Social Neuroeconomics: The Influence of Microbiota in Partner-Choice and Sociality

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Abstract:

By focusing on the studies of primate behavior and human neuroscience: we describe how different neurological processes are the base of proximate aspects of social--decision making. We also review the fact that distinct aspects of animal behavior are not under conscious or abstract control and that instead they may be regulated by adaptive 'rules of thumb'. In particular, by describing the microbiota-gut-brain axis We elaborate on suggesting that microbiota has an influence on within individual aspects of social decision making and in particular facilitating social interactions. Finally, we present comparative evidence of the ro1c of microorganisms as modifiers of aspects of kinship, reproduction and group-members recognition, suggesting how microbiota also has an influence on between individual aspects of decision making, which are themselves primary aspects of cooperation. ln summary, we propose that modem socio economic choose theories may still benefit form alternative theoretical framework that consider the human being as complex organism with intrinsic constraints and capacities product of its evolutionary history, and not just as an exclusively-cognitive decision maker acting independently of its closest partners and commensals: its microbiota

Keywords: Neuroeconomics, microbiota, probiotics, decision making process, social neurosciences.

INTRODUCTION

A concern for the study of the choices individuals make to achieve their goals, given their allocations of scarce resources, or Economics [I], has long been of considerable interest to sciences as diverse as comparative Psychology, Biology and Ecology. From the biological perspective, the appearance of 'On the Origin of Species by Means of Natural Selection' by Darwin [2] allowed that an ever present philosophical and political debate on the value of individual strategies versus those made available by group-living [3] found a niche within scientific thinking and could be gradually introduced as a pillar of the modem theoretical debate on the theory of evolution [4, 5, 6]. Certainly, one of the most relevant topics of interest in modern biology is concerned with an understanding of the theory of evolution as a process based on 'selfish principles' (sensu Dawkins [7]), versus, interpretations focused on benefits (i.e., in terms of fitness) obtained by means of cooperative and/or reciprocal behavior (5]. This debate has been reproduced in the understanding of the origins, benefits and costs of sociality, leading to new interpre-tations suggesting the beneficial nature of different levels of bio-logical organization, or a theory of 'Multilevel selection· [8] . How-ever, once there is the possibility of obtaining benefits at two different levels of biological organization, how can higher-level units (e.g. a group) ensure cooperation from lower level units (i.e. its composing members), thus ensuring the transfer of fitness from lower (a, a cost to group members) lo higher levels [9]" One likely answer is that individual units composing higher-level associations are able to identify and select their cooperative partners. In this sense, theories such as kin-selection [l OJ and reciprocal altruism [11] have been proposed as rich explanatory frameworks for how cooperation (with the possibility of having costs at the individual level) leads, to group-level stable interaction and the evolution of cooperative and organized groups of individuals (i.e. societies) Nevertheless, while crucial for the understanding of the 'ultimate' causes of cooperative behavior, other frameworks may be more. suitable to answer questions on the proximate cause or control- ling processes of cooperative behavior [12]. For instance, if behaviour is restricted by the, potentialities of the nervous system and individuals must exert short-term choices (i.e. choosing among distinct potential partners). Selecting whether investing their limited resources (e.g. energy; time) in cooperative interactions with specific individuals or not, then knowledge gained on the interaction between neurophysiological processes and individual decision-making strategies could illuminate proximate aspects, of cooperative interactions. In this context, some of the best available instruments for understanding the short-term constraints and capacities of decision-making may be made available via a focus on neuroscience as a tool for the analysis of behaviour relevant to the allocation of resources, in the form of neurobehavioral economics, This, via an examination of neurobiological aspects of behaviour, one of the main the themes of our review is based on the proximate causes, or underlying control-processes of several facets of neurobehavioral economics and social decision-making. However, traditional economic approaches conceive individuals as rational: selfish, and most importantly, unemotional maximizers [1 31 of utility: the 'level of satisfaction· derived per unit of a given good [1 4J. indeed, evidence based on this meaning or rationality can be found across several species, from simple to complex-ones [14]. Yet, another aspect of rationality involves the degree of abstract cognitive computations involved in a particular decisiot1-making process. One way of thinking about this alternative is by using cognitive frame-works such as intentionally and/or theory of mind, which in general, suggest that subjects of different species possess different degrees of knowledge about the 'contents' of the cognitive processes occurring in another organism at a given point in time. Since different species develop distinct degrees of abstraction of the factors involved in aspects of their decision-making processes, partner- choice may not necessarily be based on complex cognitive computations, but on evolved behavioral rules of thumb allowing for 'close to optimal' choices or strategies at different points in time and in different contexts . Based on the recent advances on the relationship between animals and their microbiota (i.e. the community of microbe, in a particular habitat, such as tbc microbiota of the mouth'), another important theme of this review is a focus on the influence of microbiota on aspects of within, as well as between- individual decision-making processes.

