación.

Palabras clave: imitación de gestos, facilitación de repertorios idiosincrásicos, gorila de costa.

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The evidence of imitation in great apes presents a paradoxical picture. The conventional experimental approach to animal imitation uses the 'two-action method', in which subjects witness one or other of two equivalent methods of solving a problem for reward: imitation is defined as a statistically significant tendency to match the method observed (Dawson & Foss, 1965; Galef, Manzig, & Field, 1986; Palameta & Lefebvre, 1985; Zentall, 2001). Imitation of this sort has been reported in both chimpanzees and gorillas (Stoinski, Wrate, Ure, & Whiten, 2001; Whiten, Custance, Gomez, Teixidor, & Bard, 1996). The actions concerned, however, are simple ones that the observing animals can use already. The change that is effected by observation is in the relative probability of deployment: because the observed action is likely to be applied first, and because it does indeed work, the animal learns to use it in future. In cognitive terms, this process can quite simply be explained as a matter of *priming* elements of the animal's existing behavioural repertoire by means of observation (Byrne, 1994, 1995), followed by individual learning by reinforcement. The term 'response facilitation' has been used to distinguish it from more complex forms of imitation, and draw attention to the similarity of process with learning by stimulus enhancement (Spence, 1937). By such means, the animal may learn to apply a particular (known) method to a new problem, but not acquire a novel method: the imitation allows contextual learning, rather than of production learning (Janik & Slater, 2000). Experimental evidence is extremely slender, in contrast, for the claim that great apes can learn new responses by imitation (Heyes, 1993; Tomasello, 1996; and see commentaries to Byrne and Russon, 1998). The most that has been shown is a tendency for several chimpanzees, part of a "language training" programme, to perform 3 familiar actions in a particular order that they watched repeatedly (Whiten, 1998). The sequence was in fact irrelevant to achieving the goal, and simpler explanations than imitation may be possible, linking these data more closely with superstitious behaviour of animals than with skill acquisition by imitative learning (Dickinson, 1980). Thus, belief that chimpanzees and other great apes can learn new skills by imitation rests on observational field data and the copying of human actions by captive great apes (Byrne & Byrne, 1993; Byrne & Russon, 1998; Russon & Galdikas, 1993, 1995). Observational data, whether from fieldwork or captivity, are often regarded sceptically: Tomasello has proposed that *none* of the complex skills of wild chimpanzees are based on imitative learning, and that in fact chimpanzees and other great apes have no such capacity (Tomasello, 1990). This challenge cannot yet be refuted by any adequately controlled experimental data.

In puzzling contrast, great apes have long been accepted as able to learn arbitrary, novel bodily gestures by imitation, on the basis of experiments in which gestures are copied "to order". This technique was first used with a single home-reared chimpanzee (Hayes & Hayes, 1952), but sparse documentation of the results made interpretation problematic. However, the Hayes' experiment was replicated with two nursery-reared zoo chimpanzees by Custance, Whiten and Bard (1995), who confirmed the basic phenomenon. In this so-called "do-as-I-do" research design, subjects are first trained to copy gestures that are demonstrated to them by the experimenter; then, arbitrary gestures, not previously demonstrated, are introduced as a test of the ability to imitate. Custance *et al.* (1995) asked two independent, naïve observers to judge after each demonstration

which of 48 possible actions the behaviour of the subject most resembled, and found significant matching for several gestures. However, often the chimpanzees' imitation was imperfect. More recently, the same set of stimuli were used with an orangutan, a subject which had been language-trained by humans (Miles, 1986) and was given spoken commands in English: as with the chimpanzees, detectable but imperfect copying was found (Call, 2001).

It therefore seems that chimpanzees and orangutans have the cognitive capacity to imitate relatively complex actions shown to them, yet it is not clear that they are able to put this capacity to use and imitate actions in the service of immediately functional natural goals. This contrast has led Tomasello, Kruger and Ratner (1993; see also Call & Tomasello, 1994) to introduce the concept of "mimicry": the copying of novel actions without understanding their purpose or mode of function. Great apes, these authors suggest, can mimic actions but cannot put this ability to use in achieving practical goals, because they lack adequate understanding of intention and mechanism (Tomasello & Call, 1997). Since the evolution of a complex cognitive skill that has no biological function is a priori unlikely, this implies that mimicry has evolved in great apes for some unspecified function other than skill learning. Yet long-term field studies have not suggested any other likely biological function for mimicry, nor any field data that it occurs (Goodall, 1986; Nishida, 1990).

