The evolution of human diets according to the extant primate gut morphology and taste perception

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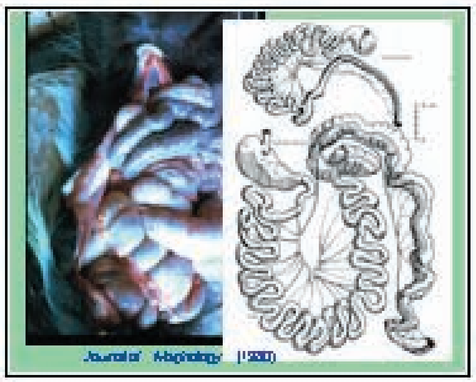
Many thanks to the organizers

When I was a student in biology – in the sixties – there was very little interest in dietary adaptations; and the passionate discussions I had with friends were based on a few disapointing considerations – such as: we do have canines, so we MUST eat meat vs pro-vegetarian assumptions– and I was expecting to find a solid basis by studying the diet of wild primates, and I did so for about 40 years, the last decades being spent in cooperation with anthropologists, ➔ in this team of the Paris Museum that I was leading for a while before I retired as an emeritus researcher and go on with my colleagues ➔ and the co-authors of this presentation.

Several data on the diets of homininae have been provided by fossil evidence, mostly teeth, whereas I will focus on gut morphology and taste responses that might not appear as evidence of evolution, since soft parts such as the digestive tract are not generally preserved in fossils; however comparative anatomy of the extant primate species can provide interesting clues.



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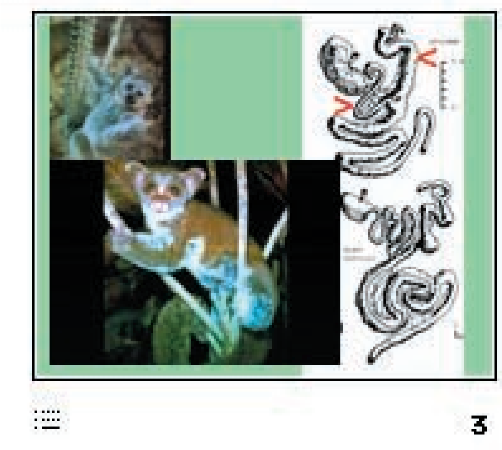
➔ Here is the initial aspect of a fresh digestive tract.

➔ To obtain accurate measurements and such clear drawings as the series we published in 1980, it was necessary to carefully unfold and measure each part –all measurements reported on the drawing– and, for calculation of the surface area of the internal mucosa ➔ I carefully flattened the open guts after muscular layers were relaxed, taking care of not extending each part that was pinned under water,in a large dissecting tray.

Of course, such a work with wild species –necessitating to shoot some animals– would not be politically correct in the present context, even with special permits that were always obtained. But that was the method used by zoologists in the 19th century and up to 1970-1980. Furthermore, until a recent period, monkeys have been hunted for food by local populations in most rain forests of Africa, thus it was quite easy to obtain the digestive tract that is a neglected food…



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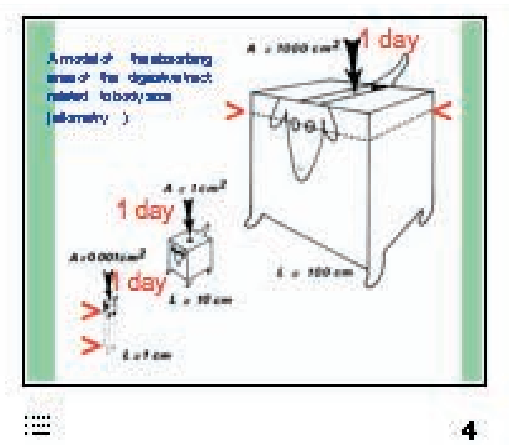
I will just show two examples of specialized primate species whose diets were studied in Madagascar in 1970, and in Gabon, in 1971.