In light of the above, the review is organized a, follows: first, it suggests how cooperative and altruistic forms of resource-allocation are as common, or even more common. than selfish or non--cooperative individual strategies. By focusing on studies on primate behaviour and neuroscience, it describes how different neurological processes arc the base of proximate aspects of social decision making. Second, i1 underlines the fact that distinct aspects of animal behaviour are not under conscious or abstract control and that in- stead they may be regulated by adaptive 'rules of thumb '. Third, by describing the properties of a microbiota-gut-brain axis and the primary anatomical afferent and efferent connections between microbiota and the brain, it suggests that microbiota has an influence on within-individual aspects of social decision making. It also suggests how, by means of its action on the parasympathetic nervous system, microbiota may have an influency on aspects of relaxation, therefore facilitating social interactions. Finally, it presents com-parative evidence of the role of microorganisms as modifiers of aspects of kinship, reproduction and group-members ' recognition, suggesting how microbiota also has an influence on between individual aspects of decision making, which are themselves primary aspects of cooperation

SOCIALITY AND COOPERATION

Costs and benefits off sociality and time-, constraints on social interaction. Cooperation occurs when individuals assist or support each other; when specific actions or traits of some subjects ate beneficial to the fitness of other individuals; when interactions are beneficial, at the same time. for two organisms, and even when behaviour is in fact costly to an actor but beneficial to its recipient [1 5]. Social-living itself entails both costs. and benefits. In low¬ productive environments, lactating females may need to reduce the variety of their social relationships to focus their social time on their primary associates I 16 1, optimizing their time and energy budgets. Moreover, both Altmann [1 7] and Nicolson [1 8] have independently suggested that due to characteristic, of behavioural interactions leading to dominance hierarchies, female primates suffer important costs in terms of reproductive success. Dunbar [19] for example, observed that for every rank-unit of dominance lost {i.e., increasing a subject's subordination) female gelada baboons (Theropithecus gelada) lost an equivalent of 0.5 births during their life cycle, whereas Almann et al. [20] reported that, in Papio cynocephalus, differences in females· dominance hierarchy were associated to differences of up to 2.5 months in the age of menarche and 1 .5 months in inter-birth intervals. In addition, bene- fits due lo sociality and cooperation al different levels have been observed in different species, both among kin-related (e.g. howler monkeys: Allouatta seniculus [2 1)) and non-related individuals (e.g. chimpanzees: Pan troglodytes, [22]), Social relationships arc beneficial because they may also act as: kind of 'buffer' for the stress produced by the interaction of subjects with both their social and their physical environment. In human [23j and nonhuman primates [24], the quality or the social environment has a significant influence on the patterns of hormone production. such as glucocorticoids (i.e., stress hormones), progesterone [25], and oxytocin; [26].

Extensive work as that by Stephens and Krebs [14] has focused on the study of strategies that animals display to acquire the energy necessary to sustain their basic physiological processes and behaviour, either considered from a perspective of the optimality of their individual behaviour or in a socially-dependent way, focused on the simultaneous interactions of foragil1g methods performed by different subjects (i,e,, their economic interdependence of costs and benefits [27]). Time-use is particularly important for organisms: it regulates the circadian rhythms of hormones like testosterone, estradiol and cortisol [28]. However, while time has long been a topic of interest to neurophysiologists, t11e question of how docs a primate or human brain perceives ii is unclear. One hypothesis is that there may be multiple neural clocks, besides the suprachiasmatic hypothalamic nucleus (the master clock), specialized in either sho1t or long durations distributed across areas of the brain, which underlie our psychological perception of time [29] . Animals living at non-equatorial latitudes may perceive substantial variations in day-length across the year·, thus, daylight hours can be a substantial constraint behavior and partner choice [30]. A considerable amount of time is often used in reinforcement of social relationships, a proportion which is, never the less dependent on the u se of feeding-time and food-quality [31]. Thus, an individual 's use of time will also depend on its physiological state. One important example of the relationships between sociality and constraints due to physiology and the use of time is explicit during the phases of female reproduction. Female gelada baboons, for example_ must increase their feeding rates, as their dependent of spring grow older [16], reducing the breadth of their social interactions when the quality of the grasses, they eat are not optimal. In the case of humans, one study suggests that the current epidemics of obesity may be related to ancestral foraging adaptations. For Rowland et al., [32 J some of the selective pressures leading to the evolution of human brains must have involved adaptations solving the type of economic problems found in ancestral environments. In such environments, the unpredictability of time until next meal should have led to adaptation; for eating less when the costs for acquiring food were high, but more importantly, to eating more when the costs of food acquisition were low. Therefore, the current obesity problem faced by several western societies could be based on the human organism's incapacity (i.e. adapted to food-uncertainty) to deal with the contemporary conditions of food availability (i.e. virtually without extractive of searching costs amd based on, often, poorly- nutritious items, that nonetheless have a great caloric value), with a net result of an obesogenic environment.

Kinship

One of the most influential models accounting for the evolution of cooperation, represented by the work of Hamilton [1 OJ is that describing the possibility of obtaining benefits in terms of inclusive fitness by aiding genetically-related individuals If related organ- isms share large proportions of their genes, then cooperative interactions could be selected even if one organism reduces its own survivorship during performance of an action. The key here is who the recipients of its genes behaviour are. If the behaviour of a subject can enhance the fitness of related individuals, then a great proportion of its genes could reach future generations due to its action, even if chis occurs through the reproduction of the altruistic individual's kin. Many primate societies have evolved cooperative group, structured by kinship [33). Across different groups of primates, coalitions with kin can have an impact up on female's reproductive success [19]. However, a prerequisite for the selection of cooperative interactions based on kinship is that animals must have the necessary adaptations that allow them to discriminate between non-closely related and closely-related individuals, or kin versus non-kin. For Silk [34), some of those mechanisms may be acquired during development, when constant association and interaction may provide cues for kin-recognition.