An unusual opportunity to examine this puzzling issue arose during a long-term study of gestural communication (Tanner & Byrne, 1999), conducted by one of us on a zoo-housed group of western lowland gorillas (*Gorilla g. gorilla*). One individual, a nursery-reared gorilla whose gestural repertoire was already very well documented (Tanner, 1998; Tanner & Byrne, 1996, 1999), occasionally appeared to enjoy copying the actions of zoo visitors. As the ability to imitate gestures had not previously been reported in gorillas, we seized this opportunity and carried out a version of the do-as-I-do procedure, filming the entire procedure, but giving no reward to the subject, either for general cooperation or for any particular kind of response. Here, we present a detailed analysis of this experiment, focusing on the question of whether the gorilla's imitative behaviour truly reflects the capacity to learn novel actions by imitation alone, or some simpler ability.

Because only a limited number of gestures had been presented to the gorilla, it was important to examine the behavioural data with great care. Rather than rely on inter-observer agreement of just two independent, naïve coders as in previous studies, we treated each demonstration of a gesture as a separate "experiment", and asked 20 observers to examine segments of pre- and post-demonstration videotape for possible instances of the demonstrated action. Videotape from immediately *before* the demonstration was used as a control for the gorilla's general mood and activity level. For each gesture, observers first watched a videotape of the experimenter giving the demonstration, to establish the potential target for imitation. Then, they viewed two segments of gorilla behaviour, but were not informed which had preceded and which had followed the demonstration; they were asked to judge whether imitation of the demonstrated action occurred in either or both segments.

One question for our subsequent analyses was simply: (1) Can naïve observers

detect an effect on the gorilla caused by demonstration of a novel gesture? That is, when behaviour matching the demonstration is perceived, is this only in post-demonstration segments. Or, if matching behaviour is sometimes perceived in pre-demonstration segments, is the match more frequent or more veridical in post-demonstration segments? Beyond this issue of detection, we asked: (2) How high is the fidelity of matching, in behaviour perceived by observers to be imitative? That is, does the apparent imitation closely match the demonstrated action, or is there only a loose correspondence? These questions focus on the *presence* of gestural imitation in a gorilla, of the sort reported in chimpanzees and orangutans. Because this individual was part of a long-term study of gestural behaviour, we were able to go beyond those studies, and ask (3) is there any evidence from the individual's past history to clarify the *nature* of any imitation detected.

METHOD

Subject

Zura, a female western lowland gorilla (*Gorilla g. gorilla*), was 12 years old at the time of these observations (July 11, 1994). The gorilla group of the San Francisco Zoo then consisted of 6 individuals: 2 adult males (36yr, 18yr), 3 adult females (36yr, 13yr, Zura 12yr), and one juvenile male (5yr). Zura had been nursery reared in Columbus, Ohio, for the first 14 months of her life, before transfer to the San Francisco Zoo, and interacted with zoo visitors to a greater degree than the other gorillas in the group, often attracting visitors' attention with gestures and vocalizations clearly directed toward them.

Data collection procedure

The gorilla enclosure at San Francisco Zoo has an outdoor area of 2300m², measuring 38m by 50m at its maximum parameters. It is naturalistic, with vegetation covering all surface areas, several large living trees as well as dead trees and large stumps, and two artificial rock hills with arches and cave-like areas beneath. The enclosure is below viewer (ground) level, except for one large windowed viewing area. The experiment was carried out during Tanner's routine videotaping of the group's social interaction. Normally, Tanner did not interact with the gorillas in the course of observation. Zura would sometimes come over to observe Tanner and her camera operator (Tanner's husband), but rarely made displays to them or threw things at them, as she did at strangers who attracted her attention.

