Neuroeconomics :

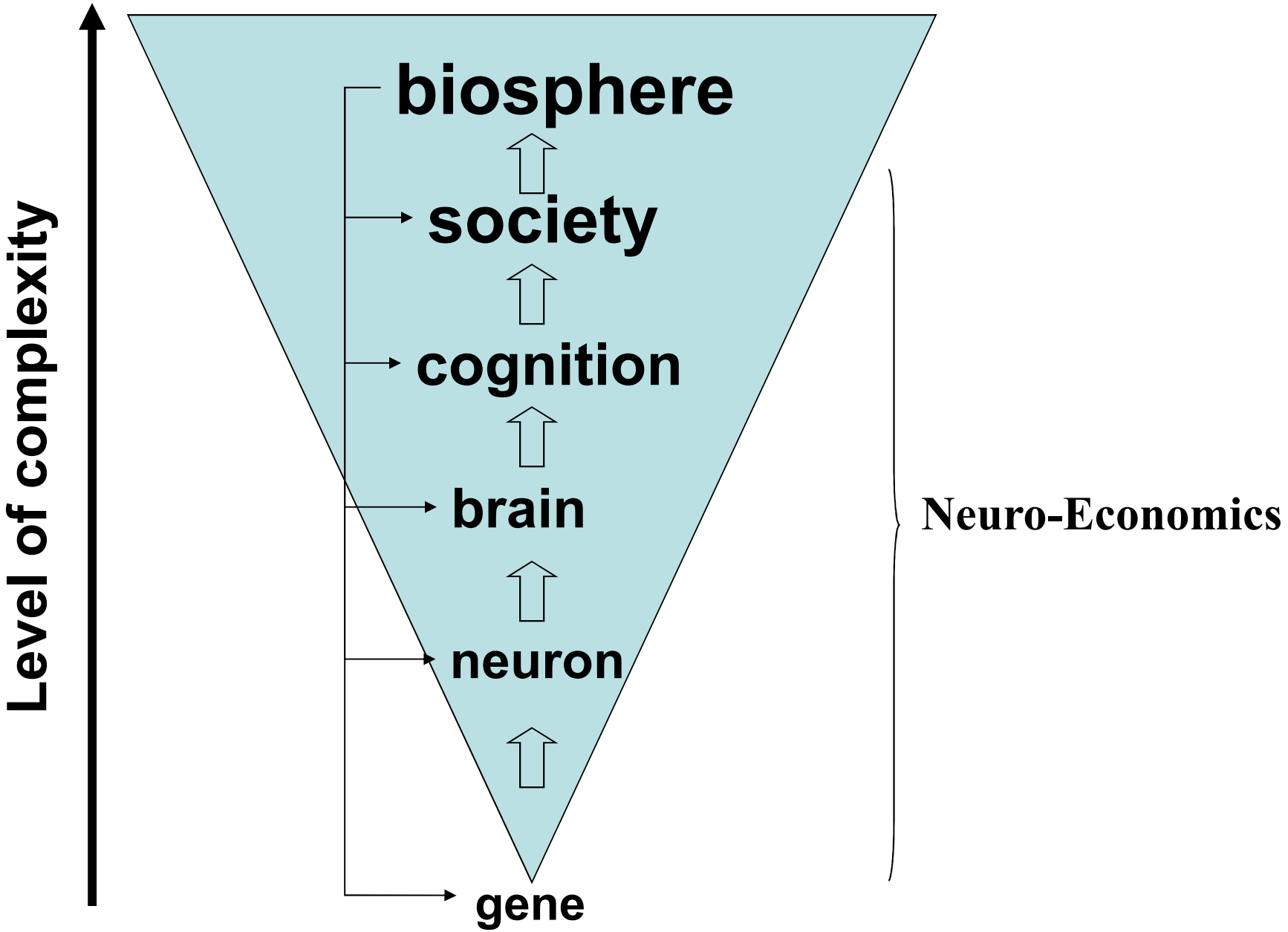
Neuroscience of decision making

Lecture N9

Evolutionary perspective.

Vasily Klucharev

-Higher School of Economics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Neuro-Economics

Ontogenetic origin of cooperation

- Young children are motivated to participate in joint activities: When a cooperative activity breaks down (such as when the partner suddenly stops participating), 18-month-olds and 2-year olds, actively try to re-engage the partner in order to continue the joint activity rather than attempt to continue the activity by themselves (Warneken et al. 2006, Warneken&Tomasello 2007).

- Thus, children do not view their collaborative partner as a social tool to achieve their own goal but rather in a truly collaborative light.

- This is in contrast to chimpanzees, which do not show this motivation for jointness in their collaborative behavior (Warneken et al. 2006).

- When working jointly with a partner on a task that should result in both actors receiving a reward, 3.5-year-olds continue to work until the partner has received his reward even if they have already received their own reward earlier in the process (Hamann et al. 2012).
- Moreover, when 3-year-olds need to break away from a joint commitment with a partner, they do not simply walk away but “take leave” from the other as a way of acknowledging and asking to be excused for breaking the commitment (Grafenhain et al. 2009).


Double Tube
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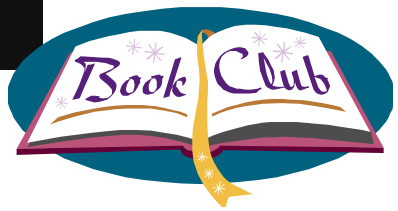
Sympathy and helping.

- By 14 to 18 months of age, children readily engage in instrumental helping such as picking up an object that an adult has accidentally dropped or opening a cabinet door when an adult cannot do so because his hands are full.
- They do not do these things in control situations that are similar but in which the adult does not need help; for instance, they do not pick up an object the adult has thrown down intentionally or open a door he approaches with no intention of opening it (Warneken & Tomasello 2006, 2007).


Book Club

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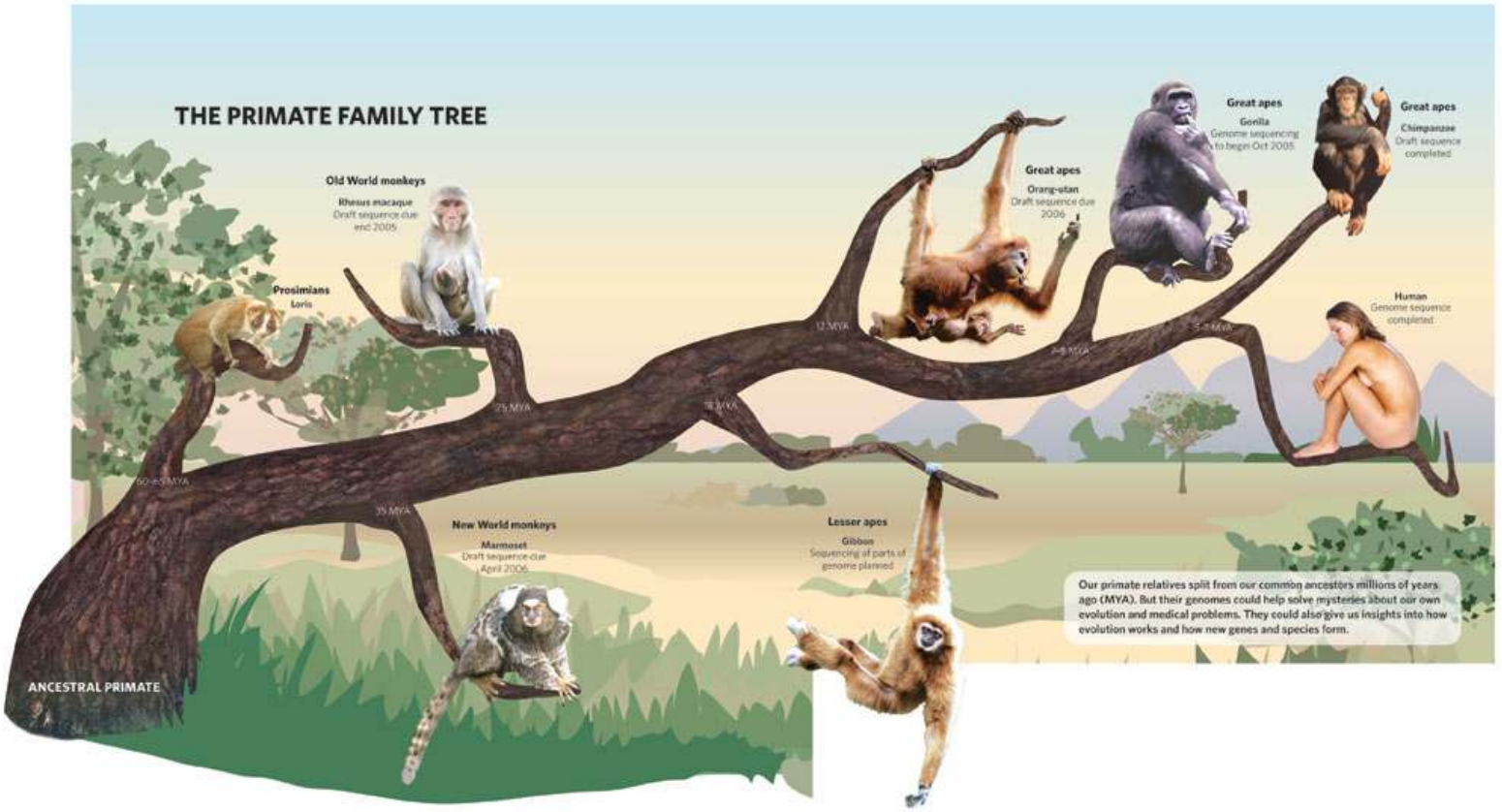
Chimpanzees will help both humans and other chimpanzees.

Michael Tomasello



Cooperation in Great Ape Societies

Helping, sharing, and reciprocity.

- chimpanzees will go to some effort to help humans (Warneken et al. 2007).
- chimpanzees will also release a hook to send food down a ramp to a desirous conspecific, if it is clear that they cannot get the food themselves and if the recipient actively signals his need (Melis et al. 2011) .
- chimpanzees giving tools to others that needed to rake in food for themselves (Yamamoto et al. 009). They give the specific tool that the conspecific needs from an array of possible tools (Yamamoto et al. 2012).

Chimpanzees and other great apes do share food with others under some circumstances:

1. Mothers share food with their offspring (mostly a passive sharing in which they allow the offspring to take food from them, Ueno & Matsuzawa 2004).
2. If the food is not very highly valued and not easily monopolizable (e.g., a branch full of leaves), then a group of apes may peaceably feed on it together, and occasionally there may be some more active sharing among friends (de Waal 1989).
3. If the food is very highly valued and somewhat monopolizable (e.g., meat), then typically subordinates and nonpossessors beg and harass dominants and possessors until they get some, again with some instances of more active sharing (Gilby 2006).

But all of this food sharing is more active and reliable in situations involving some form of reciprocity.

Collaboration.

1. As in many mammalian species, chimpanzees form alliances and support one another in fights (Harcourt & de Waal 1992).
   - Whereas in many monkey species it is typically kin that support one another, among chimpanzees it is mostly nonkin (Langergraber et al. 2011).

2. Second, like many mammalian species, great apes engage in various forms of group defence.
   - Small groups of male chimpanzees actively patrol their border, engaging agonistically with any individuals from neighboring groups that they encounter (Goodall 1986).