Some of the neural mechanisms for kin-recognition may be based on capacity, such as 'self-referent phenotypic-matching·, observer where an individual uses its own characteristics to evaluate aspects of another subject's phenotype, enabling kin versus, non- kin classifications [35, 36], However, with the exception of chimpanzees, which may have a capacity to identify kin using visual cues [37], there is still meager evidence of these capacities in non-human primates, Importantly, there is evidence suggesting of neurological structures in phenotype matching. Krill and Platek [38] studied the activation of the human dorsal anterior cingulate cortex (dA CC) in an experimental setting that evaluated the affective distress associated to social exclusion, Their subjects reported the greatest distress response, when they felt excluded by individuals with whom they shared more facial similarities, suggesting that group-membership or group-identification influenced dACC activation during social exclusion.

Reciprocity

The apparent conflict between the classical theory of natural selection and widespread instances or cooperation (e.g. altruistic behaviour). is at the base of the study of sociality. On the one band, instances of cooperation are also observed among unrelated individuals, but then. how can non-related individuals avoid being

cheated after cooperating with a non-related individual? One important suggestion has been the strategy of direct reciprocity. ln interactions among unrelated individual's cooperation may be a fitness-enhancing strategy when individuals can directly and repeatedly interact with each other. Then, by alternating roles of provider and recipient of a cooperative act, subject's may set the conditions when cooperating 'now' is beneficial in light of assuring future cooperation [l l]. On the other hand, there is the related concept of altruism. Altruism is defined as behavior that benefits other individuals while being detrimental to the fitness of the altruistic subject [11]. Therefore, if performing altruistic acts reduces individual fitness, then one would not expect that individuals per-forming such strategic would be able to successfully transmit genes to future generations, yet this can be an important strategy of some societies, including humans. Kurzban [19] suggests four condition required for altruism to provide reciprocal benefits lo either kin or non-related individuals: one, there must be sufficient variance in the needs of interactive individuals over time two organisms must interact with each other regularly; three subjects must be able to distinguish each other and remember the outcome of past interactions: four, they must adjust their current responses contingently: according to the results of those past interactions. The best example of the action of all these conditions in reciprocal altruism is given by \Wilkinson [40] in his study of patterns of blood –sharing by vampire bats. The individuals of this species (Desmodus rotundus) are unable to survive long periods of time without food. and often, they end their 'night-shifts' without having located a suitable animal Lo suck for blood. Upon returning to their roost with and empty stomach, some of these subjects use food-begging gestures by which better-fed individuals can regurgitate and share some of their food, allowing the former to survive the night. Thus, blood- sharing among vampire bats depends on previous interactions and, since animals are able to identify each other and know with whom they shared blood in the past, they tend to beg for blood primarily to such individuals, promoting continued sharing and reciprocal exchange.

Remarkably, human exchange of goods occurs even when the probability of futures encounter is low. People often give things while aware that the probability of reciprocation is null or low, and this can even extend to interactions among complete strangers. who

may never have met or will again. Chase [41] developed such pos-sibility in an evolutionary context He suggests that cooperation among large human social networks is possible than lo indirect reciprocity. for Chase, a, the human group-size incremented and the need for larger territories grew, the number of infrequent social contacts grew as well, Thus, if direct reciprocity (as described above) was the only cooperative strategy available, exchanges would take place only among individuals with high possibilities for meeting again; yet humans rely strongly on the possibility of future interaction. For chase the evolution of indirect reciprocity in humans could have been based in the fact that, in order to avoid starvation, the increasingly large human group sizes inhabiting productive but patchy environments (i.e. discrete areas, rich in resources but separated by distance), would require the expansion of foraging territories and its constant monitoring by different foragers. In these conditions, both goods and information would be highly valuable, such conditions could then select the individuals offering information, which others could reliably use to arrive at resource;

found far from their immediate vicinities. By this means, a cooperative act by a given individual 'A' towards subject 'B' could eventually be reciprocated by the cooperative act of individual 'C' thus being an indirect form of reciprocity. Nevertheless, subjects could still transmit inaccurate or entirely false information, So, how could indirect cooperation as found in humans ever establish? Among different and plausible options (reviewed by Hamunet-stein [42]), one alternative (possibly based on neurophysiological mechanisms) is altruistic punishment. Fehr and Gacchtcr f43] advocate the fact that even if they have to pay a cost for doing so, humans arc willing to punish unfairness or uncooperativeness in the behaviour of other people, suggesting that such altruistic punishment could be a potent driver or cooperation in human groups. De Qucrvain el al. [44] also studied the neural basis of this behaviour. Using Positron Emission Tomography (PET) imaging, the Quervain and colleagues scanned subjects brains during an economic exchange task. In it subjects could detect uncooperative counterparts and thus could apply effective or 'symbolic' punishment. Their results suggested that effective punishment, but not symbolic punishment produced an activation in subject's dorsal striatum area and that individuals with a greater activation of the dorsal striatum were disposed to incur greater costs (in tem1s of money) to punish defectors. Therefore, given that altruistic punishment activated brain regions also related to reward these authors suggested that altruistic punishment was, in fact reinforcing at the neural level. Finally, indirect reciprocity is also dependent on a neurocognitive factor: subjects must be able to restrict their immediate impulses for reaching particular goals or commodities in the present time in order to gain access to even larger rewards in the future [45]. Studies suggest that human children begin to develop two strategies for archiving this capacity close to the age of six years old [46]. While this capacity for self-control was once thought to be exclusive of humans, It is now suggested to be present in a variety of nonhuman primate species.