On several occasions in the past, Zura had been observed to imitate facial and lip movements of visitors but this had not been possible to document formally. On July 11, 1994, Tanner took advantage of a quiet period at the zoo to model an action (slapping her cheek repeatedly with one hand, repeated twice). Zura watched intently, and began to respond with cheek slapping, albeit using both hands and followed by other, different gestures. When Tanner repeated the original slapping motion once more,

Zura again responded after a few seconds, this time slapping with only one hand as Tanner had done.

Tanner opportunistically repeated this procedure over the next 30min, inventing a series of gestures. Whenever Zura seemed responsive to the observers, Tanner performed demonstrations of an action several times while the camera operator recorded Zura's activity; during this period, Tanner continued to give intermittent demonstrations. For each gesture, demonstrating and recording ceased when either Zura appeared to have been somewhat successful at imitating it, or when she looked away or moved away as if uninterested. Then, before moving on to demonstrate the next gesture, a video record was made of Tanner demonstrating the gesture she had previously been modeling for the gorilla.

Demonstration stimuli

A total of 7 gestures were demonstrated to Zura during the session. These actions were chosen in an attempt to meet two criteria: (a) they should be physically possible, but (b) they should not be species-typical actions of gorillas, nor in Zura's existing repertoire of idiosyncratic gestures. (Note that, because of the opportunistic nature of the experiment, there was no chance to review the extensive data on Zura's repertoire over 5¹/₂ years of study, so the second criterion meant in practice that the demonstrated gestures were unlike any of Zura's regular actions.) The gestures were as follows:

1. *slap cheek*. Palm of one open hand, held vertical, repeatedly slaps same-side cheek.
2. *slap shoulders*. With arms bent at elbows, repeatedly slap both ipsilateral shoulders with palms of hands.
3. *hide eyes*. Palms of both hands, slightly curved, placed horizontally over eyes.
4. *slap top of head*. Palm of one hand, held open, slaps top of head.
5. *swing arm up*. one arm, slightly bent at elbow and with hand open, swings forward and up above the head;.
6. *rub stomach*. Open hands, held horizontal, rub stomach with vigorous up and down motion.
7. *thumb pulled from under teeth*. Thumb is extended from fist then pulled away from under upper front teeth.

Behavioural analysis

Firstly, all videotape showing Tanner's demonstrations was edited out and made into a tape for naïve coders to view as a guide to behaviour that might have been imitated. Then, videotape of Zura's own actions was divided into seven segments, each consisting of the time from when Tanner first performed a demonstration of an action for Zura until the demonstration of a new action. Each of these post-demonstration segments, which differed in length, was matched with a segment of control videotape

of equal length. The control segment for each episode consisted of the videotape of Zura's behaviour immediately preceding the same demonstration; the aim was that Zura's overall demeanour and motivational state would be similar in each pair of segments. These 14 segments (7 post-demonstration, D; 7 control, C) were edited into a review tape, with each segment numbered; whether D or C came first for each demonstration was randomized on the tape, and all sound was eliminated to avoid influencing the coder by verbal comments from the human observers.

Twenty people were recruited as coders: none had prior experience of analyzing animal behaviour or experience of watching gorilla behaviour in particular. Each was individually given standard instructions on a printed sheet. The instructions explained that the review tape consisted of seven pairs of episodes, and for each pair they should look for a certain gesture. Before viewing each pair, they should closely study the demonstration of that particular gesture, as given by Tanner, on a separate videotape. Then, when watching the two episodes of Zura's behaviour, each time they thought they saw her make the demonstrated gesture, they should note the exact time code (shown on the tape). The instructions emphasized that imitations might vary somewhat from the original, in such things as: exact area of body where hands make contact, exact hand shape, direction of motion, speed, one versus two hands, arms crossed versus separate. They should rate each of these instances on a scale of 1-3, where:

1. The action very closely resembles the demonstration;
2. The action resembles the demonstration in several dimensions, but is not an exact copy;
3. The action bears only a rough resemblance to the demonstration, but it could possibly be an imitation.