3. Collaboration in the acquisition of food.

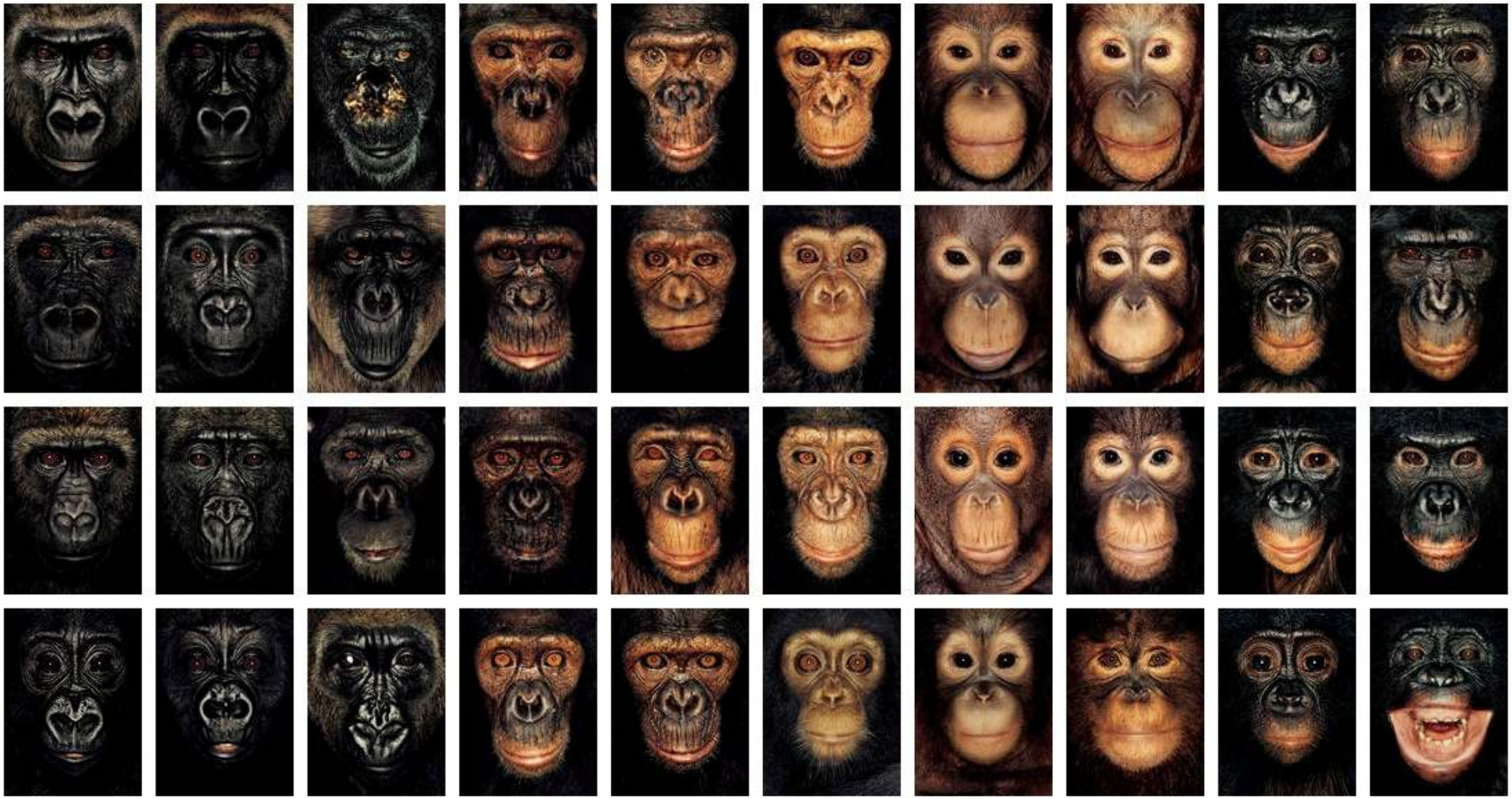

© Warneken, Chen & Tomasello (2006)

- Chimpanzees do coordinate their actions with a partner to achieve individual goals.

  But they do not seem interested in achieving joint, social goals, and if their partner becomes passive and unengaged during a joint activity, they make no effort to reengage their partner in order to continue that activity (Warneken et al. 2006).

- Chimpanzees know which individuals are good partners for them and they subsequently choose those partners in preference to others (Melis et al. 2006).

- When given a free choice of how to obtain food, chimpanzees choose a solo option over a collaborative one, whereas 3-year-old children more often choose the collaborative option (Rekers et al. 2011).



James Mollison

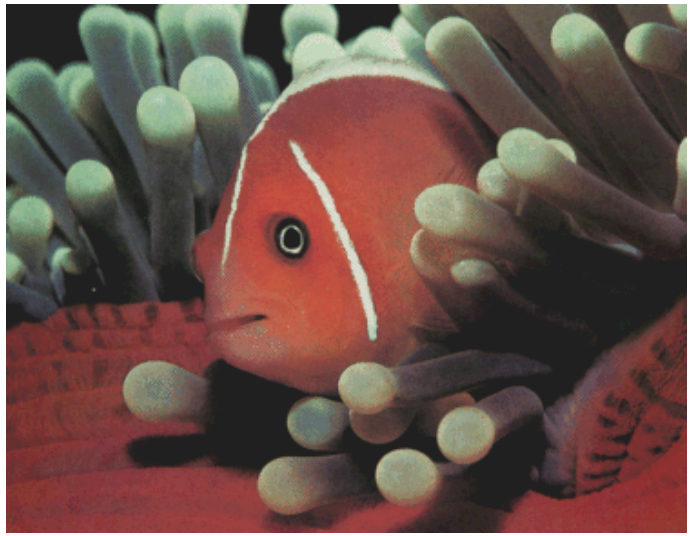
Neuroeconomics

Redouan Bshary

UNIVERSITÉ DE NEUCHÂTEL

- **Mutualism** is a biological interaction between two organisms, where each individual derives a fitness benefit (i.e. increased survivorship).

Similar interactions within a species are known as co-operation. It can be contrasted with interspecific competition, in which each species experiences reduced fitness, and exploitation, in which one species benefits at the expense of the other.



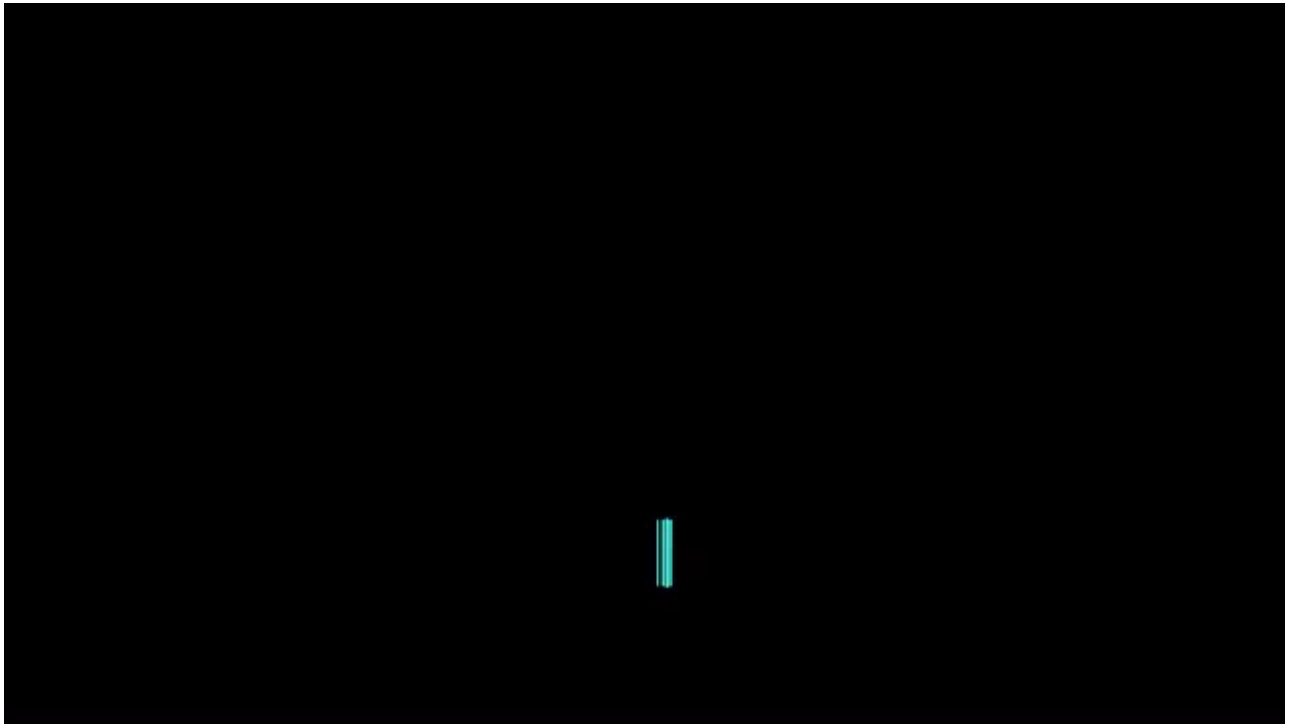
A case study: mutualism between the cleaner *L. DIMIDIATUS* and client reef fish

- Cleaners (*Labroides dimidiatus*) are small marine fish that feed on the external parasites of larger fish.
- Each cleaner owns a “station” on a reef.
- The cleaner nibbles the parasites off the client’s body surface, gills and even the inside of its mouth.
- Sometimes the cleaner is so busy that clients have to wait in line.
- Client fish come in two varieties:
  - **Residents** belong to species with small territories; they have no choice but to go to their local cleaner.
  - **Roamers or “choosy clients”**, hold large territories or travel widely, which means that they have several cleaning stations to choose from. They want short waiting times, excellent service and no cheating.

Bshary &Noë, 2003


شرکت ملی پخش فرآورده های نفتی ایران
ISNA


Rokus Groeneveld ©



- Individual cleaners (*L. dimidiatus)* may have more than 2000 interactions per day, eat about 1200 parasites per day, and may reduce the parasite density on clients by a factor of 4–5 (Grutter 1999).
- Clients without access to cleaner fish showed a higher stress response to capture than clients with access to cleaner fish.

Bshary &Noë, 2003

A pure market game

- Sometimes two or more clients seek the inspection of a cleaner fish simultaneously.
- In such cases, individual clients compete directly over access to the cleaner fish.
- This competition takes place only through inviting the cleaner for inspection, not through aggressive displacement (Bshary 2001).
- Cleaners regularly cheat clients by consuming client mucus.

Experimental evidence indicates that cleaners can recognize individual clients (Tebbich et al. 2002).

Bshary &Noë, 2003

Frans de Waal, 2005

Roamers (choosy clients)

CLEANER FISH nibbles parasites in the open mouth of a large client fish. Roaming client fish rarely return to the station of a cleaner fish after they have been kept waiting (*left graph*) or cheated (*right graph*), meaning that the cleaner took a bite out of the client's healthy tissue. Cleaner fish therefore tend to treat roaming clients better than residents, who have no choice of cleaning stations.

The probability of a client returning to the same cleaning station for its next inspection was high (median of 13 individuals: 60%) if it was inspected, but low (median: 0%, n = 13) if it had been ignored in favor of another (choosy) client.

Asymmetry in possible sanctions:

- About 15% of client species are predatory (they hunt fish that are the size of cleaners).
- Thus, the effects of cheating on the partner could be highly asymmetric:

  an predator only loses a little bit of mucus, whereas an exploited cleaner loses its life.
- For the 85% nonpredatory client species:

  the cleaner can cooperate as well as cheat whereas the client has no option to exploit the cleaner to its own advantage.

•Residents
•Roamers
•Predators

Bshary &Noë, 2003

Market theory makes the following predictions:

- Cleaners should give priority to Roamers (choosy) clients over resident clients.

  The reason is that choosy clients can visit another cleaning station rather than queuing for service. Resident clients have no strategy available to push a cleaner into giving them priority of access.

- Cleaners should give priority to predators and do not cheat them.

Bshary &Noë, 2003

Cleaners demonstrate a good business practice:

- Cleaners treat roamers better than they do residents:

  If a *roamer* and a *resident* arrive at the same time, the cleaner almost always services the roamer first.

  Residents have nowhere else to go, and so they can be kept waiting.

- The only category of fish that cleaners never cheat are predators, who possess a radical counterstrategy, which is to swallow the cleaner.