Biological Markets

Contrary to kin-selection and reci11tocity, focused on cooperation among similar organisms, biological market theory is focused on how different classes or even distinct species develop systen1s of cooperation. The theory has therefore, focused on the origin of collaboration within asymmetrical relationships, and its characteristics suggest that the range of phenomena covered by this theory may have important roles in the evolution of mutations partner choice and mating interactions 152-56]. The operation of biological markets is focused on how animals belonging to different classes may possess distinct kinds of commodities. Its main premise is that animals with opportunities to increase their payoffs by means of cooperation will most likely have access to different potential partners, but if other subjects are required for achieving those benefits then individuals, must also compete for access to social partners. Therefore, such conditions will open possibilities for the operation of bargaining strategies, and thus for market-effects [57], Then, in a way similar to how products are exchanged in human economies, biological markets theory suggests tl1at the bargaining power of a given class or subjects offering a givm1 commodity will depend on how scarce a given community is in a particular exchange-scenario. A substantial advantage of the theory is its suggestion that subjects can have dynamic roles in an exchange scenario: exchanging the same type of behaviour with some individuals but receiving different kinds of benefits in its exchange with other type of subjects [58]. For example, two kinds of commodities have been described in the interactions of female chacma baboons; (Papio cynocephafus ursinus): grooming and handling of infants, which were interchanged in a non-symmetrical way [59]. Bouts of grooming given to mothers were exchanged for allowance of her infant's handling. The length of the grooming bout (or price paid for handling in- fants) depended on how many infants were in the group; when there were many, the required price was low and vice versa. This was identified as a market effect. However, the effect, dependent on the 'supply' of infants, could be overrun by the dominance status of females present in the group. Females that had a much higher status than mothers with infants did not need lo exchange equivalent grooming bouts to gain access to those infants. In another example, Statrtmbach [60], observed that when subordinate Macaca fascicularis individuals where trained to gain access to a food-provider device, other individuals which were not capable of operating the device by themselves adjusted their behaviour toward these 'spe-cialists' . In order to gain benefits; acquired by the animals stopped chasing them when they were near the food device. Similar results were obtained in a recently study (based on the general design of Stammhach), which, importantly, added knowledge lo the way initial gains in the bargaining power achieved by the only food-provider in a monkey troop decreased after a second subject in the group learned the way to open a box with food [6 1].

PARTNER-CHOICE: SIMPLE RULES OR COMPLEX PROCESSES?

Some important conceptions describing strategic decision- making or this way subject, allocate their resources among alterna-tive uses amulet upon the assumption that individuals can predict the actions, or 'step into the shoes· of other, [62]. One of the most influential theories explaining the evolution of the human brain has been driven by the idea that. in primates. the problems posed by ecology (e.g. finding food and males) were not (he main pressure selecting for larger brains, hut instead, that a need for tracking the inter-individual phenomena taking place in the social group could have selecter for greater 'social intelligence ·. Several of the every- day problems of nonhuman primates require that individuals keep track of their social environment. Thus one first focus of theories oil social intelligence was based on a Maquiavelhan intelligence hypothesis. This theory suggests that a need to anticipate and respond in accordance to the strategic behaviour of other individuals could have selected for greater cognitive capacities to predict social behaviour [163]. In tum, Dunbar 1 64 j expanded this idea advocating for a theory of the evolution of a 'Social Brain', suggesting that the increasing complexity or the social environment was here selecting for more 'brain power for predicting or calculating a range of possible strategies of other individuals · behaviour, and therefore, that social cognition must have been one of the selective pressures underlying increments in brain si,,;e. Several neural structure, have been associated with the possibi1ity: the amygdala and the prefrontal cortex in particular [65], Noé [66] observes that, just as Barkow er a!. [67] suggested, the amygdala may have an important role within one of mind· s modules focused on detection of non-cooperators (i.e. cheaters), and therefore, that a ' fear of deception · could have evolved in the amygdala via a generalization of its role in fear activation. Other component of such modules could be located in the ventral prefrontal cortex and the anterior cingulate cortex (ACC) [6 8]. In the opinion of Parr et al. [69], spindle or von Economo cells in the ACC may have a role in the processing

of self-conscious emotion, like guilt, shame, pride and embarrassment, which could in tums evidence of a regard for others. Given that these neurons are abundant in humans, and found in apes like bonobos, chimpanzees and orangutans, hut not in monkeys, they suggest that their lo cation in the prefrontal cortex and their recent phylogenetic emergence may be evidence of their important relation to social decision-making. These anatomical and functional variations may underlie crucial cognitive differences. While many species arc capable of amazing feats to enhance their short-term utility (i.e. in terms of satisfaction of immediate needs), higher cognitive capacities such as episodic memory [70] and higher-order intentionality [7 1] may he exclusive of apes and humans. For example, a lack of episodic memory, i.e., an incapacity for travelling within! he mind across different time-associated memories (i.e. constructed based on self-experience). may restrict monkeys to short-term decisions; rendering them unable to reflect on past self-- experience for their decision -making proccs5es. In turn, organisms lac-king higher order intentionality, may not have a capacity for generating abstractions, about the contents of the mind of others (i.e. a theory of mind of other organisms i72]), restricting their capabilities for predicting and responding to strategies employed by cooperators or competitors [62]. These discrepancies suggest that several species may not be able to qualify their behaviour based on may not be experience, or, in other words, to abstract an objective understanding of the principles explaining their own decision-making processes. One further consequence would be that other- regarding feelings and empathy could be capacities present only in ape, and human, [73], and thus 'moral-thinking' (understood as generalized or universal principles about what constitutes 'good' and 'bad. '[74]), could be an exclusively human capacity.