A specific, hypothetical example of how to apply the 1-3 ratings was given. Finally, coders were warned that many gestures might be seen that did not resemble the demonstrations, and these should be ignored.

Thus it was possible for a coder to pick out zero, one or several instances of putative imitations, in both the experimental and matched control segments of tape. Each case would then be rated as close, somewhat inexact, or only rough versions of the original.

RESULTS

We have structured our analyses in order to converge on potential evidence in the gorilla's behaviour for imitative learning, in the sense of the ability to copy arbitrary novel actions. Thus we move from the most general issue, of whether watching the demonstration had any measurable effect on the gorilla's gesturing, to the most specific question of whether the gorilla thereby acquired a distinctive gesture, closely resembling the demonstrated action, that she had not done before.

Frequency of Behavioural Matching after Observation

We first ask whether observers can detect the effect of demonstration. That is, can any effects, specifically in the direction of the observed gesture, be detected that would enable confident identification of which segment came before and which came after a demonstration. Each observer's ratings of the post-demonstration (D) and control (C) segments were compared, for whether the gesture in question was considered present, how often, and at what level of matching to the demonstration. We treated as a "detection" any of the following cases:

1. If the gesture was noted *only* in D, not in C.
2. If the gesture was noted in both D & C, but the *highest* quality match to the original demonstration was in D.
3. If matches of equal quality were noted both D & C, but *more matches of the highest quality* were noted in D.
4. If equal numbers of the highest quality were noted in D & C, but *more matches overall* were noted in D.

Table 1(a) shows the resulting frequencies of detection, analysed with the Binomial statistic (two-tailed; ties were discounted, thus total N varies). For 5 out of the 7 gestures, it is clear that there was a highly significant increase after the demonstration in behaviour which matched the demonstrated action, so that by some criteria imitation did occur in these cases. For gestures #3 (hide eyes) & #6 (rub stomach), however, no such increase was found.

Quality of Behavioural Matching after Observation

We next consider whether the gorilla's behaviour post-demonstration showed specific signs of resemblance to the gesture demonstrated. With numerical superiority no longer an issue, we treated as positive evidence either of the following:

1. If the gesture was noted *only* in D, not in C.
2. If the gesture was noted in both D & C, but the *highest* quality match to the demonstration was in D.

Table 1(b) shows the resulting scores, analysed with the Binomial statistic (two-tailed; again, ties were discounted). For gesture #2 (slap shoulders), no increase in quality was found, and we conclude that the effect on this gesture was a purely quantitative one. However, for 4 out of the 5 gestures in which we had found a post-demonstration increase in matching behaviour, there remains a highly significant effect. Naïve observers do find a higher resemblance to the demonstrated action in behaviour that occurred after the demonstration.

Demonstrations were given throughout the test period for each gesture, and these varied in length for different gestures: it is thus possible that the fidelity of copying by

the gorilla varied with the number of demonstrations seen. To evaluate this possibility, we computed the time between the first demonstration and that behaviour rated by coders as closest to the gesture actually demonstrated. As can be seen from Table 1, there was no sign of any such relationship.

Relationship between Frequency and Quality of Behavioural Matching

In principle, finding a qualitative increase in resemblance to the demonstrated gesture after watching the demonstration might be a side-effect of quantitative change. Suppose a gesture in the gorilla's existing repertoire is facilitated by seeing a demonstration which somewhat resembles it, and consequently this gesture is performed many more times post- than pre-demonstration. Given stochastic variation in animal behaviour, among these many instances there is statistically more likely to be one which closely resembles the (novel) demonstrated action than among the few cases pre-demonstration. However, low-quality matches would also increase sharply.

We thus go on to ask whether the observed increases, in higher quality matches to the gestures that were demonstrated, were associated with a general increase in quantity of all matches, good and poor; or, is it specifically actions that closely resemble the demonstrated gesture that increase in frequency? Here, only those 4 experiments are relevant in which a qualitative rise in matches to demonstrated behaviour was noted. The critical issue is whether all increases in judgements of high-fidelity matching, in the post-demonstration period D compared to the control period C, were associated with increases in overall quantity of lower-grade matches. We set aside all such cases. Table 1(c) shows the remaining data, again analysed using the Binomial statistic, showing that in all 4 cases it is specifically high-quality matches that are increased after the demonstration. Evidently, the fact that observers noted behaviour post-demonstration that more closely matches the demonstrated action was not due to any general, quantitative increase in the frequency of actions only vaguely similar to the demonstration.