Bshary &Noë, 2003

Cleaners and coral fishes – a case of biological market

Biological market theory

- **BM** (Ronald Noë and Peter Hammerstein) theory predicts that changes in the supply-demand ratio should result in directional shifts in cooperation or in the exchange values of goods and services.
- Biological market theory predicts that partner choice can lead to selection for specific traits. Skills that are important in the selection of cooperation partners:

  (i) judging the partner's quality,

  (ii) a memory for the partner's quality and location,

  (iii) searching strategies,

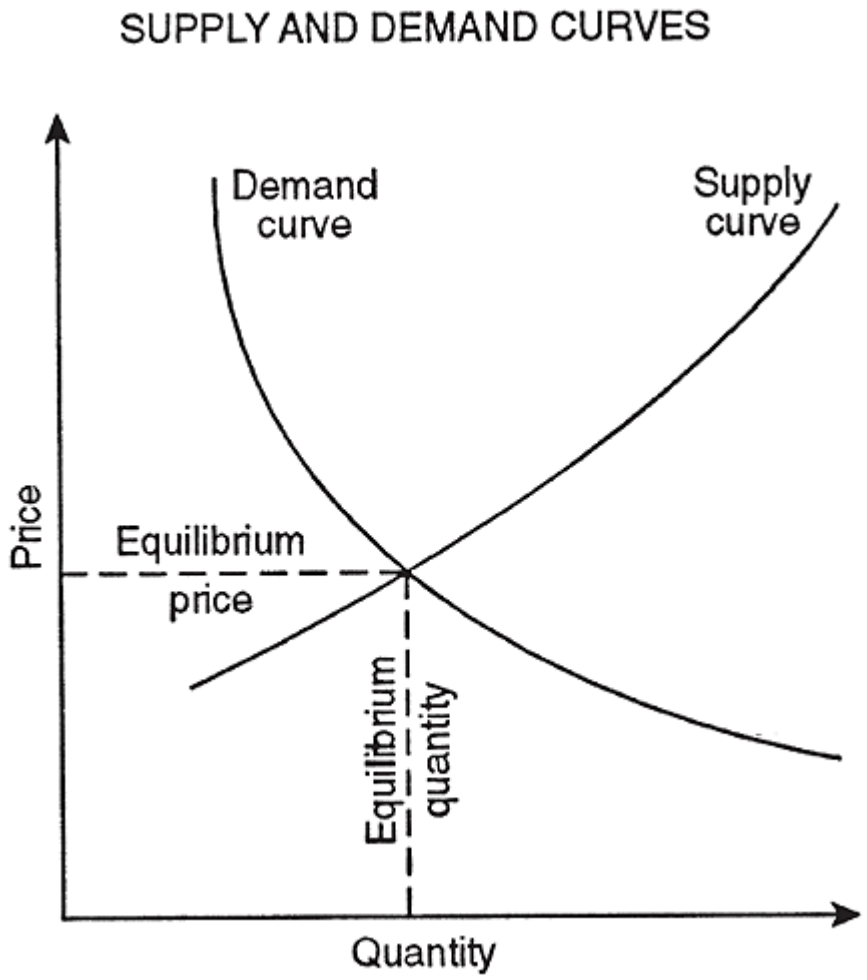
  (iv) judging the honesty of signals and so on.

Adjusting to market value:
Supply and Demand in ECONOMICS

In classical economic theory, as demand for an item increases, prices rise.

When manufacturers respond to the price increase by producing a larger supply of that item, this increases competition and drives the price down.

Modern economic theory proposes that many other factors affect price, including government regulations, monopolies, and modern techniques of marketing and advertising.



This relationship is thought to be the driving force in a free market.

Biological Markets

BABOON FEMALES pay a price in grooming to get a peek at a new infant; the fewer the infants, the longer the grooming time required. The value of commodities—baby baboons in this case—increases as their availability decreases.

Frans de Waal, 2005

- Grooming behavior (e.g. searching somebody's fur for parasites) is a kind of social behavior that helps the relationships among the members of the flock.


TTC

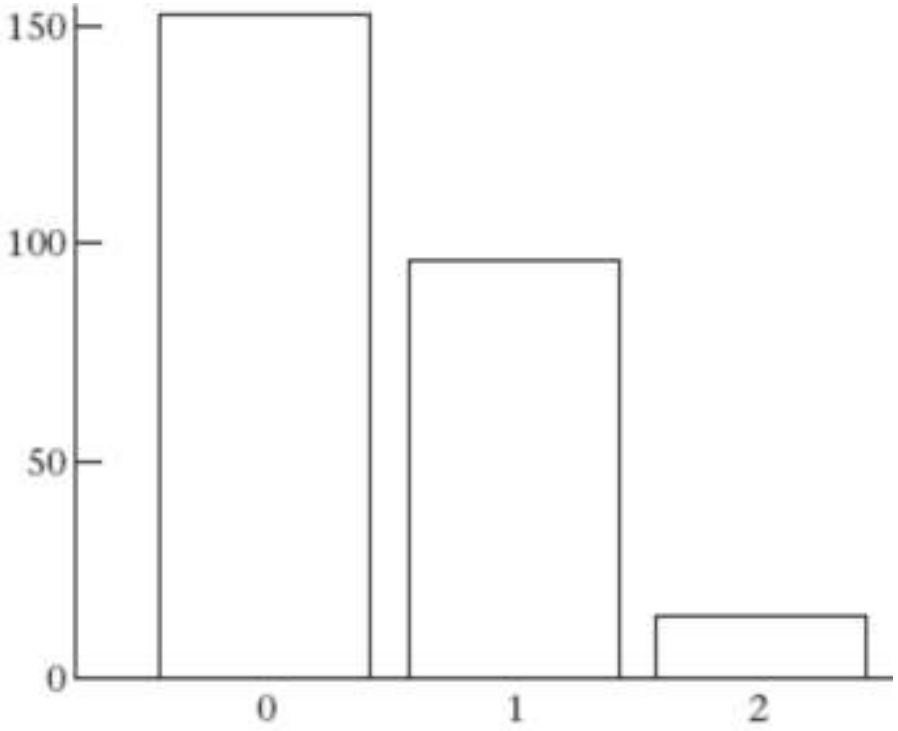
Infant market:

- It is easy to observe and score.
- Trader classes are easy to identify (mothers versus handlers).
- Levels of supply (number of young infants) fluctuate through time.
- Demand is consistently high, as all adult females are keen to interact with young infants.
- Handling is not ‘free’. Baboon mothers are notably reluctant to allow their offspring to be handled, probably because of the potentially high costs to their reproductive success (Nicolson 1987).

Barrett & Henzi, 2002

- After a relaxing grooming session, a mother may give in to the groomer's desire for a closer look. The other thus buys infant time.
- Market theory predicts that the value of babies should go up if there are fewer around.
- Louise Barrett and Peter Henzi found that, indeed, mothers of rare infants were able to extract a higher price (longer grooming) than mothers in a troop full of babies.

Barrett & Henzi, 2002



Infants as a commodity in a baboon market

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Variation in median grooming bout duration (s) with availability of infants present in the troop

Barrett & Henzi, 2002

Supply and demand determine the market value of food providers in wild vervet monkeys

- The law of supply and demand affects the exchange rates in nonhuman ‘‘trading’’ in a similar fashion as in human economic exchanges.
- The exchange of commodities in primate groups is a trading on a market with exchange rates fluctuating from day to day depending on supply and demand.

Supply and demand determine the market value of food providers in wild vervet monkeys

Cédric Fruteau[a,b], Bernhard Voelkl[b], Eric van Damme[a,c], and Ronald Noë[b,a,c]

- Grooming can be exchanged against grooming itself, but also against other goods or services, lending it currency-like characteristics.
- Commodities bought with grooming include tolerance at food sites, access to newborns, compliance of females, and support in conflicts.
- Experiment:
  - **phase 0** - an initial phase in which baseline data on grooming was gathered
  - **phase 1** - a single low-ranking female produces a bonanza of food for herself and her group members by triggering the opening of a container over a period of 9 weeks
  - **phase 2** - a second provider was introduced in group, another low-ranking female with a second food container that only she could open.