The differences described above suggest that even in the most complex species, partner-choice and other instances of social decision-making may not necessarily be based on abstract knowledge of the contents of the mind of other individual, hut instead, that these may he based on evolved 'rules of" thumb'. Here we understand there as 'proximate behavioral programs that animals appear to follow and which lead them to behave in ways that often approximate optimization ', for example, cases of mate preference based on coloration, (ultimately determined by parasite-load), or incest avoidance, determined by preference of the most-dissimilar mates; among many others f75]. In general, simple strategies would be maintained by natural selection as long as they provide benefits for their possessors (even in species with complex neurological systems), while more complex strategies requiring more processing time or cognitive-power would probably not be favored by natural selection, something observed in the way even humans use 'simple heuristics· in choices where traditional economics would predict other, more rational outcomes 166_1. 111 these lines, Barrett and Henzi [68] suggest that the increments observed in brain size, structure and mental capacities of primates may have evolved driven by a need follow short-term variations in that 'value· of both social and environmental commodities or that rules of thumb (like associate preferentially with your oldest daughter") that did not require complex cognition could explain the fom1ation of long-term relationships [76], ·while many primate species are able to recognize other individuals or their own kin [33]. this is not the equivalent as suggesting that they will have a 'concept' of what it means to be related·, but only that they may be good at distinguishing their closest associates from other group members [77]. Even be· behavior at the group level, such as collective movement has been explained by simple rules involving patterns of social affiliation between individuals [78]. The next section is aimed at suggesting some of the primary mechanisms by which microbiota may influence aspect, of social decision-making within an organism.

MICROBIOTA, GUTS AND BRAINS: EMOTION AND SO- CIALITY

Important neurological structures underlie our long-term, strategic planning and/or conscious decision-making processes. However, we also make fast-decisions, some of which are performed without an excessive amount of strategic, anticipatory or abstract planning in fact, even while awake and active, many of our re-sponses may not reach consciousness. We know how we can ride bicycles, drive a car or walk, and at the same time have an intense conversation over an interesting topic with the person next to us while never being consciously aware of exactly how, or by means of which exact route, we have safely reached our destination. While humans haw, exceptional mnemonic and analytical capacities which most of up can apply to understanding the abstract contents codded in auditory signals. several other stimuli and responses involved in face to face social interaction (e.g. chemical, tactile emotional, among others) arc not (at least immediately) analyzed in terms of abstract intentions or motives. Yet most healthy adult humans are able to provide fast and accurate responses that more or less fit the general hd1avioural or emotional qualities of such situations. The possibility that efficient inter individual communication requires stimuli or than the abstracts contents of language may be one of the underlying reason, explaining why, intense online sociality (as expressed in the intensity of use of social-networking websites) is not a predictor of either the amount of 'offline ' social relationships or their emotional quality [79] Recent studies suggest that microbiota and particularly the microbiota found in the gut of several animal species, including humans, has roles determining some aspects of behavior, ln this context, the relevant questions of this section ate: l) what are the primary anatomical efferent and efferent ways by which microbiota establishes feedback communication with the CNS?; 2) How does microbiota influence the proximate events underlying social-decision making processes within an individual?

ANATOMICAL COMMUNICATION PATHWAYS

Recent studies show the importance of the relationship between gut and brain, and of the maintenance of homeostasis within a microbiota gut-brain (MGB) axis in health and disease, These studies show the role that diet, stress, physical activity and other environmental factors can exert on the stability and quality of the intestinal microbiota and their effects on host's health and disease in the modulation of behavior [80]. Microbiota in the intestinal environment. a diverse and dynamic ecosystem, has developed a mutualistic relationship with its host, playing a crucial role in the development of the hosts innate and adaptive immune responses, Microbiota servers the host by protecting against pathogens, harvesting otherwise inaccessible nutrients, aiding in neutralization of drugs and carcinogens, and affecting the metabolism of lipids, Gut bacteria modulate intestinal motility harrier function and visceral perception [81 J, Today, neuroimaging, electrophysiological. and pharmacological techniques in combination with molecular and genetic tools, have begun elucidating the neuronal mechanisms underlying cognitive and emotional processes. The ability to obtain images of the living human brain through various imaging devices has greatly enhanced our capacities for studying the brain and gut interactions in health and disease, This factor has aided in the recognition of the possibility that the gut-brain axis provides a bidirectional homeostatic route of communication based on neural, hormonal, and immunological routes, one that, when dysfunctional, may result in pathophysiological consequence,, Such bidirectional signaling between the gastrointestinal tract and the brain is vital for maintaining homeostasis, and is regulated at the neural (both central and enteric nervous system), hormonal and immunological levels [82], In fact, this modulation of the gut-brain axis has been interpreted as a possible large, for the development of novel treatments for a wide variety of disorders ranging from obesity, mood. and anxiety, lo gastrointestinal-sickness [83],