Here are the digestive tracts. In the sportive lemur, *Lepilemur*, I found the shortest small gut ever seen for an animal of about one kg – less than 10 cm –. It is associated with an extremely long cecum allowing fermentation.

For *Galago elegantulus*, whose staple food is gum and other tree exudates that also need bacterial fermentation, the cecum is also extremely developped ....

These various gut shapes are related to specialized diets; however, there are also variation depending on the animal size…



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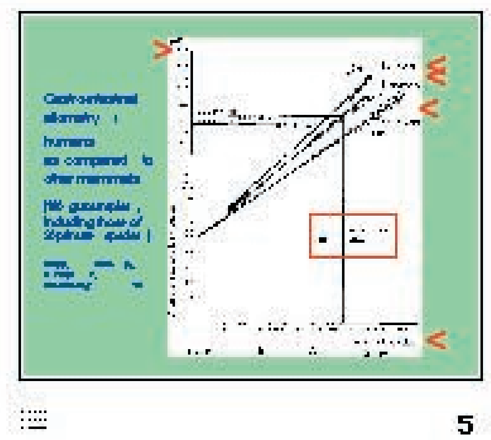
To explain such variations, this is my cubic model. In these cubic animals, the absorptive gut mucosa is represented by the aperture **A** allowing to fill up the animal in one day.

The shape is quite different according to the size, and, for the smallest cubic species measurig one centimeter, **A** would be one thousandth of a square centimeter.

However, these different shapes result from a very simple relationship between the surface areas (the square of the body length) and the volumes (the cube of body length)...but, according to the Kleiber's law concerning basal metabolism, the large species have a lower energy requirement, illustrated by the broken line , whereas, for the smallest cubic animal energy requirements are much higher, thus the area of the absorbing mucosa should be slightly larger than one thousandth of a square centimeter.

Both **form and function** depend of the size of the animal, as was demonstrated in many other examples, especially about the brain size of primates by Pr Robert Martin.

Let us consider the results obtained with the digestive tracts of primates species including humans....



The three regression lines of this graph are those that we published with David Chivers in 1980, using the measurements of the area of digestive tracts of 180 samples (mostly primates) located on a logarithmic scales, in relation to body size that is the cube of the body length

When considering all species with a diet including mostly leaves (although leaf monkeys always include some fruits in their diet), we got a linear function with a slope of nearly **L** (the body length) to the cube. The shaded parts show the 95% confidence limits for the slope.

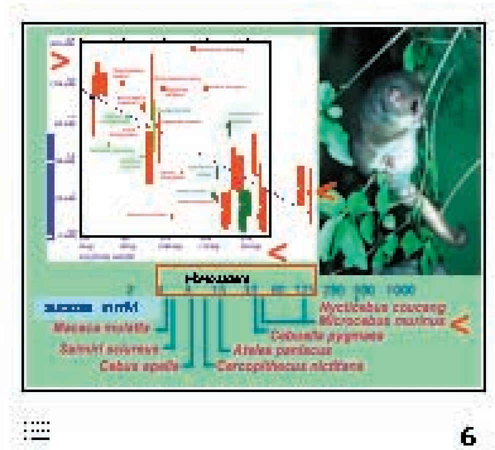
Slopes are quite different with frugivorous species such as chimpanzees and macaques, whereas, for species eating mostly animal matter (that's insects for primates or meat for some carnivorous mammal that were included in the computation), the linear function has a slope of about **L** to the square.

…..I also show here the results for human digestive tracts, that we obtained in 1981 at the forensic medecine service of the Cambridge hospital. These fresh samples were treated exactly as we did for non-human primates and other mammalian species (that is relaxed and flattened in a dissecting tray).

All human samples show the same relationship between body size and gut area as that of all species grouped under a global term of **frugivores**, that is feeding mostly on fruits, but also including seeds and some invertebrates, and even sometimes meat, like the small pieces eaten by the chimpanzees after a hunting party,.