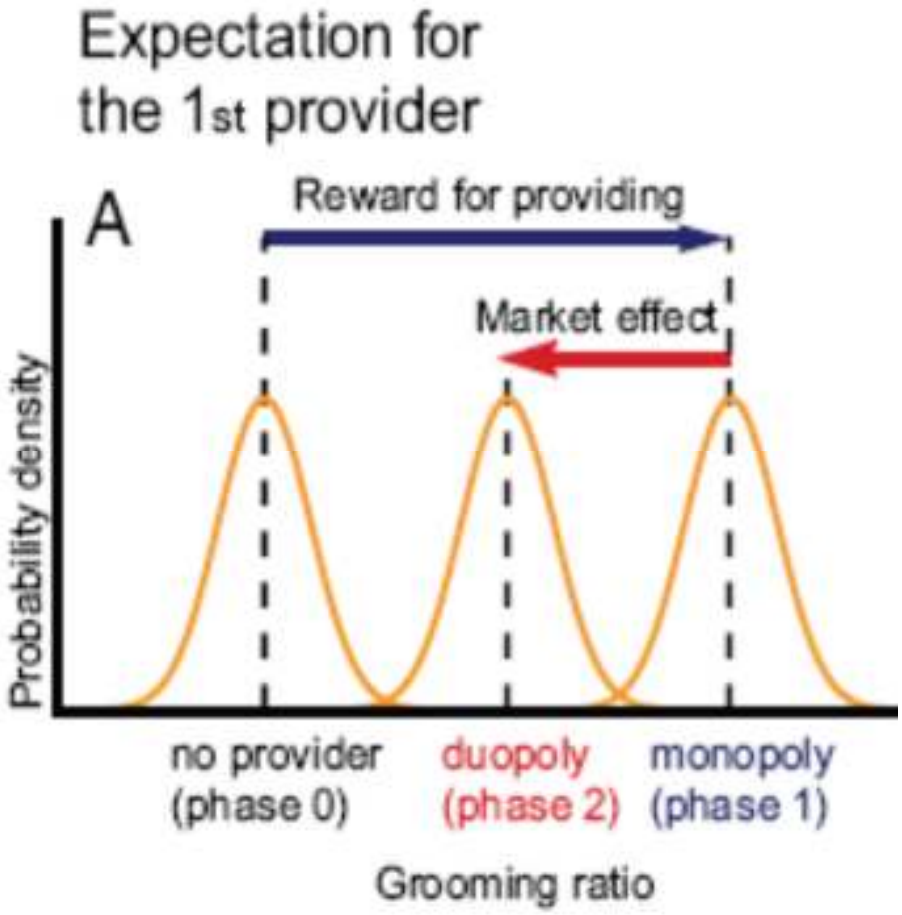
Fruteaua et al 2009

Fruteaua et al 2009

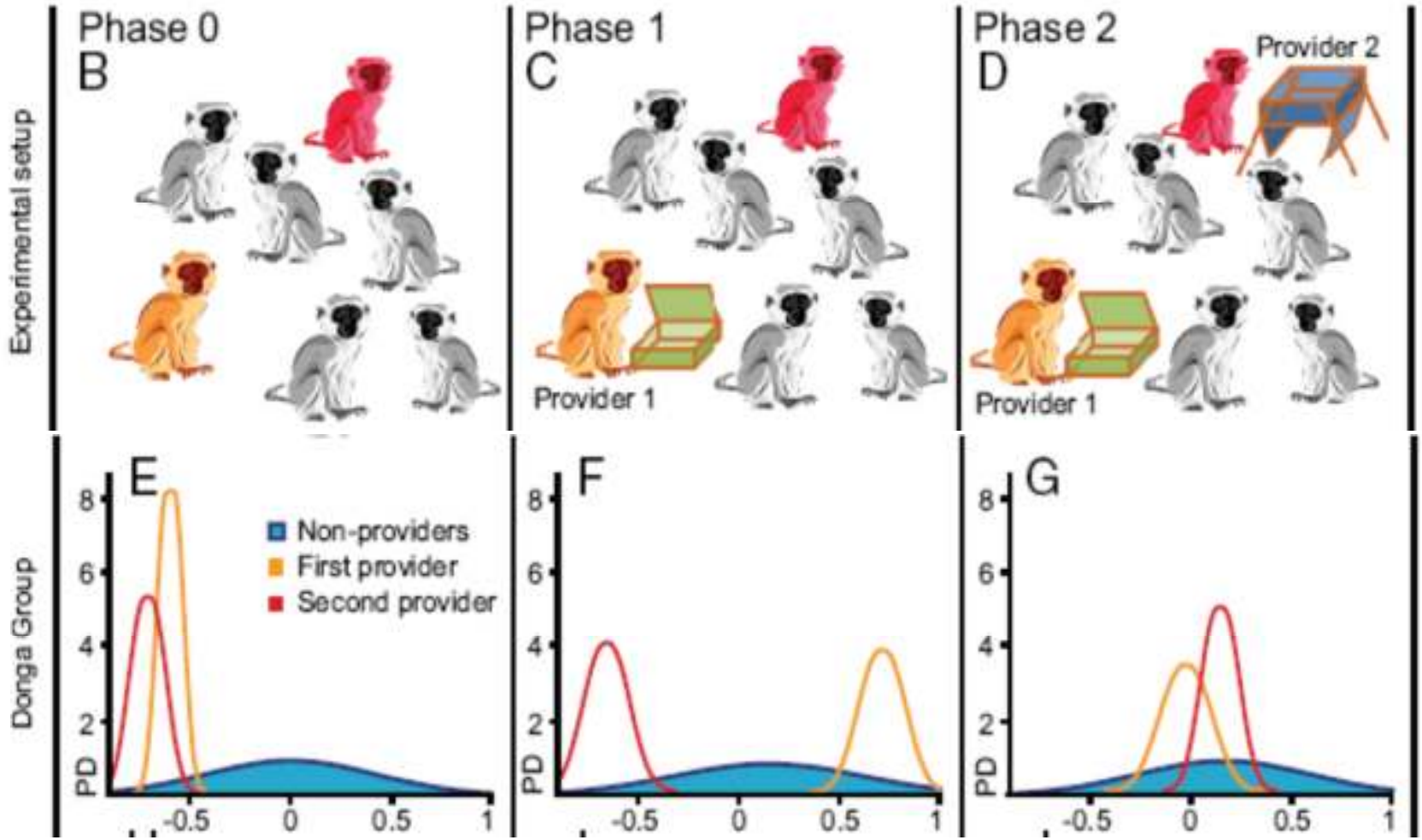
Fruteaua et al 2009

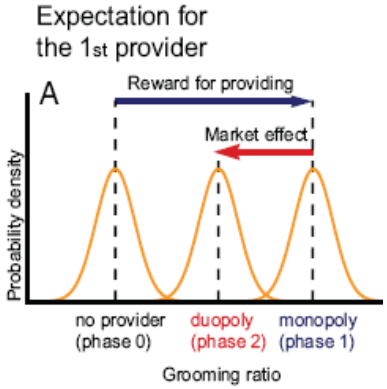
- In economic terms a monopoly is replaced by a duopoly. Agents enjoying a monopoly should obtain stronger leverage over their exchange partners than members of a competitive duopoly.
- This leads to main prediction: grooming ratios should increase in favor of the provider in phase 1 and decrease again with the introduction of a competitor in phase 2.

Fruteaua et al 2009



In summary, we can expect (*i*) baseline grooming ratios to be skewed in favor of more dominant individuals, (*ii*) grooming patterns to change strongly in favor of the first providers, but to become less favorable again when the second providers are introduced, and (*iii*) providers to open the containers preferably in the presence of those grooming them most.





Mean estimates of the grooming ratios for the food provider

Results

- The differences in grooming ratios between the non-test phase 0 and phase 1 were significantly greater for the first providers than for the group of nonproviders (P 0.001).
- The positive effect on the grooming ratios of the first providers was half as strong after a second provider was added in each study group, confirming a central tenet of biological market theory.

Biological market approach

1. Explain adaptations that are the result of “market selection.” Market selection explains the evolution of mechanisms enabling partner choice as well as adaptations that increase the chances of being chosen in cooperative systems.
2. Predict changes in exchange rates of commodities due to changes in the supply/demand ratio between these commodities.

Supply and demand

- Biological market theory - each individual is involved in shopping for the best partners and selling its own services that is modulated by supply and demand.

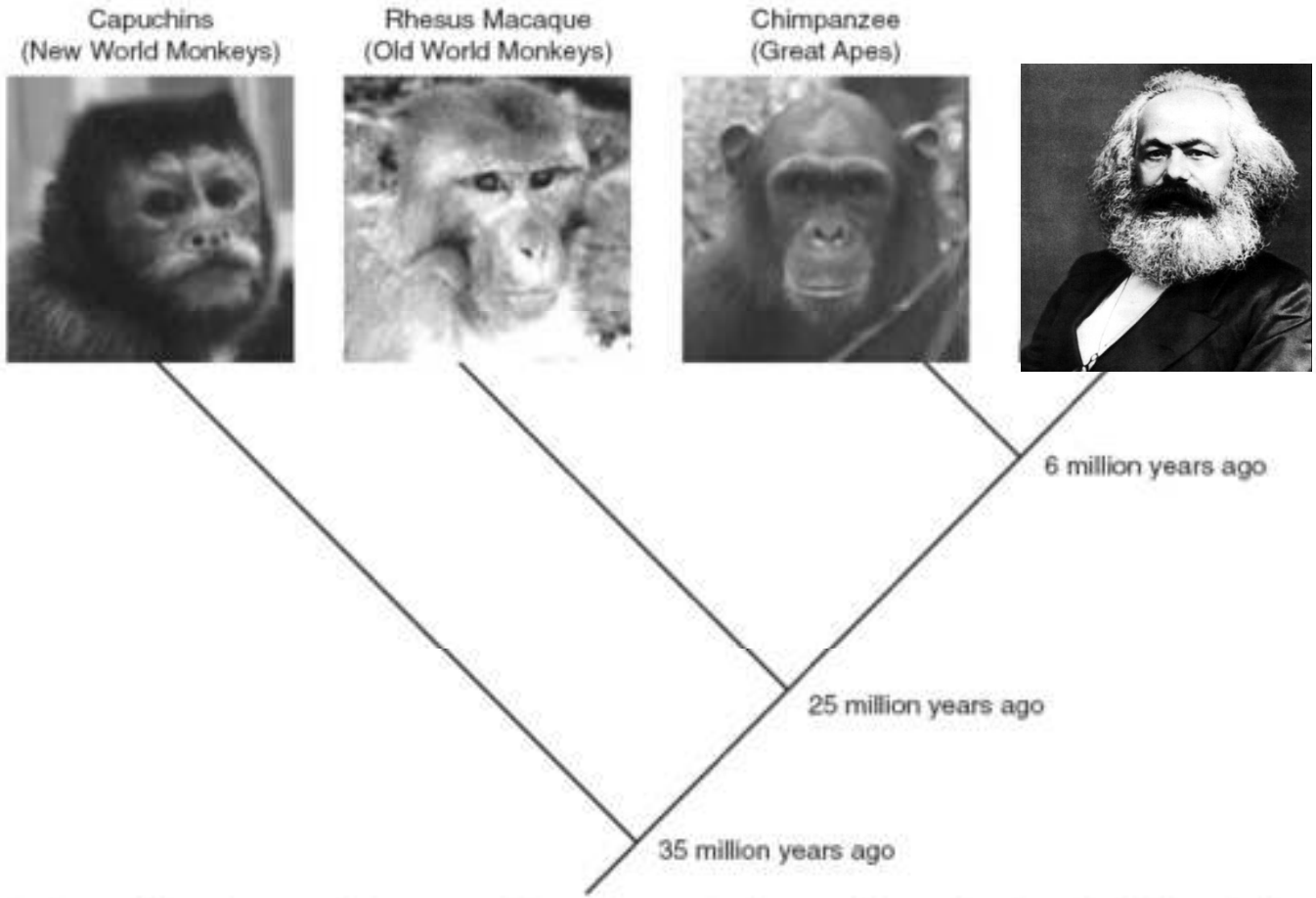
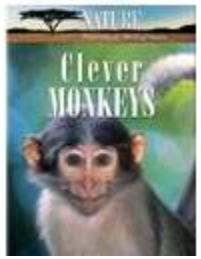


FIGURE 7.1 A schema of the primate evolutionary tree. Our subject species, the capuchin monkey, branched of from the human Old World primate line about 35 million years ago.

Capuchins - “ the chimpanzee ” of the New World primates

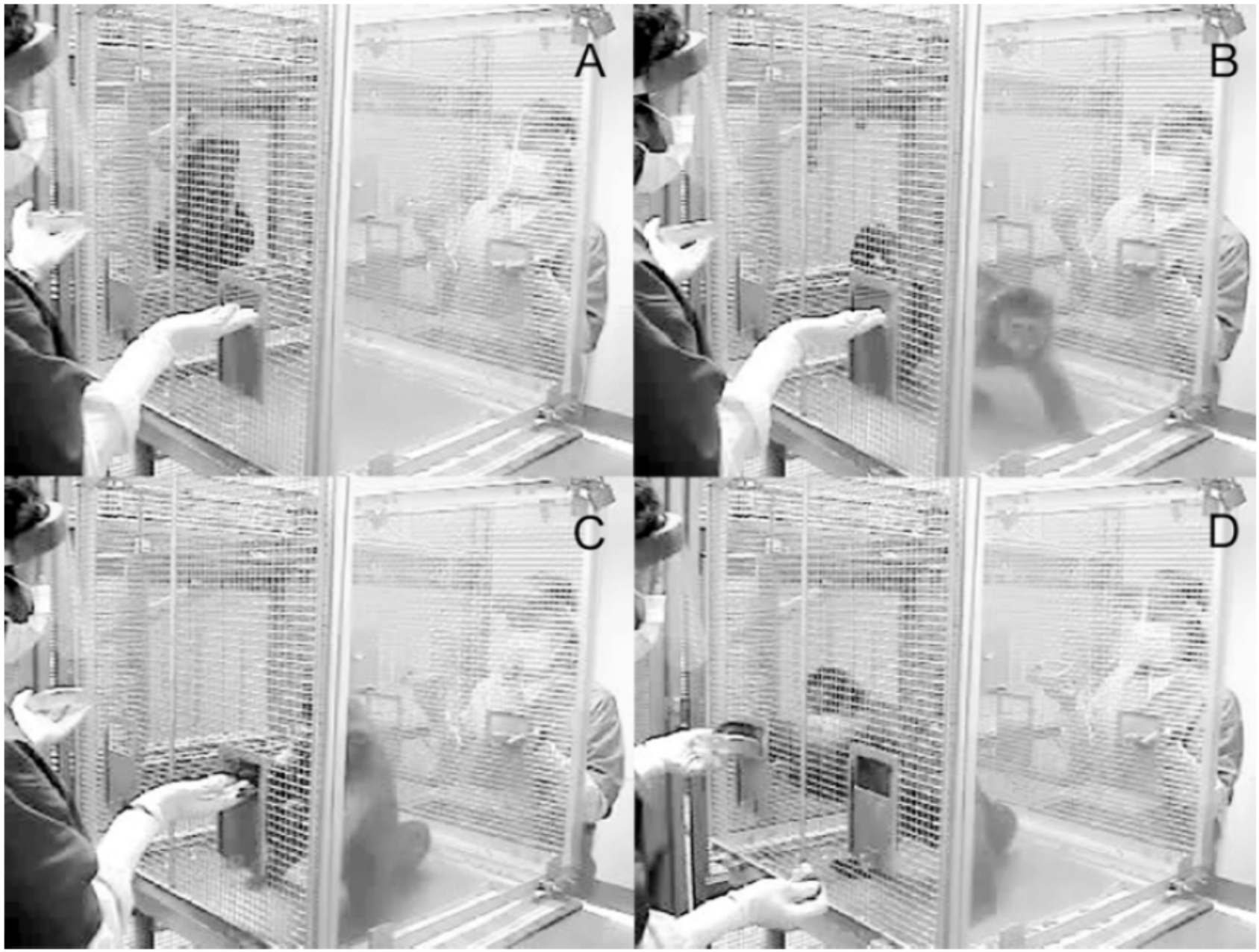
- Capuchins have extremely large brains relative to their body size
- Capuchins live in relatively large social groups as larger as 40 individuals.
- Capuchins are an extremely tolerant species sharing food with many members of the group.
- They can successfully recognize the goals of other individuals and can learn socially from the actions of others.