The state of the gut has a profound influence on our healtl1, It is from a healthy gut that we enjoy neurological and psychological stability, necessary for establishing effective evaluations of the characteristics of our environment, including social interactions in accordance with current social events, ln terms of its development, both our gut and brain originate early in embryogenesis from the same clump of tissue [84}, While one section develops into the central nervous system, the other section migrates further to be- come the gut's 'brain' or enteric nervous system (EN S) [85 J , It is only until later phases when the two system, connect via the via the agues nerves derived from Latin meaning wandering the longest of all cranial nerves, Because it passes through the neck and thorax to the abdomen, the vagus has the widest distribution in the body. The ENS is located in sheaths of tissue lining esophagus stomach, small intestine and colon, It is packed with neurons, neurotransmitters and proteins that zap messages between or support cells similar to those found in the brain [86], The ENS has several functions, including: control of enteric mobility regulation of fluid exchange and local blood flow, regulation of gastric and pancreatic secretion, regulation of gastrointestinal endocrine cells, immune defense reactions, and entero-enteric reflexes [87], It contains somatic and visceral afferent fibers, as well as general and special visceral efferent fibers [88], It exits the medulla oblongata in the groove between the olive and the inferior cerebellar peduncle it leaves the skull through the middle compartment of the jugular foramen, where it has upper and lower ganglionic swellings, which are the sensory ganglia of the nerve [89], There are two types of output from the ENS to the CNS, The first has its cdl bodies in the ENS and sends axons through the anatomic nerves to terminate in the celiac, mesenteric and hypogastric ganglia. The second type has cell bodies in the dorsal root ganglion in the cranial nerve ganglia and its fibers send signals from all art>.as or the gut to areas in the spinal cord and brain stem [90], These fibers represent up to eighty-percent of the nerve fibers in the vagus nerve and they transmit their sensy signals to the medulla. which initiates vagal reflex signals that return to the gastrointestinal tract. The gastric branches innerve the stomach, The right vagus forms the posterior gastric plexus and the left forms the anterior gastric plexus, The branches lie on the postero-interior and the antero-superior surfaces, respectively, The celiac branches are derived mainly from the right; nerve, They join the celiac and supply the pancreas, spleen, kidneys, adrenals, and intestine, The hepatic branches originate from the left vagus, They _join the hepatic plexus and through it, they are distributed to the liver [9 1],

A ROUTE FOR AN INFLUCENCE OF MICROBIOTA ON WITHIN-INDIVIDUAL SOCIAL DECISION-MAKL.VG

Another aspect of our approach to decision-making specifically underlines the role of the vagus as one of the nerves most closely related to a form of purely-emotional decision making, in this sense, Porges [92] suggested that the my clienated branch of the vagus nerve, exclusively found in mammals. is relevant to understanding some non-endocrine bases of sociality, Porges suggests that as a subdivision of the parasympathetic nervous system con- trolling the fine-tuning of the autonomic response (e,g. when exerting an inhibitory effect upon breathing, facial muscles or heart rate) the vagus nerve can b<e conceived as the system responsible for providing the relaxed states necessary for effective social interaction and therefore that its evolution is related to that of the affects, emotion and contingent social behaviour [93], Afterwards, visceral sensations can be assigned to a system that relays vagal, gloss pharyngeal, facial, an d spinal afferent activity by way

of the brainstem parabrachial nucleus to the ventrobasal complex, and then to the insular cortex, The fundamental commonality of pain, temperature and other bodily sensations us interceptive perception has baton recognized just rete11tly [94], This interconnection between the gut, its microbiota and the central nervous system is bidirectional involving a complex interaction between immune, endocrine and neural conduits, ln the vagus, neural terminals arc activated by gut peptides that are fashioned by enter endocrine cells, and neuro- transmitters or its precursors (e,g, tryptophan) can be produced by microbiota, reaching the gut's surface (i.e, epithelia) and the producing a cascade or effect Relayed in the nucleus tracts solidarity of the brainstem, the amygdala and insular cortex may gather this information as self-referential stim that can in tum interconnect with spindle cells and form the basis of interception [69], Therefore, insular cortex plays an important role in !he conscious perception of the body's sensations, while the dorsal anterior cingulate cortex (dACC), with its connection to effector systems mediate

effective responses and motivational drive, Indeed evidence indi-cates that the anterior insular cortex contains interceptive repre-sentations that substantialize all subjects ' bodily feelings, and other dam strongly suggests that the ai1tcrior insular cortex has a fundamental role in human awareness [95], Recent functional anatomical work in primates and in humans has described an afferent neural system representing m any aspects of the physiological condition of the physical body [96].

MICROBIOTA, ITS ROLE lN KINSHIP, REPRODUCTION, AND GROUP MEMBERSIIIP

Just as we have described for the case of enteric microbiota, there is evidence that microbial communities have important roles as mediators of animals· capacities for distinguishing between group members, kin, and potential mates [97]. Organisms with a capacity to recognize some of the phenotypic characteristic of their peers should be able to distinguish between social and antisocial subjects and thus identify individuals or social conditions [98] prone to the establishment of cooperative relationships. Among

social insects for example, community living (i.e. nest specify) may lead to common gut bacteria, and therefore to kin-recognition mechanisms mediated by the action of microbiota. In comparison to individuals from other nests (i.e. different environments) relatives raised in the same environment possess more similar bacterial communities. Given that bacterial metabolism can render by- products providing the genera l scent of a given colony, then colony- specific bacterial communities provide strong evader, that gut microbiota is involved in mechanisms of kin recognition [99]; without the involvement of a complex decision-making CNS. A vertebrate species capable of distinguishing their kin using odour is the green Iguana. In an experimental selling iguana hatchling from different mothers were separated during incubation but immediately put together (after hatching) in a communal (social) enclosure to allow for social interaction. As a result kin-related individual associated with each either, while non-related individuals did not Moreover, physical contact with siblings (or their faces) was necessary for individuals originally separated from their relatives to be recognized by their own kin [100]. Both amphibians [101] and birds [102] can acquire their microbiota from their parents, with important effects on their survivorship. Birds can also acquire microbiota from both their sibling during their time at the nest [! 03], or more actively by means of holding diverse materials in their cloaca, likely obtaining benefits in terms of priming their immunological system [104, 105].