Of course our data could be re-interpreted in various ways, and there have been other proposed interpretations using our primate data; but I am quite convinced by our original model, which is just indicating a dietary tendency for humans, which is presently correspondind to most standards of a healthy diet recognized by the scientific community.

...In much recent years, this research on the relationship between size and function was also applied to **taste responses** ….



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Here are some of the primate species that have been tested, either by Dieter Glaser, or by Bruno Simmen, for their ability to perceive sugar, with a two-bottle test,.

The small primate species, on the right side, are able to discriminate from pure water only concentrated solutions, up to 500 Mm (that is 120 gram of sugar per liter), whereas most of the large species (on the left), have a high taste acuity (they do perceive sugar at very low concentration)….

… and *Homo sapiens* is among those who perceive nicely sweet solutions (you know that), but with large individual variation in taste sensitivity, and large differences among various populations

Although I was quite reluctant to consider the allometric relationship, with an aparently so weak correlation, Bruno Simmen (who was working at this time in the lab of Bob Martin) plotted all primate species that have been tested for sensitivity to sucrose, and he obtained a significant correlation between sugar concentration perceived and the species' body weight **;** and we also added data concerning *Homo sapiens* that fits with the regression line obtained for the other primates.

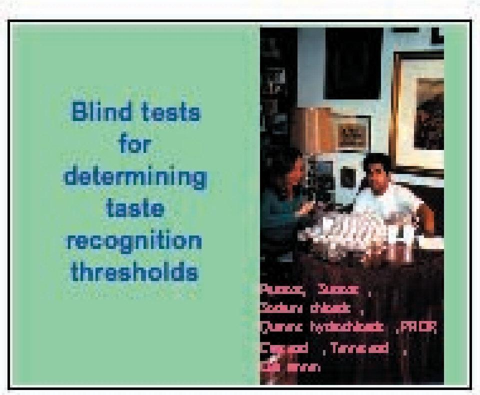
In spite of a large dispersion of the data, due to peculiar adaptations in various environments, **one can wonder why** there is such a difference between large species, the most sensitive to sugar, and small species with a rtelatively low taste sensitivity?

There is an explanation that fits with the observed facts. Sensitivity towards sugars is the result of coevolution, during the Cenozoic, of primate species, together with plant species bearing fleshy fruits (the Angiosperms). Fruits with a high sugar content being prefeferred, their seeds are dispersed in the feces of primates, thus selective pressure would have been exerted on both the **sugar content of fruits and primate taste sensitivity**. In this context, the higher sensitivity of large species allows to feed on a wider array of fruits, even those with low sugar concentration, and this **widens the array of food plants eaten by large primates**, permitting to fulfill higher calory requirements.

~~Conversely, no allometric relationship was found when considering sensitivity to a bitter substance such as quinine: a result that was expected, due to the toxic effect of several bitter alkaloids. In this case, the large variations between primate species in terms of bitter taste sensitivity are essentialy related to the occurrence of such substances in their environment, an obviously adaptive process.~~

A very surprising aspect concerns taste responses of the lesser mouse lemur, *Microcebus murinus* whose taste threshold varies throughout the very marked seasonal cycle in Madagascar, when the animal is lean and when it is accumulating fat . This type of adaptive response is also related to the necessity of widening the range of food choices, to get a maximum of calories, and have fat reserves for the dry season. Accordingly two different taste threshold have been determined , but these are behavioral responses, and there is no change in the peripheral taste signal.