Trading Capuchins ….

FIGURE 7.2 A frame-by-frame demonstration of a single trading event involving one of our capuchin actors (Jill). The capuchin begins by placing a token in the experimenter's hand (1). The experimenter then takes the token away (2–3) and delivers a piece of food (4) which the capuchin then takes from the experimenter's hand (5–6).

On each trial, the monkey had a chance to trade a token with one of the two experimenters. Each trial began when the two experimenters were in position on either side of the cage. In one hand the experimenters
held the good that they were offering to the monkey; their other hand remained open for the monkey's token.


A
B
C
D

Trading with capuchins

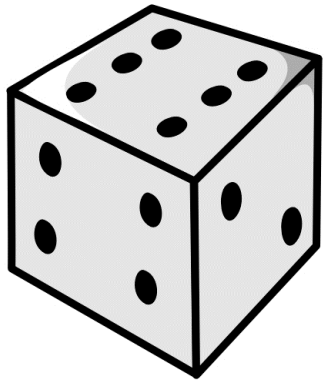
- Capuchin monkeys (as well as other primates) can be quickly trained to trade tokens for small food rewards.
- Capuchins make choices *between multiple different traders*, each of whom delivers different kinds or amounts of goods when presented with a single token.
- An **economic market** – in which they could establish preferences across different bundles of goods.
- Thus, we introduce **price** and **wealth changes** and examine how such changes affected capuchins ' purchasing behavior.

Do capuchins obey price theory as humans do?

- Two goods that the capuchins liked equally – pieces of jello and apple slices .
- Next: dropped the price of one of the two goods by half.
- The majority of capuchins actors shift their consumption to the cheaper good, like humans, obey the tenets of price theory.

Capuchins also try to maximize their expected payoff in the market.

- Chen *et al* ., 2006 presented capuchins with a choice between two traders offered the same kind of good – apples.
  - 1st trader - offered one piece of apple and then handed over that one piece.
  - 2nd "risky" trader – began with two pieces of apple and then, with 50% probability, either handed over both pieces or took one of the two pieces away for an offer of only one piece.



- On average the "risky" experimenter gave 1,5 pieces of apple on average, while another experimenter gave only 1 piece.
- Like rational actors, capuchin traders reliably to prefer the risky experimenter.
- Thus, capuchins shift consumption rationally in response to price shifts and prefer gambles with the highest average payoffs.

DO CAPUCHINS DISPLAY THE SAME BIASES AS HUMANS?

- Human consumers appear to evaluate their choices not only in terms of their expected payoffs
- In particular, human participants tend to be loss averse – they avoid getting payoffs that appear as losses relative to their reference points more than they appear to seek out gains relative to their reference points (e.g., Kahneman and Tversky, 1986; Tverky and Kahneman, 1981).

Problem 1—The Asian Disease

Imagine that the United States is preparing for the outbreak of an unusual Asian disease, which is expected to kill 600 people. Two alternative programs to combat the disease have been proposed.

√ If Program A is adopted, 200 people will be saved.

If Program B is adopted, there is a one-third probability that 600 people will be saved and a two-thirds probability that no people will be saved.

Which one of the two programs would you favor?

If Program A′ is adopted, 400 people will die.

√ If Program B′ is adopted, there is a one-third probability that nobody will die and a two-thirds probability that 600 people will die.

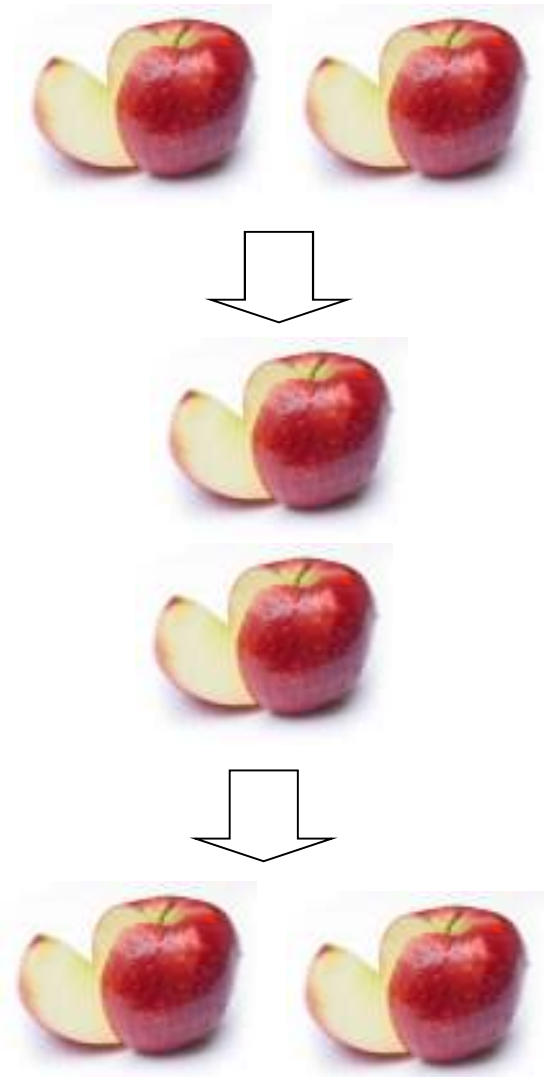
Are Capuchins Reference Dependent and Loss Averse?

- Monkeys got to choose between two experimenters who both delivered the same average expected payoff of 1,5 of apples.
  - The first experimenter gave the monkeys less than they had expected based on their reference point.

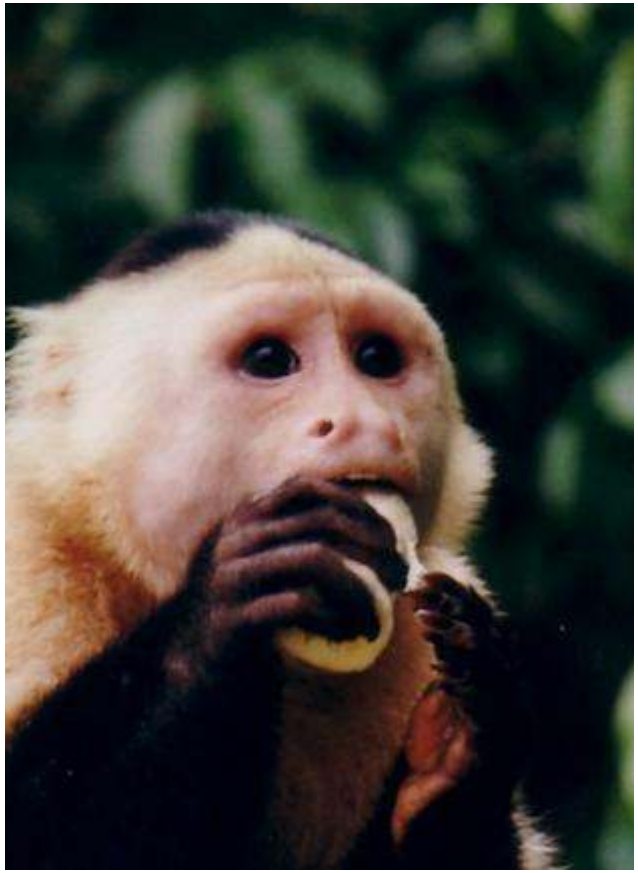
  This experimenter began every trade by showing the monkeys two pieces of apple. When this experimenter was paid, he either delivered these two pieces of apple as promised, or removed one to deliver only a single apple piece.

  - The second experimenter, in contrast, gave more on average than the monkeys expected.

  This second experimenter always began by displaying a single piece of apple but then, when paid, either delivered this one piece as promised or added a second piece for a payoff of two apple pieces.



- Monkey consumers reliably preferred a gain condition.
- Like humans, capuchins appear to take into account reference points – in this case, what they initially are offered.
- Thus, capuchins appear to share fundamental biases that humans display: framing effects, with different descriptions of the same problem leading them to make different choices.



Endowment effect

- The endowment effect—the tendency of human decision makers to systematically overvalue objects that they own over objects that they do not yet own.
- Kahneman et al. (1990) gave human participants a new object (e.g. a mug) and then offered them the chance to sell this object or trade it for an equally priced alternative good (e.g. a set of pens).

  Participants consistently refuse to trade their owned object and demanded approximately twice as much money to sell the object as buyers were willing to pay to obtain the object.

Figure 1. A photograph depicting the token exchange method in capuchins. Here, one capuchin subject, Auric, trades a token for a food reward.

- **Experiment 1** presented monkeys with food items in place of their 12 tokens and allowed subjects to trade these food items back to an experimenter who offered an equally preferred food item in exchange.
- **Experiment 2** checked monkeys' willingness to use food as tokens – they were allowed to trade their endowed good for a treat of far greater value, the FFRU (slice of marshmallow fluff-filled fruit roll-up).
- **Experiment 3** checked whether monkeys may be reluctant to trade their endowed food due to the cost of transporting the endowed food to the experimenter for exchange.
- **Experiment 4** checked whether monkeys exhibit an endowment effect simply because trading takes more time than eating the food.

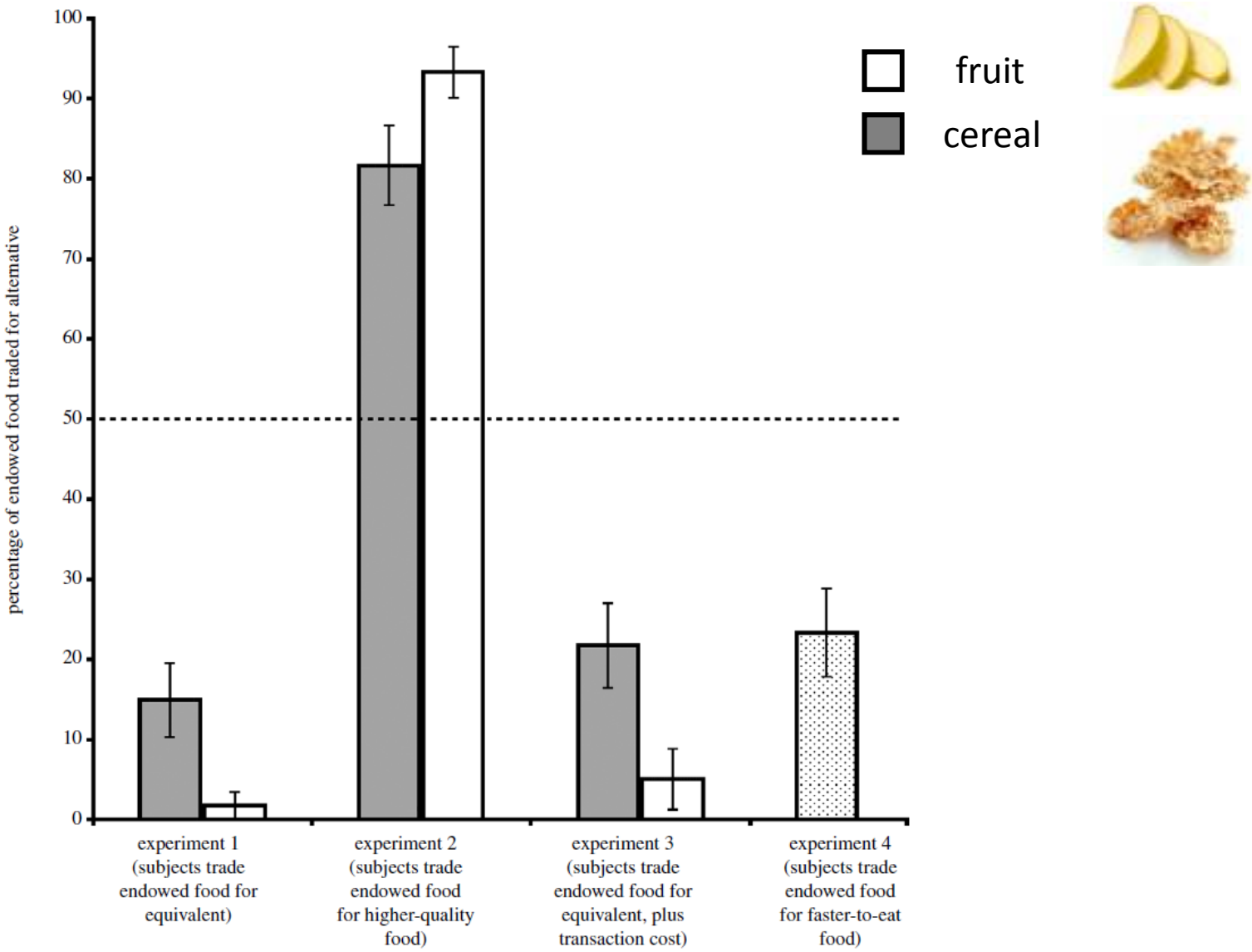


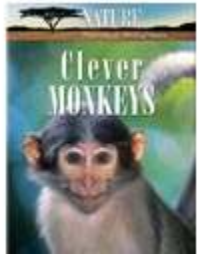
Figure 2. Percentage of endowed food traded by the subject for the alternative food in each condition, pooled across subjects ($n=60$ for each bar). Error bars represent 1 s.e. In experiment 1, when sujects could trade an endowed good for its equivalent, subjects preferred the endowed good over the good available through trade. This preference to consume endowed food, rather than exchange it for an equivalent, persisted despite increasing the size of the offer to account for the cost of the transaction (experiment 3) and the time of the trade (experiment 4). However, subjects were willing to trade food in exchange for a highly valued alternative (experiment 2). Grey bars, cereal; white bars, fruit; dotted bar, in-shell nut.