A good amount of evidence suggests that odour [1 06], regulated in mammals in large part by the Major Histo compatibility Complex (MHC), can have an important role in kin-recognition j97J. However, both individual-specific or group-specific odour ' tags' may also be by-products of bacterial symbioses in other animals groups. A fomentation hypothesis· [I 07] suggests that a diversity of mam- mal, arc able to recognize other individual, using odours based on individual profiles of volatile fatty acids present in their anal-pocket secretions In the Indian mongoose for example, such contents include six short-chained. odorous carboxylic acids that arc produced from sebum and apocrine secretions by actions by the action of individual-specific communities of bacteria, giving each subject a characteristic odour [1 08]. Similar volatile acids produced by fermentation are also suggested Lu be present in the anal secretions of the red fox (Vulpes vulpes), lions, bush dog (Speothos venaticus), tigers (Panthera ligris) , maned wolf, domestic dogs and domestic cats.

Another relationship between microbiota and kinship in mam- mal s is vertical microbial transmission during lactation [109],

Within milk, female mammals provide nutrients, that are not directly used by the is offspring but that instead, feed microbial organ- isms that are able to process this milk further, allowing infants to use the nutrients provided [11 0]. New evidence suggests even in humans, where smell is one of the most reduced senses [1 1 1], body odour microbiota and discrimination or recognition of relatives are interconnected. For example, an experimentally-set group of mothers unaged to recognize the odours of the children they had given bi11h to, but not the odours of their adopted children, whereas children managed to recognize their full brothers and sis-ters but not their half-sibling or adopted brothers or sisters [11 2]. ln tum, evidence suggests that odours produced by bacteria (for example from the axilla) can be used by humans to adequately identify, based only on odour samples [113].

1n general, species with the highest population densities, larger groups and promiscuous, mating system have a higher pathogen prevalence, which may be contro lled by means of social barriers like social structure [1 14]. Microbiota can influence mating by provoking bacterially-induced alterations in nuclear genes coding for the production of sex pheromones, or by generating molecules that may act as, ex attractants [115]. A large number of species use chemo signals for mare recognition and attraction, perhaps, given that such as of stimuli can be reliable indices of a mate resistance to disease and genetic compatibility, making them a fruitful beacon for studies with a focus on sexual selection [1 1 6]. For in- stance, common fruit-flies (Drosophila melanogaster) can develop a preference for mating with flies that grew in an environment similar to their own (i.e. eating the same type of food}. When D. melanogaster individuals raised in an environment similar to their own given antibiotics, the specificity of their preferences disappear. Flies raised in specific conditions drastically-modified their preferences and stymied mating with t1ies raised in any type of environment, suggesting that their fanner preferences were mediated by the presence of microbiota [1 1 7J. During mating individuals can ac4uiri:, pathogens due to the intimacy of the act itself, or become infected simply by means of contact with droplets: in tum, promiscuity can increase the variety of acquired pathogens [118], This may occur in the case of matting in common lizard, (Zootoca vivipara). In this species, females can mate with either a single or multiple males. Thus, poly-androus females showed a higher diversity of microbial species in their cloaca. suggesting that this result was a direct effect of sexual transmission of bacteria by multiple mates [J 1 9], In birds, this type of studies are interesting since they provide good models for the study of sexual transmission of microbes. This, given that birds' cloaca facilitate the incorporation of both gastrointestinal pathogens and endosymbionts into ejaculates[1 20]. An experimental study on zebra finches (Taeniopygia gultata) [121] found that both social and sexual behaviour allow for the transmission of bacteria. In this study, experimentally inoculated bacteria into the cloaca a11d feathers of different il1dividuals found their way into subjects (most likely due to the role of preening and bacterial ingestion), and across subjects by means of sexual transmission, particularly when males were the initially-infected sex. Microbiota has an important influence as modifier of individual's odour, and thus a ccrucial role in the way animals. Bacteria may be located in moist, wan and organically-rich sites on the body surfaccs or 'scent glands' of several mammalian species [97], providing a role for microbiota as a means for mate recognition, This is particularly important in human mate-choice related to the MHC Such interrelation has been relatively supported, primarily bassed on the hypothesis that genes affect the composition of microbiota, for example, by means of antigen-elimination of bacteria [97], In no other area may the possibility of microbiota tram mission be closer to our every-day understanding of behaviour, as in the possibility that mouth-to-mouth kissing could serve as an adaptation for tcstil1g the irnmw1ological compatibility of mates [97] and a likely means for the avoidance of teratogens viruses (e.g. cy- tomegalovirus) during offspring-development [122].