Pre-existing Repertoire of Subject

Can we therefore be absolutely sure that these 4 cases reflect imitative learning of novel action patterns? The only alternative explanation is that the specific gesture demonstrated was *already* in the gorilla's repertoire, to some rather high degree of fidelity. This possibility has not been considered in any of the previous studies, none of which had long-term data on the repertoires of their subjects. Those studies therefore relied on choice of 'novel' gestures for experimental testing: in practice, that meant using actions that the subjects had not been seen to display over several days, and which were not part of the species-typical repertoire. Similarly, in this study Tanner chose the experimental gestures with the aim of novelty, on the basis of her experience of gorillas at the San Francisco Zoo, and of Zura in particular. However, in this case film records of Zura's behaviour over 5 years were available, and we used them to examine the possibility that rare (and perhaps overlooked) gestures might match the demonstrated 'novel' ones. We tackled the issue in two ways.

Firstly, we asked whether any observers did occasionally note a demonstrated gesture, to a high criterion of matching, in control (pre-demonstration) periods. Were actions, *closely* matching the behaviour that had not yet been demonstrated, ever recorded? In fact, this was found to be the case in 4 out of 7 gestures: for gestures #1 (7 out of 20 observers), #2 (5/20), #3 (13/20) and #6 (6/20), observers did indeed report the highest level of match to the not-yet-given demonstration. Note that #2, #3 and #6 have already been set aside as lacking good evidence of imitation.

We then turned to Tanner's long-term database of the San Francisco gorilla group, a catalogued collection of video records extending over 5¹/₂ years, to ask whether

Table 1. Coder identification of gestural copying.

(a) Increase in quantity or fidelity of matching			
Gesture ¹	N ²	Errors ³	Detection probability ⁴
1 (83s)	20	0	>0.001
2 (35s)	20	2	>0.001
3 (29s)	20	6	ns.
4 (6s)	20	0	>0.001
5 (56s)	19	0	>0.001
6 (21s)	20	10	ns.
7 (72s)	20	1	>0.001
(b) Increase in fidelity of matching			
Gesture ¹	N ²	Errors ³	Detection probability ⁴
1 (83s)	13	0	>0.001
2 (35s)	4	0	ns.
3 (29s)	5	4	ns.
4 (6s)	20	0	>0.001
5 (56s)	18	0	>0.001
6 (21s)	14	7	ns.
7 (72s)	19	0	>0.001
(c) Increase in fidelity of matching without accompanying quantitative increase			
Gesture ¹	N ²	Errors ³	Detection probability ⁴
1 (83s)	7	0	>0.05
4 (6s)	19	0	>0.001
5 (56s)	13	0	>0.001
7 (72s)	19	0	>0.001

¹ Time in seconds between first demonstration and behaviour rated as 'best copy' by coders.

² Naïve, independent coders whose judgements of putative imitation differentiated between pre- and post-demonstration segments of videotape.

³ Cases where, using the criteria specified in the text, the coder's judgements would fail to detect the post-demonstration segment on the basis of some, more or better imitations of the target gesture in the experimental than the control period.

⁴ Binomial statistic, two-tailed.

anything closely resembling the demonstrated gestures had been recorded for Zura. The key gestures to examine were #4, #5 and #7, since the others were all perceived by coders in control tape sequences. In all of these three cases, cases of close resemblance were in fact detected in the long-term database (see Table 2). Gesture #4 was “slap top of head”, something Zura normally did not do; however, on one prior occasion she had been observed to quickly pat the top of her head, in the course of a series of other gestures. Gesture #5 was “swing arm up”, and while this had never before been identified as a specific gesture, on several occasions Zura performed essentially similar actions as part of other activities, such as locomotion or reaching for objects. Gesture #7 was “thumb pulled from under teeth”. This bears a fairly close resemblance to a not infrequent gesture in Zura’s idiosyncratic repertoire, “blow kiss” (Tanner & Byrne, 1999). In the control segment preceding demonstration of gesture #7, Zura happened not to give the “blow kiss” gesture, accounting for the coders’ positive ratings.