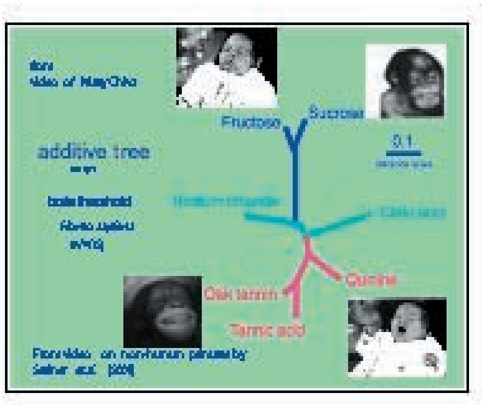
All the non-human primate taste thresholds have been determined with a two-bottle test, a very long procedure allowing to find a significant difference between consumption of pure water vs a solution of sucrose, fructose, quinine, etc... But for humans, the procedure is much faster...



with a blind test and immediate responses of the subject, allowing to obtain data from a large number of individuals in a sub-population. That's what we did in various countries (here is one of my student in Spain, during a program of the European Union). The solutions are in increasing concentrations and can be discriminated once the taste threshold is reached.

The different compounds tested include several sugars, organig acids and bitter substances, without any preconcieved ideas about what is classically described, with little physiological support as the four basic tastes (sweet, salty, acid and bitter), but keeping in mind that each chemical elicits a particular taste signature in the peripheral taste system.

Even sucrose and fructose do not elicit exactly the same type of taste signal, and this has been investigated through the correlations observed in 412 humans.....



In this additive tree, the short distance separating fructose and sucrose means that, the higher the taste treshhold for sucrose of an individual, the higher his threshold for fructose. That is to say that the taste signals are partly similar and that's also why sweet tastes are generally considered as a unique basic taste.

Conversely, there is no (or very weak) co-variation of sugar perception with the bitter taste of quinine .

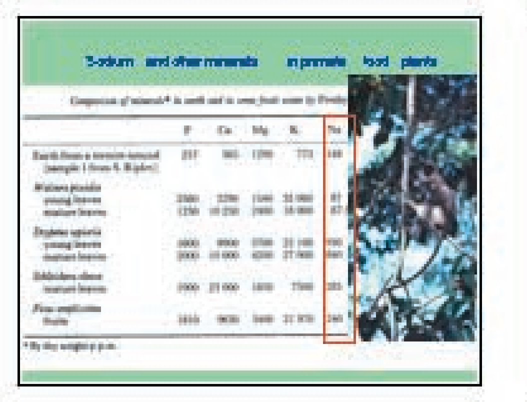
Bitter taste perception is correlated with that of astringent tastes of tannins, or to other substances evolved in plants to deter folivorous animals.

In short, there are several naturally occurring compounds (shown **in red**) that should be avoided for potential toxicity, opposed to beneficial substances, such as sugars (in dark blue) providing energy. And human babies have a gusto-facial reflex → allowing to ingest sugars and a to avoid (or spit out) alkaloids or other bitter compounds.

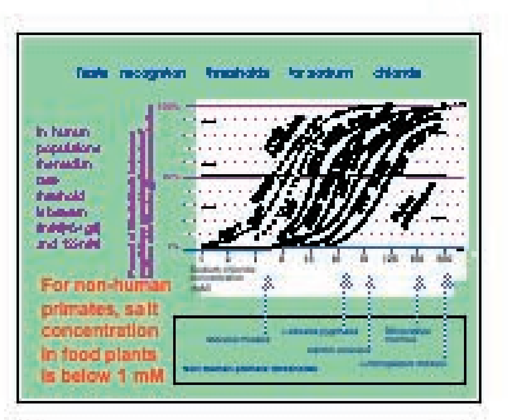
→ The same type of gusto-facial reflex, genetically determined, has been observed by Steiner and his collaborators in very young non-human primates, and this reflex is quite certainly the result of co-evolution of primates and plants in the cenozoic environment.

→ Indeed, with my colleague Göran Hellekant (of Madison University), we constructed for non-human primates, very similar trees of correlation, using, instead of taste thresholds, the signals **directly recorded on the taste nerve fibers of various primate species**. These trees showed the same dichotomy between beneficial signals, versus those of alkaloids and tannins.

But what about signals elicited by salts → especially that of sodium chloride, which is not clearly correlated with other taste signals and is classically described as THE basic salty taste?