Both direct (i.e, with physical contact between individuals) and indirect (i.e. mediated by any environmental feature) patterns of microbial transmission [123] and thus, social interactions can enhance the similarity of microbiota across individuals, For many group-living mammals, recognition of individuals (e.g. based on by-products of their skin glands [1 24J and the action of microbiota [107]) is a crucial capacity leading to enhanced within-group cooperation and the possibility or multilevel selection [125] . Wild rabbits (Oryctolagus cunirnlus) for example, present inguinal pouches containing characteristic microbiota composed of bacteria’s cherichia coli, and Streptococcus facials, as well as volatile fatty acids like acetic and isovaleric acid [1 26]. In one study. rabbits o f a given pen were attacked by the group's dominant male after they were smeared with the inguinal gland secretion, of males of a different pen, suggesting that these secretions carry information coding for some form of group membership [127] Very similar results were obtained in a study using lemurs as sub-jects, describing how lemurs had stronger scent-marking responses towards the smell of foreign individuals compared to responses activated in response to the scent of familiar subjects [l28]. In a similar way, olfaction is crucial for the social life of spotted hyena, (Crocuta cmcuta). Hyenas also have scent glands which they use to mu-k the boundaries of their territories and discriminate the sex and relatedness of conspecifics [l 29]. This property has been further confirmed by gas chromatography of fatty acids and esters composing such scents, confining the suggestion of a clan-specific scent signature [130] used as a group-membership tag or social odour [1 31].

Both human members of the same family [1 32] and individuals from the same chimpanzee community 1 1 33 i can be grouped ac- cording to the inter-individual similarly of patterns of their gat microbiota. This is important because social traditions in both species can serve as both a means for the transfer of microbiota, and discriminating between subjects based on membership to a group (i.e defined by its specific social traditions) [1 34]. Evidence suggests that the taste of spices potent is produced by secondary phy-tochemicals that. with minimal nutritional or caloric value, evolved as protection against organisms trying to ingest them [1 35], including microbes and fungi [136]. Across, different latitudes, spices with the greatest bacterial inhibition power (e.g., onion, garlic mid chilies) are the most frequently employed, and countries in which his man’s apply morn spices per dish are those with the highest annual average temperatures, , suggesting that spices were incorporated from the origins of the most prominent Mesoamerican and Indo- European ethno-diets, likely being assimilated to recipes in order to slow the spoilage of food at ambient-temperature I l 3 71, Resembling humans, several nonhuman species practice different ways of self-medication (i.e., zoopharmacognosy: [138]) a; prevention of future illness or therapeutic agents [13 9]. Evidence in apes suggests that many secondary compounds of the plants found in their diets can control parasitic infections and reduce already-present gastrointestinal symptoms of illness[1 40]. Moreuver, the observation that the same plants are often used by both humans and apes raises the possibility that ancient hominids could possess similar knowledge on self-medication [1 41], which. when socially-transmitted across many generations, could evolve into the diverse ethno-medicinal and ethno-culinary uses characterizing different contemporary human cultures. A rather interesting study by Fincher Et al. [1 42], using human world-wide epidemiological and culn1ral data, has suggested that even after different variables wen: accounted for, a high regional prevalence of pathogenus was strongly mid positively correlated with cultural indices of collectivism (i .e. collectivistic cultural values).

CONCLUSION

The preceding discussion suggested that behaviour can he influenced by proximate causes that may not be subject (B intense cognitive scrutiny, but may, nevertheless, lead individuals to performing behaviour approaching optimality. It also suggested that microbiota may influence processes of both within-individual decision making and social- and reproductive-partner choice.

For some behavioural contexts, conscious deliberation, can be a rather slow and sometimes cumbersome process not suited for particular scenarios. species social behaviour may often be of a less 'immediate' nature (ie. in terms of the average speed of reaction required), it is by no means 'dismissible '. in terms of its impact on fitness. On the contrary different theories suggest how important the subtleties of social life may be in the context. of evolution. Our review suggests that microbiota may influence these processes at two levels. On the one hand, there is growing evidence suggesting that being an intrinsic part of mammalian bodies, bacterial processes arc deeply involved in partner choice. On the other hand, once choice has been made and partners' microbiota communities interacted theory of emotion· 1 921 presents a compelling argument that, in view of the growing evidence of the action of a MGB axis, may serve as a probable link between the evolution of emotions sociality. By means of this interaction, microbiota could exert influence in the process by which both gut-based stimuli parasym-pathetic activation and other perceptions involved in social

registered by other senses are evaluated and integrated in CNS, activating the most pertinent responses. Thus, if microbiota interacts with a subjects· brain and helps individuals to identify their closest associates, then such processes may underlie the bases of the construction u r the inter-individual forces and emotional bonds that may translate into fitness effects (e.g. by inclusive fitness). Consequently. much could be learned from designs restricting the action of microbiota within an individual then evaluating effect of such intervention into that subject's social interactions [105]. If, for example, an impairment of the of microbiota could result in a concurrent impairment of partner-recognition, mate-choice, or general quality of social life, then, one could question the extent by which, evaluations, and particularly, cognitive strategies, are in effect or 'in control' of the social chemises that species, primates make a daily basis. Moreover, if close present more bacterial communities' profiles than other individuals interacting more sparsely, then such similarity could be employed as a for the strength of the bonds between subjects. and thus, having another for the strength of social bonds and/or group- membership. such a measure could provide important insights into the basis of group-level cohesion, All of the above also that modern socioeconomic choice theories may still benefit from alternative theoretical frameworks that consider the human being as a complex organism, with intrinsic constraints and capacities of its evolutionary history, and not just as an exclusively - cognitive decision maker acting independently of its closest partners.

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