DISCUSSION

The gorilla Zura was able to imitate gestures demonstrated by a human model, in the sense that (1) naïve coders could detect the behavioural effect of the demonstrated gesture to a high level of reliability, and (2) this effect specifically increased the resemblance of her behaviour to the form of the demonstrated gesture. This gorilla’s gestural imitation therefore resembled that of the home-reared chimpanzee of Hayes & Hayes (1952), the two nursery-reared chimpanzees studied by Custance et al (1995), and the language-trained orangutan of Call (2001). Zura’s imitations were typically not high fidelity copies of the gestures demonstrated, although they could be readily identified in context—as was also noted by Custance et al (1995) for chimpanzees and Call (2001) for the orangutan. Using the same logic as those previous studies, the conclusion must be that at least some gorillas have the cognitive capacity to imitate manual gestures. Moreover, whereas previous experiments used reinforcement techniques to teach the procedure to the subjects, Zura copied spontaneously and unrewarded. Although based on only 5 individual great apes, each with a very different history, gestural imitation appears remarkably consistent: variations in rearing (zoo nursery vs. human home), training (“language” vs. none), species (chimpanzee, gorilla, orangutan), testing (reinforcement trained responding vs. spontaneous) and analysis (informal, two independent observers, group of independent observers) do not seem to influence the basic phenomenon. However, note that none of the subjects were mother-reared individuals: a high orientation of behaviour towards humans may be essential to elicit the capacity.

Since there are no obvious species differences in gestural imitation among the individuals so far studied, we can use Zura’s data to hypothesize the likely mechanism of gesture copying in all great apes. Neither Custance et al (1995) nor Call (2001) make a sharp distinction between copying of novel and of familiar gestures: both are treated as imitation. Indeed, Custance et al note that in some cases the behavioural match with a model was achieved by replicating an action already in the repertoire, and Call states that some of the actions tested closely resembled signs the orangutan used in interaction

Table 2 Characteristics of best copies.

Gesture	Characteristics of best copy	Possible origin of copy
1 Slap cheek	Single, open hand slap of cheek, using same motion path, repeated at same rate as demo. But: opened mouth while slapping, used opposite hand.	Single case, matching in all features except mouth opening.
2 Slap shoulders	Both hands slap shoulders with open palm, repeated at same rate and 7 times, as demo. But: left hand copy less clear than right, and made contralaterally.	Numerous cases where Zura made body- or shoulder-slapping gesture with crossed arms.
3 Hide eyes	Both hands cover eyes, then rapidly removed. But: hands held in loose fists, not flat, and arms crossed, kiss sound made.	Commonly made gesture (with kiss sound) of both hands to body, made over eyes earlier that day.
4 Slap top of head	Open-handed slapping of top of head. But: steady beats, whereas demo paused between slaps.	Among several head-touching gestures, one case where arm flung up and one hand put briefly on top of head.
5 Swing arm up	Swinging motion replicated with open hands, repeated at same speed as demo. But: two arms used, crossing body, while single non-crossing arm shown.	Two cases of single arm swung up, once apparently gesture towards other individual, once while solitary.
6 Rub stomach	Both hands placed and moved vertically on stomach, with left hand on top, at similar tempo. But: hands slightly bent, scratching rather than rubbing motion.	(Note: not perceived as imitation by coders.) Two-handed scratching of body areas seen commonly.
7 Thumb pulled from under teeth	Right fist placed at opened mouth and rapidly withdrawn repeatedly. But: hand cupped in first repetitions, motion more hitting than place-and-withdraw; thumb under teeth not copied.	(Note: perceived as imitation by coders, but blow-kiss not present in control tape.) Gesture matched Zura's common "blow-kiss" action pattern.

with his caretakers. In these cases, imitation can be treated as contextual learning, and the simplest explanatory mechanism would be priming of the pre-existing repertoire (i.e. response facilitation), as in the case of the experimental studies of imitation in apes, discussed earlier.