9 → This is an example of the minerals present in the diet of wild primates in Sri Lanka, → and especially sodium content measured in parts per million of the dry weight of various food samples. The amount, smaller than 1000 ppm, corresponds, in the juice of a fresh *Ficus* fruit eaten → to about 0.001 g of salt per liter, a very low concentration, not detectable by the taste buds of any primate species.

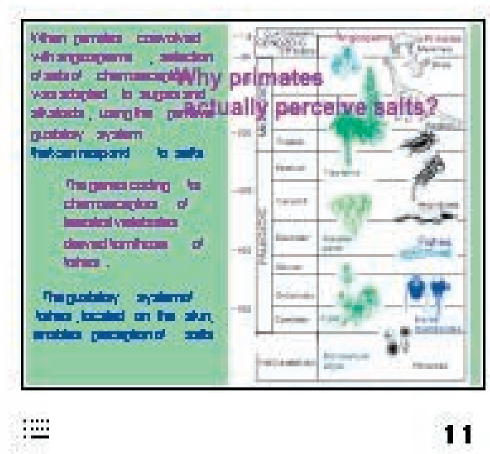


10 → For instance, here are (below) taste thresholds for sodium chloride of some non-human primates, tested with the classiclal two-bottle test...

They are compared, on the same logarithmic scale, to thresholds of human populations → , for whom the median threshold is above 8 mM (that is 0.4 g of salt per liter). The graphs show cumulative percentages of tasters, and there are significant differences between populations that we attributed to recent dietary adaptations, especially among the Inuit (the most sensitive to salt) whose diet is at risk of an excess of sodium chloride.

However, non-human primate species, would never have been subject to evolutionary pressure concerning the taste response to salt → , since the concentration of sodium chloride in all forest foods is below 1 mM, that is far below what the taste system can actually perceive.

And, contrary to what occurred with the sugars and the fruit of angiosperms, co-evolution could never have occurred in this case →



→ Accordingly, **why** can we actually perceive so nicely sodium chloride?

→ If we consider the long-lasting process of the parallel evolution of plants and animal species, we know that, as vertebrates, we evolved from fishes, as it is remarkably illustrated in the recent book of Neil Shubin, based on palaeontological records.

The tasting ability of fishes is still remarkable, especially for salts → that are detected by taste buds located all over their skin.

When terrestrial mammals evolved, the genes coding for chemoreceptors persisted, but the taste buds were located exclusively inside the mouth.

Primates, that, during the Cenozoic, co-evolved with Angiosperms bearing sweet fruits –hence the complex adaptation to sugar perception– have a taste sytem resulting from that long evolutionary process, and, in any case, this **primitive taste system responds to salts**.

....And this is a fabulous conclusion, because some humans (maybe before *Homo sapiens*) discovered the extraordinary taste of the salt deposits along the sea shore, and salt was certainly the first food additive ever used. It was probably associated with the first cooked food, considerably improving the tasteof early dishes.

~~As cooking improved the taste of roasted foods, adding salt became such an habit in our societies that, presently, unsalted foods seems tasteless. This ability to perceive salts had great consequences to human cultural evolution.~~

....And a quite parallel conclusion can be drawn about Ptyalin in saliva

.... since recently, Perry, Dominy, and their collaborators observed that the gene coding for this amylase (that break the starch molecule) is duplicated, and likely to determine higher secretion of ptyalin in the human societies where starch is eaten in large amounts.

This gene is also present in non-human primates. However non-human primates eat raw foods for which ptyalin is not efficient for breaking the starch globules protected by a thin enveloppe of cellulose. But it was certainly very useful to the first Hominins that began to cook food, as Richard Wrangham would have said...

Hence, **as for salt perception** the presence of ptyalin in primates was a fortuitous **lucky occurrence** that now contributes to make bread and rice a staple food to most human societies.

Isn't it nice?

Thank you.