Trading has the hallmarks of cooperation:

(i) two or more individuals exchange goods and services in such a way that the participants involved are usually better off after the interaction, than before it,

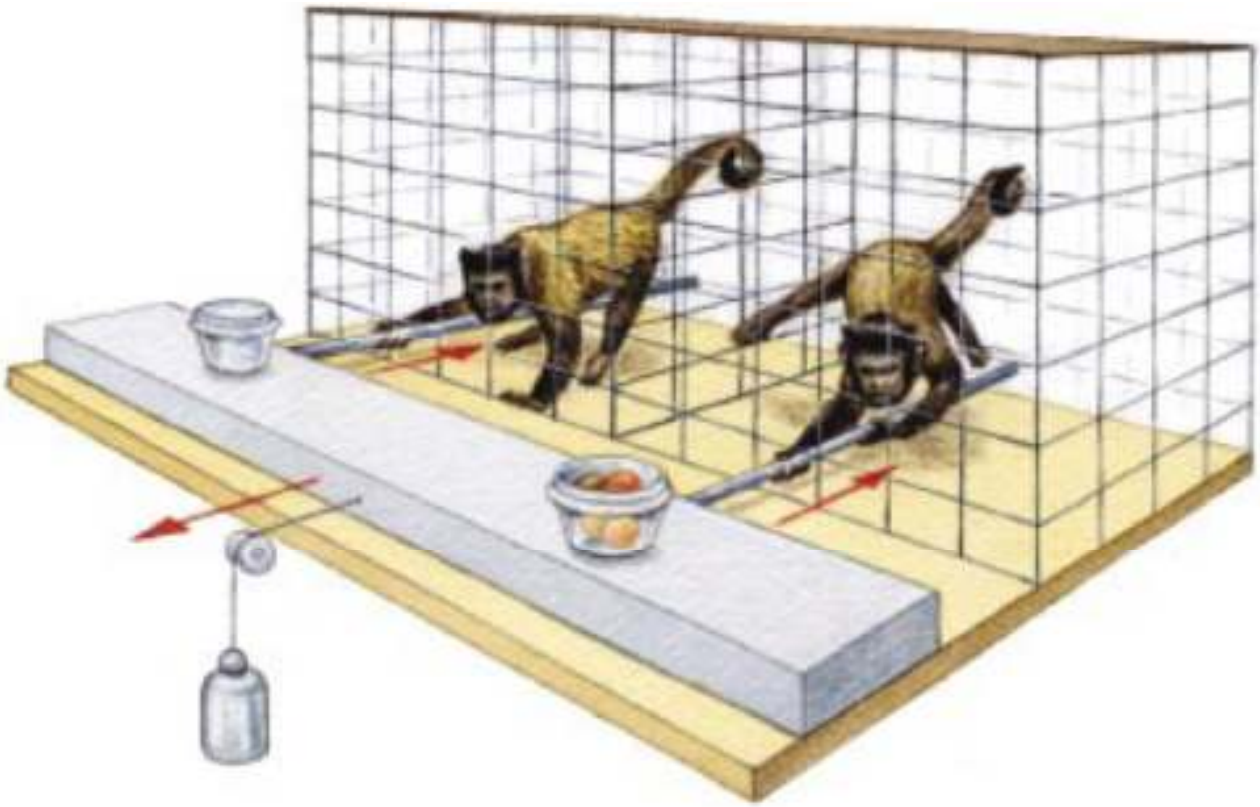
(ii) the participants have to invest something in the interaction without a full guarantee of net gain.

- Broadly speaking ‘cooperation’ – all activities that result in net benefit to both the actor and the recipient(s).



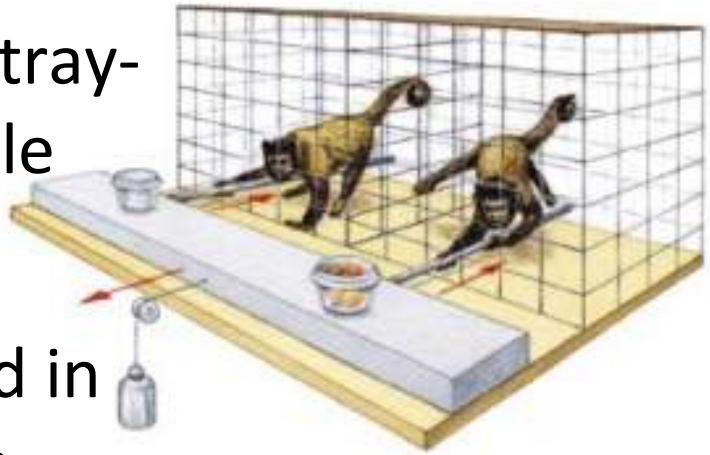
Cooperation of Capuchins

TRAY-PULLING EXPERIMENT demonstrates that capuchin monkeys are more likely to share food with cooperative partners than with those who are not helpful.

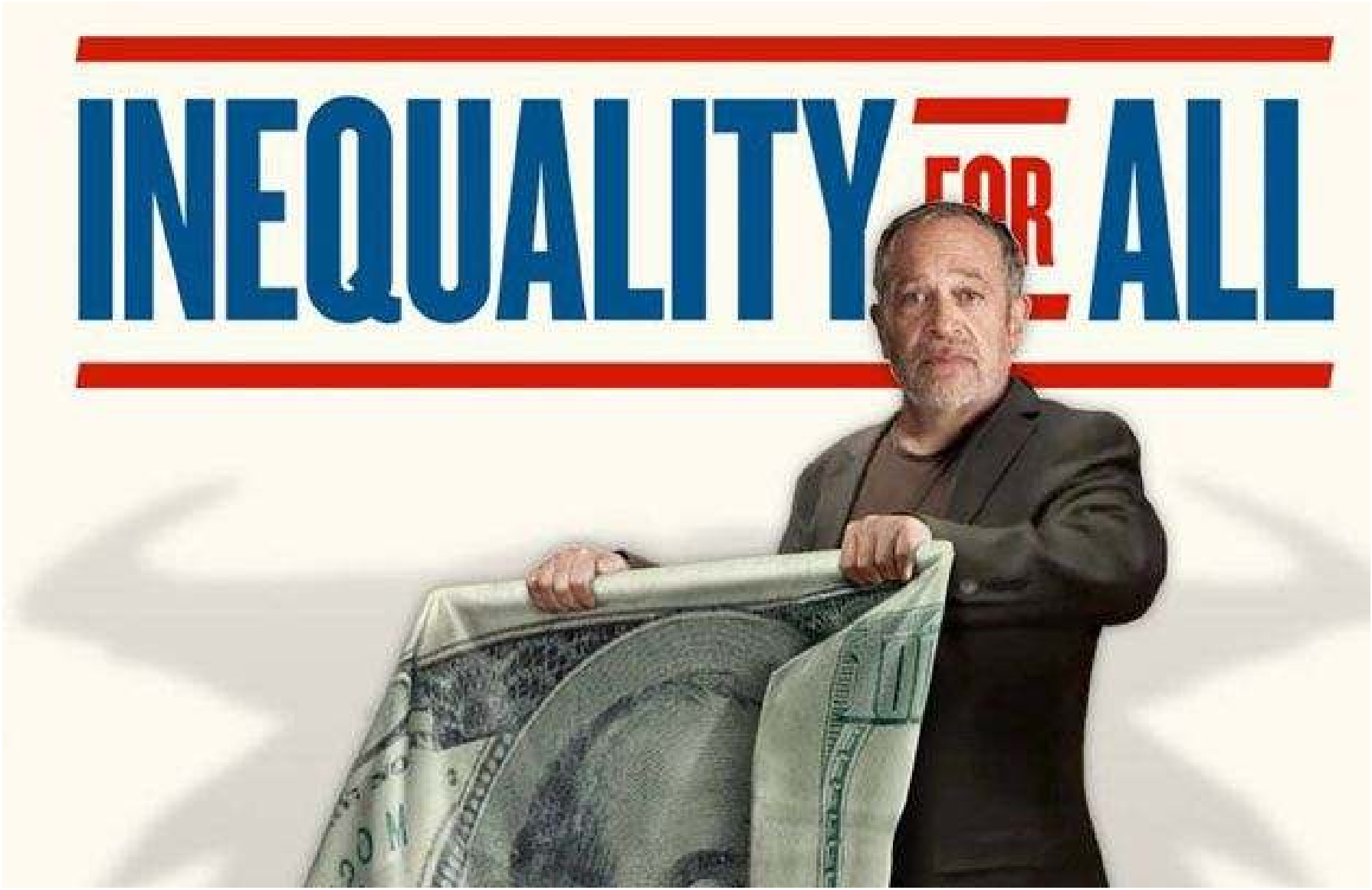


TRAY-PULLING EXPERIMENT demonstrates that capuchin monkeys are more likely to share food with cooperative partners than with those who are not helpful. The test chamber houses two capuchins, separated by mesh. To reach their treat cups, they must use a bar to pull a counterweighted tray; the tray is too heavy for one monkey to handle alone. The "laborer" (*on left*), whose transparent cup is obviously empty, works for the "winner," who has food in its cup. The winner generally shares food with the laborer through the mesh. Failing to do so will cause the laborer to lose interest in the task.

- Only one monkey (the winner) of a tray-pulling pair received a cup with apple pieces.
- Its partner (the laborer) had no food in its cup, which was obvious from the outset because the cups were transparent.



- Researchers counted more acts of food sharing after collective than solo pulls: The winner generally shares food with the laborer through the mesh. Failing to do so will cause the laborer to lose interest in the task.Sharing affects future cooperation.



a film documentary “Inequality for All”

Monkeys reject unequal pay

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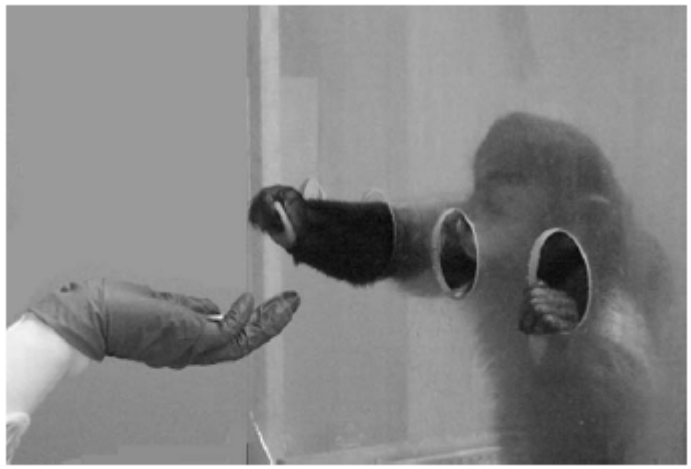
- **Equality condition** – two capuchins get the same food in exchange to a token
- **Inequality condition** – two capuchins get different food (cucumber and grape)
- "**Effort controls**" – a grape was simply handed to the partner by the experimenter (no exchange) followed by the subject herself exchanging for cucumber
- '**Food controls**' – in the absence of a partner, the subject witnessed a grape being placed in the location where the partner normally sat, after which the subject herself exchanged for cucumber.