Gestural imitation, however, may also give evidence of imitation in the more restricted sense of production learning of novel responses, learning that could allow an individual to acquire new skills by observation. Establishing such an ability is not a simply a matter of the reliability with which coders detect imitation by behavioural matching: to achieve significant matching, a gesture need only to be *closer* in visual

form to the action demonstrated than to any of the other gestures. In all studies, including this one, the quality of the great apes' matching was often rather poor. Suppose that what in fact happened in these experiments was that whichever response in the ape's existing repertoire *most resembled the demonstrated action* was facilitated, by seeing it done. In that case, although the ape would be making a gesture that it has made before rather than copying what it has seen, its actions would nevertheless be rated as more like the action demonstrated just previously than any of the other gestures presented in the experiments. In addition, the "copy" would be expected often to be inexact, as has in fact been noted.

How plausible is this concern, for previous reports? In all studies of great ape gestural imitation, coders were familiarized with just the set of gestures used in the experiments, but great apes have a very extensive natural repertoire of actions (e.g. for chimpanzees, see Nishida *et al.*, 1999), and human-reared individuals are particularly likely to have an augmented repertoire of actions. Custance *et al.* (1995) reported that "novel modifications of taught actions" and "novel responses" were given in response to about 30% of the demonstrations. However, since great apes are long-lived, deciding whether a particular gesture is part of an individual's repertoire is by no means straightforward. In addition to the very large natural repertoires of great apes, long-term studies of captive individuals have shown that they readily develop a wider repertoire of non-species-typical gestures, some of which are used in communicative interactions (Pika, Liebal, & Tomasello, 2003; Tanner & Byrne, 1996, 1999; Tomasello, George, Kruger, Farrar, & Evans, 1985; Tomasello, Gust, & Frost, 1989). In these studies, the presence of numerous non-standard gestures in individual repertoires was not necessarily evident to keepers, nor would it have been to researchers who carried out their work over short time-spans. The possibility exists, therefore, that the chimpanzee and orangutan subjects of previous imitation studies likewise had much more extensive gestural repertoires, including gestures not typical of their species, than was known at the time. The researchers had no way to be entirely sure that some or all the "novel" gestures had not in fact occasionally been made previously by their subjects.

In the present study, we had an unusual opportunity to investigate this possibility, because long-term records of gestural behaviour had been collected from the subject of the experiment over several years, as part of Tanner's doctoral study of gorilla gestural communication. We used this to assess the gorilla's ability to imitate arbitrary, novel actions by investigating the alternative possibility that even cases of imitation of apparently novel action were actually a matter of facilitation by observation, of very low frequency gestures in the gorilla's existing repertoire.

In all cases where observers reliably reported imitation, this proved to be likely: gestural imitation by the gorilla Zura is therefore most parsimoniously explained as evocation, as a result of observation, of visually similar actions that she had already performed. None of the gestures imitated by the gorilla gave convincing evidence of learning novel actions by observation at the time of the experiment. We suggest that the same conclusion may well apply to all previous, published claims of gestural imitation in great apes. Not only is this explanation of ape gestural imitation -as facilitation by visual similarity- a rather simple one; but it has the advantage of explaining why so

often researchers report imitation to be rather poor. The behaviour that is evoked would be expected to resemble the demonstrated action more than does any other action in the ape's pre-existing repertoire, but not necessarily to be identical to it.

Cognitively, facilitation can be modelled as the "priming" of brain records of environmental stimuli (Byrne, 1994; Byrne & Russon, 1998): When an animal sees a conspecific engaged with a feeding task, for instance, brain records corresponding to location, food type, and any objects manipulated during the process are primed. Primed records direct the observer's subsequent attention and exploration towards a limited set of stimuli, with resulting faster learning: classically, the process is described as stimulus or local enhancement (Spence, 1937; Thorpe, 1956). If, in addition, when an animal attends closely to conspecific behaviour, brain records for the actions it sees are also primed, then primed records would influence the observer's subsequent exploration towards use of the same actions -provided only that the actions are ones in the observing animal's current repertoire. The neural basis of response facilitation is now becoming understood, with the discovery of mirror neurons in monkey cortex which have been identified for a range of simple goal-directed actions (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Gallese & Goldman, 1998; Rizzolatti, Fadiga, Fogassi, & Gallese, 1996; Rizzolatti, Fogassi & Gallese, 2000). Mirror neurons react equally to the sight of manual gestures, whether these are performed by the monkey itself or by another individual such as a human. How animals develop mirror neuron systems is not yet fully understood, and this is clearly a greater problem when the action as done by the self would appear very different from the same action as done by another (Byrne, 2005; Zentall, 2001). Recent theories vary from proposing an innate 1:1 mapping of actions-as-seen to actions-as-done (Meltzoff, 2002), to claiming that all the appropriate mappings can be learnt by associations made naturally during normal development (Heyes & Ray, 2000); resolution of this issue is beyond the current study, but certainly gestures like "slap cheek" and "hide eyes" present very different visual stimuli when done by the self or by another.

Several predictions follow from the hypothesis that gestural imitation is based on facilitation of pre-existing repertoire. Firstly, gestural copying should occur only in species with *large behavioural repertoires*. For a species with a small, easily enunciated repertoire of actions, response facilitation is unlikely to be mistaken for an ability to learn arbitrary, novel actions by imitation. Great apes have gestural repertoires that are notoriously difficult to describe completely, as the rarity of published ethograms for great apes shows; and where an attempt has been made, the set of actions is very large (e.g. Nishida, 1999). Secondly, since experimenters investigating imitation naturally do their best to choose test actions to be unfamiliar to the subjects, *exact copying is unlikely*. Most copying will reflect the facilitation of closely similar, but seldom identical, actions in the existing repertoire. Thirdly, since movement patterns vary with each execution, some of the facilitated actions will bear a closer resemblance to the demonstrated ones than others: thus, high quality copying will often be *associated with high frequency of copying*. All three predictions are met by the data on gestural imitation in great apes: we therefore conclude that the experimental evidence for gestural imitation by great apes, our own and others', can be accounted for as response facilitation.

There are occasional suggestions that, nevertheless, great apes may sometimes go beyond response facilitation in their gestural copying. For instance, Custance *et al.* (1995) noted cases where a subject initially made a very inexact match, and then repeated it once or more in a way that more closely approximated the gesture as demonstrated. Similarly, in the present study it was noted that Zura's imitation of "hide eyes" was initially rated as not very accurate and failed to replicate eye-covering, but after several trials Zura raised her hand above her mouth and did almost cover her eyes. It is tempting to treat these anecdotal cases as "striving towards a remembered model" (compare the template-matching theory of bird song learning: Marler, 1976), and it may be that both chimpanzee and gorilla possess a little-used ability to imitate arbitrary, novel actions. The statistically reliable data of published papers, however, support no such conclusion.

We conclude by noting that the discontinuity in evidence, between copying arbitrary gestures and copying instrumental actions, is now removed. In both areas learning by contextual imitation occurs, and can be explained cognitively by the simple mechanism of priming. In both areas the case for imitation of novel actions in great apes largely rests on observational data and anecdote. To progress beyond this unsatisfactory state of affairs, experiments are needed which address -in their fundamental design- the need to distinguish any apparently positive results from the effects of response facilitation.

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APPENDIX



swing arm up demonstrated



swing arm up; Zura's action



slap top of head demonstrated



slap top of head; Zura's action



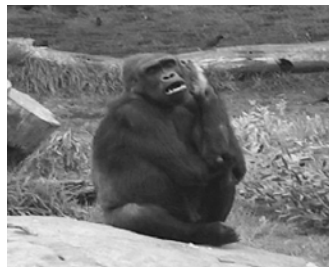
slap shoulders demonstrated



slap shoulders; Zura's action



slap cheek demonstrated



slap cheek; Zura's action