Incomplete exchanges were counted:

(1) failure to hand back the token (no token, NT),

(2) failure to accept or eat the proffered reward (reject reward, RR).

Frans de Waal Lab

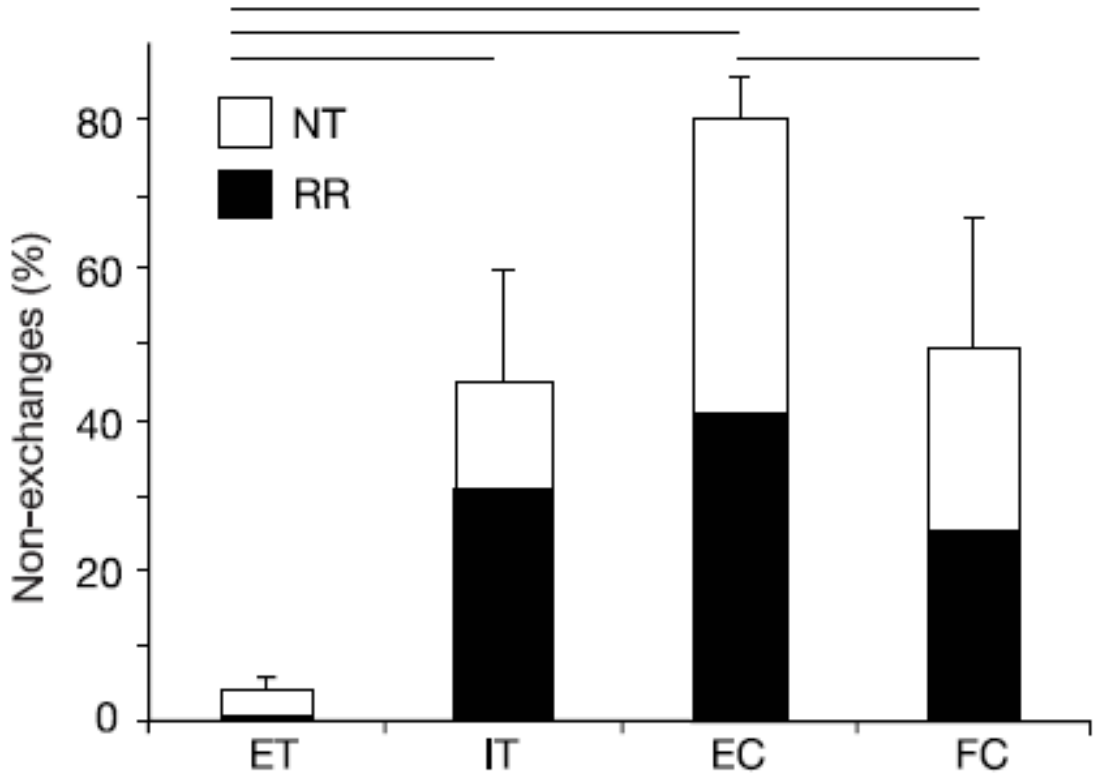
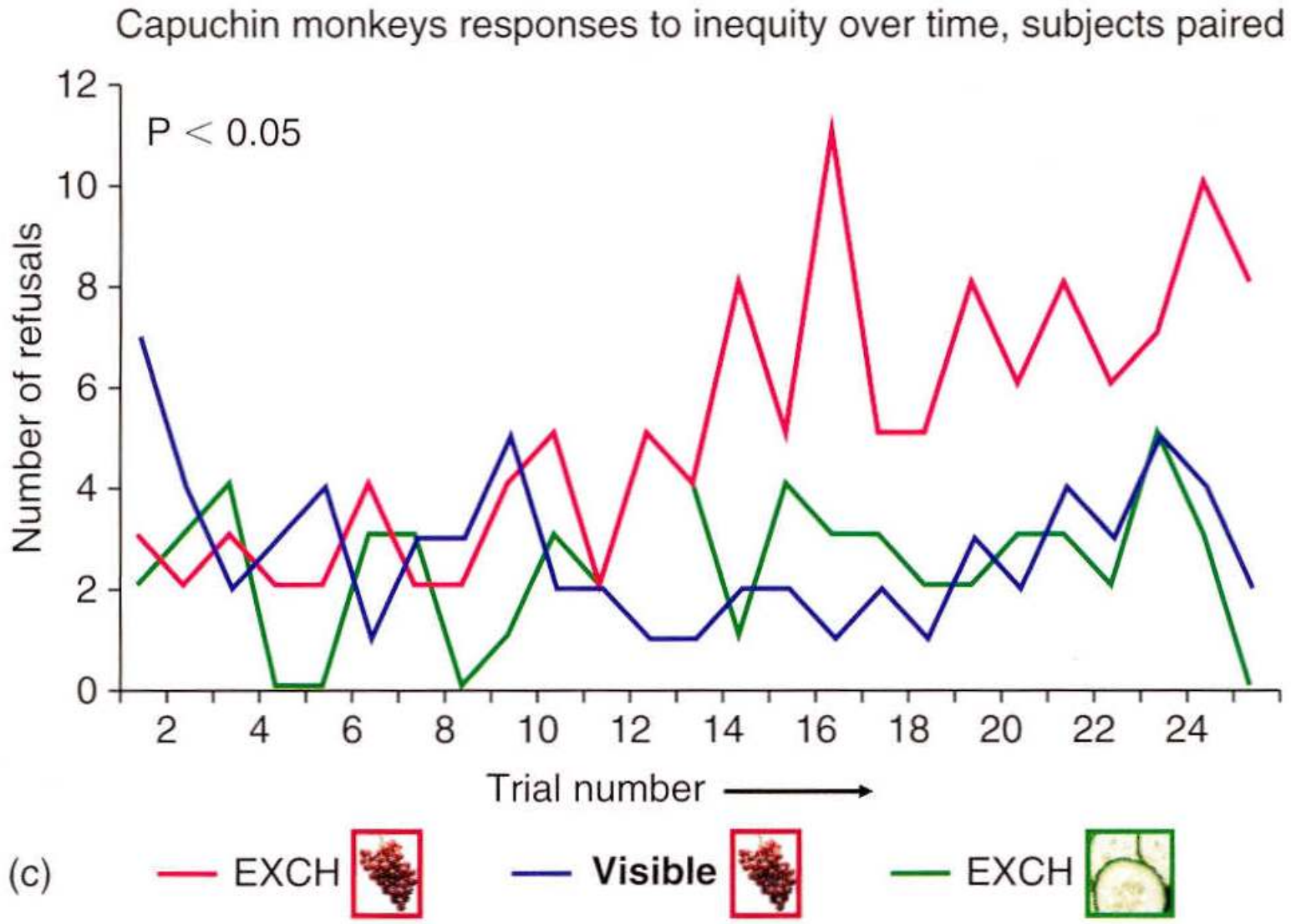


Figure 1 Mean percentage ± s.e.m. of failures to exchange for females across the four test types. Black bars (RR) represent the proportion of non-exchanges due to refusals to accept the reward; white bars (NT) represent those due to refusals to return the token. s.e.m. is for combined non-exchanges. Lines indicate significant differences between conditions (Tukey's multiple comparisons). ET, equality test; IT, inequality test; EC, effort control; FC, food control.


Capuchin monkeys responses to inequity over time, subjects paired
P < 0.05
Number of refusals
0
2
4
6
8
10
12
2
4
6
8
10
12
14
16
18
20
22
24
Trial number
(c)
EXCH
Visible
EXCH

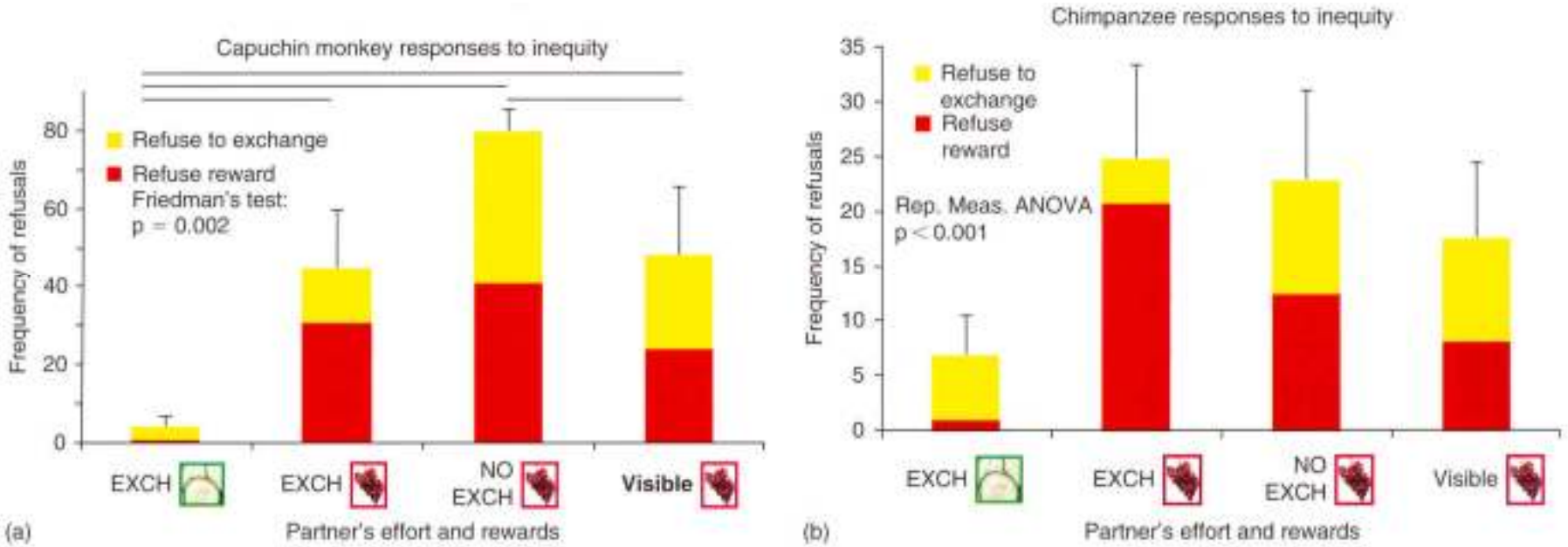


FIGURE 19.5 The distribution of refusals in the original conditions. The subject always exchanged for a cucumber, while the partner's rewards and effort required varied (indicated on the x-axis; cucumber or grape for reward, exchange or no exchange for effort). In the "Visible grape" condition, grapes were visible but no primate received one. Paler bars indicate refusal to return the token; darker bars indicate refusal to accept the reward. Standard error bars are for the total measure (refusal to return the token and refusal to accept the reward combined). Subjects were much more likely to refuse to participate when the partner received a better reward, either for the same or for less effort. Significant differences from *post hoc* tests are indicated by horizontal lines over bars. (a) Data for capuchin monkeys. Reprinted from Brosnan and de Waal (2003). (b) Data for chimpanzees. Reprinted from Brosnan *et al.* (2005).

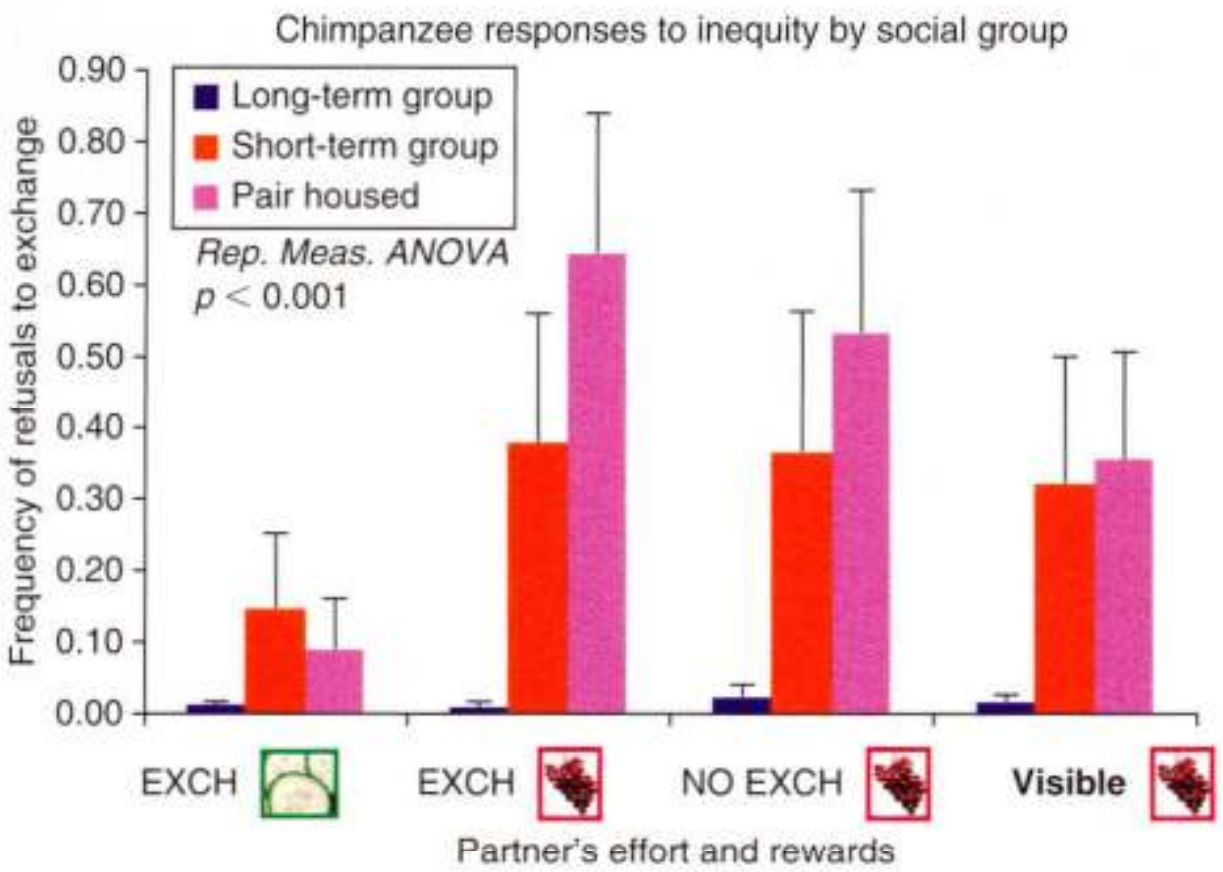


FIGURE 19.8 This figure further breaks down the data presented in Figure 19.5b, indicating that responses varied greatly dependent upon the social group. Chimpanzees from a long-term social group were much less likely to respond to inequity than those from shorter-term or pair-house situations, indicating that subjects' relationships or other social factors influence the response to inequity. Reprinted from Brosnan *et al.* (2005).

Unfair cooperation

- To reject unequal pay—which people do as well—goes against the assumptions of traditional economics.
- In the short run, caring about what others get may seem irrational, but in the long run it keeps one from being taken advantage of discouraging exploitation is critical for continued cooperation.

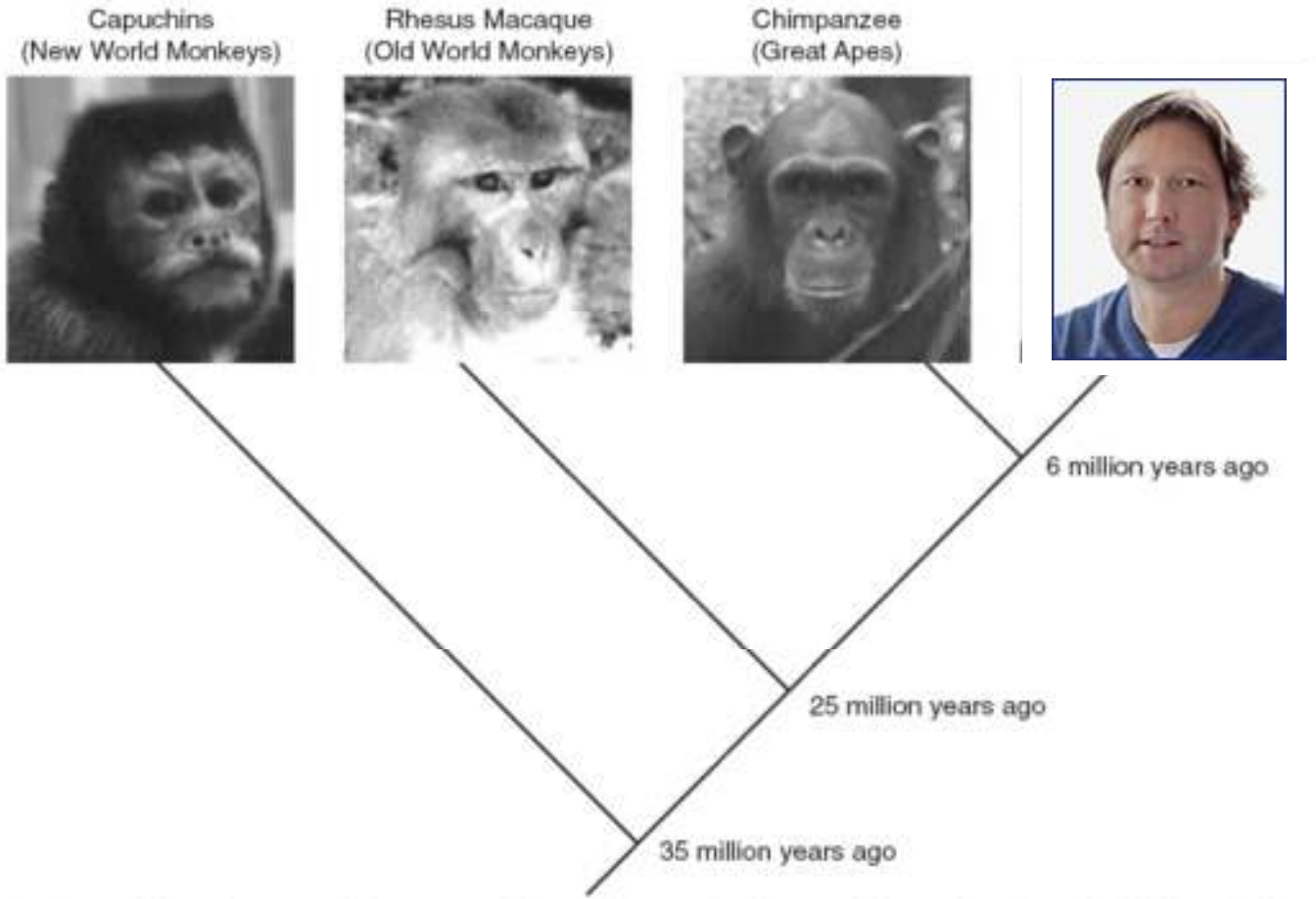


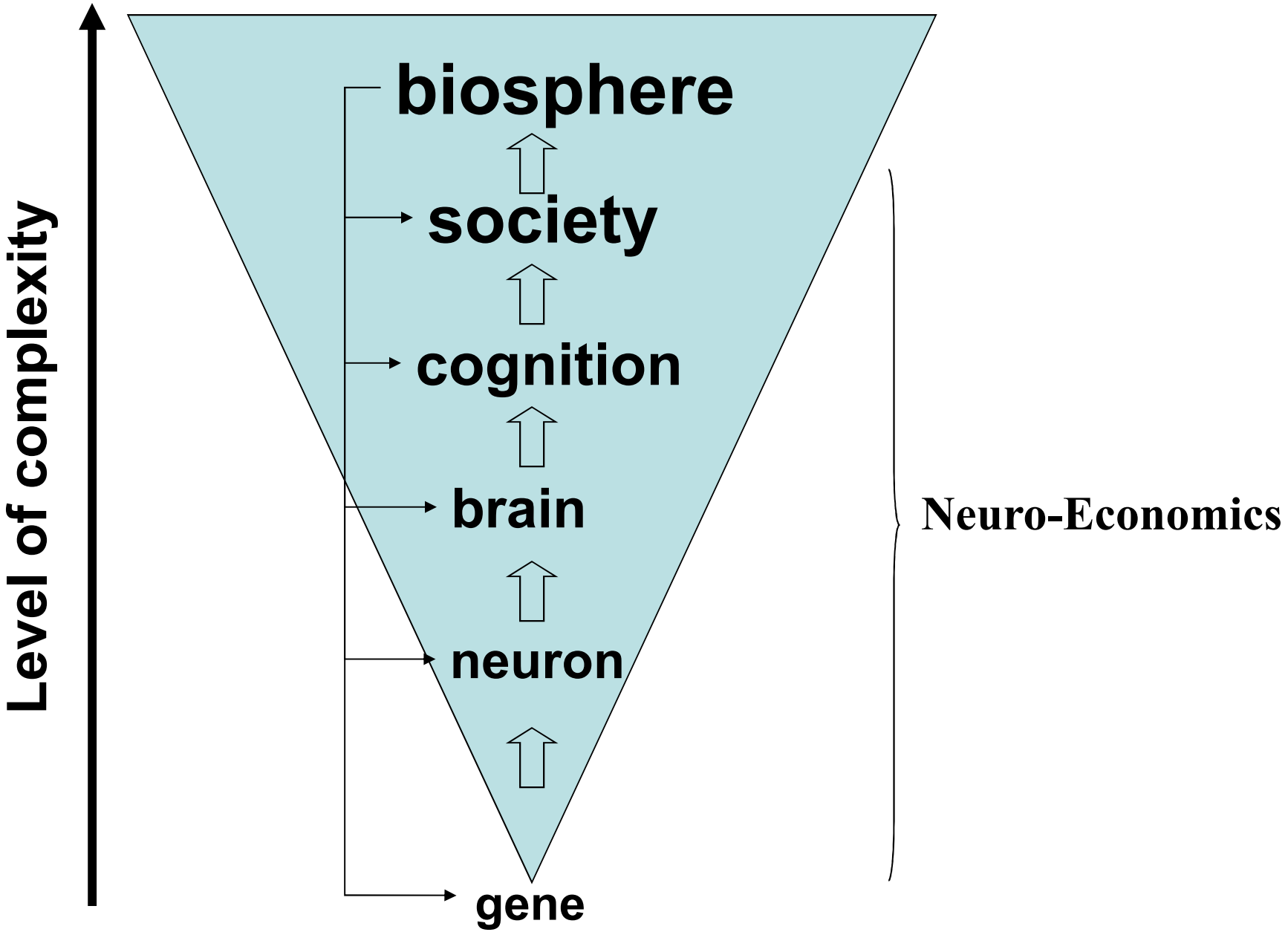
FIGURE 7.1 A schema of the primate evolutionary tree. Our subject species, the capuchin monkey, branched of from the human Old World primate line about 35 million years ago.

WHAT COMPARATIVE STUDIES MEAN FOR TRADITIONAL ECONOMICS AND NEUROECONOMICS

- Capuchins appear to obey the standard price theory, just like humans.
- Capuchins also exhibit the same systematic biases as humans – they evaluate gambles in terms of arbitrary reference points, and pay more attention to losses than to gains.
- Monkeys appear to show other market anomalies, like the endowment effect.
- Comparative studies suggest that biases are evolutionary based and emerge in the absence of experience.

Summary

- Animals are engaged in “economic” interactions affected by supply and demand for goods.
- Some animals shows decision-making biases that are similar to human.
- Sub-optimal human decisions in modern circumstances may be made using archaic mechanisms.


Level of complexity
biosphere
society
cognition
brain
neuron
gene
Neuro-Economics

Thank you for your attention!