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Evolution and Genetics Stuff

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An independent academic psychologist, based in England, who has written extensively on different areas of psychology with an emphasis on the critical stance towards traditional ideas.

A complete listing of his writings at http://psychologywritings.synthasite.com/. See also material at https://archive.org/details/orsett-psych.

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1. TROPICAL RAINFORESTS AND HUMAN EVOLUTION

1.1. IMPORTANCE OF RAINFORESTS

Scerri et al (2022) outlined the following common view: "The perception that open grasslands and savannahs were the ecological 'cradle' of humans and their ancestors has shaped both the geographical context of fieldwork as well as dominant narratives concerning early hominin evolution, dispersal and cultural development. By contrast, tropical forests, where fossil preservation tends to be poorer, have been presented as relatively pristine environments left free from human influence — habitats deemed too hostile for humans throughout much of pre-history" (p1).

These authors wanted to challenge this view: "As Homo species spread from Africa, they encountered and engaged with tropical forest biomes across South and South-east Asia, the Pacific and ultimately, in the case of our own species, the tropical Americas... Despite popular perception of vast homogeneous green canopies, the tropical forests of these regions comprise an incredibly diverse set of ecosystems" (Scerri et al 2022 p2).

The variety included wet, lowland evergreen rainforests as well as "{S]emi-evergreen forests with a short annual dry season, montane and sub-alpine forests, closed-canopy dry forests and swamp forests" (Scerri et al 2022 p2) [1]. These forests were not unchanging, even before Homo sapiens introduced "fire dynamics" and species change (Scerri et al 2022).

The different tropical forests of the time of early humans is increasingly being researched:

i) Africa - "The tropical forests of Africa were the first to be encountered by H. sapiens and its hominin ancestors. Africa's forests have particular structural and floral characteristics including an unusually high biomass of animals, which could potentially act as a food

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[1] "Some authors refer here to mega-thermal forests, defined as forest biomes where the risk of frost damage is non-existent, enabling a proliferation of species diversity" (Scerri et al 2022 p3).

resource for humans" (Scerri et al 2022 p3).

There is evidence of hominins living on the edge of forests (eg: a tooth in Central Africa dated at 2.5 million years ago) (Scerri et al 2022).

Braucher et al (2022) reported stone tool artefact evidence of hominins in the Congo Basin (in modern day Gabon) between 850 and 650 000 years ago.

ii) South-east Africa and Pacific (appendix 1A) - eg: fossil evidence of human populations adapted to tropical forest environments in southern China 100 000 years ago (Scerri et al 2022).

Louys et al (2022) dated fossils of early humans in Sumatra (present-day Indonesia) to 70 000 years ago, a time "dominated by a closed-canopy forest very similar to those present in the region today" (Scerri et al 2022 p5).

iii) Neo-tropical areas (eg: Amazon lowlands).

The Americas were probably colonised by modern humans 25 - 15 000 years ago (Scerri et al 2022). "Early human populations in the Americas have traditionally been portrayed as mobile hunter–gatherers who exploited coastal resources and large savannah game, while avoiding forest habitats as a result of the absence of large mammals and the difficulties of mobility in dense forest vegetation. Contrary to this classic paradigm, mounting evidence suggests early colonists were actively exploiting and managing trees of economic importance and quite quickly began practising early cultivation of annual crops" (Scerri et al 2022 p6). Iriarte et al (2022) used cave paintings of large extinct animals in present-day Colombia as evidence of humans in forests as these animals tended to live in the forested areas.

Scerri et al (2022) summed up: "Tropical forests clearly represent a key human habitat that can no longer be ignored in the context of deep human history. In particular, the wealth of data, methods and insights emerging from tropical forests in Asia and South America is driving a tropical research agenda that has so far lagged somewhat behind in Africa, the evolutionary home of our species" (p8). However, there are still "big questions" that need answering, including how many times did humans adapt to tropical forests, and what was the speed of adaptation? (Scerri et al 2022).

1.2. OUT OF AFRICA

The dating of humans in different regions of the world is important in understanding how Homo sapiens moved out of Africa. "Genomic and mitochondrial data have frequently been used to argue for a major exit from Africa around 65–60 thousand years ago. However, archaeological evidence from Saudi Arabia, Israel, Greece and China indicates that at least some populations occupied Europe and Asia before this time, most likely following corridors of suitable habitats resulting from ameliorated climatic conditions" (Louys et al 2022 pp1-2) (eg: Israel (Shea et al 2003); Arabia (Groucutt et al 20021); table 1.1).

The implication is multiple dispersals of humans (or related hominins) out of Africa after 400 000 years ago (Dennell 2021).

Researchers can now ask "why it took so long for Homo sapiens to successfully expand out of Africa, when the climate repeatedly enabled it" (Marshall 2021b p20).

- Fossil evidence suggests that "at least five hominin expansions into the Arabian interior, coinciding with brief 'green' windows of reduced aridity approximately 400, 300, 200, 130-75 and 55 thousand years ago. Each occupation phase is characterised by a distinct form of material culture, indicating colonisation by diverse hominin groups, and a lack of long-term Southwest Asian population continuity" (Groucutt et al 2021 p376).

- The modern desert of the area is not suited to preserving bones, which has not helped. However, stone tools had been found previously and speculations made (Marshall 2021a).

- "The remarkable discoveries from Arabia remind us that, when it comes to the study of human evolution, much of the planet is yet to be explored. The systematic study of Arabian pre-history is barely more than a decade old. Many of the researchers who work there were told not to bother because 'there was no pre-history in Arabia" and were even laughed at" (Editorial 2021 p5).

- If Arabia was inhabited since 400 000 years ago, then different hominins may have been there - eg: Nesher Ramla Homo (a possible ancestor of Neanderthals) known from one site in Israel (Marshall 2021a).

Table 1.1 - Hominins in Arabia.

1.3. BIPEDALISM

"Striding bipedalism" is the human version of walking on two legs, which was believed to have evolved once in an ancestral hominin since six million years ago. But "fossils discovered during the past decade show that multiple versions of bipedalism existed simultaneously during one or more periods of hominin evolution" (Melillo 2021 pp388-389).

This is supported by evidence from footprints in volcanic ash fallout at Laetoli, Tanzania, dated at 3.6 million years ago (McNutt et al 2021). It is accepted that the only species of hominins at the time was Australopithecus afarensis (Melillo 2021). But unusual footprints at the site open the possibility of another hominin bipedal species, argued McNutt et al (2021). There is disagreement about this interpretation (Melillo 2021).

1.4. APPENDIX 1A - POLYNESIA

Ioannidis et al (2021) analysed data from 430 living individuals from twenty-one Pacific island populations to map the migration of humans around the Pacific Islands. A sequence was proposed, "starting in Samoa and progressing rapidly eastwards through the Southern Cook Islands in the ninth century, thence to the Society Islands and Tuamotu Islands, and finally, by the mid-fourteenth century, to the widely separated islands of the Marquesas, Raivavae and Rapa Nui (also known as Easter Island)" (Kirch 2021 p477).

The spread of population from island to island showed "a 'telescoping' succession of genetic bottlenecks, known as founder events, in which small colonising populations moved from one island to discover and settle on another. Such events lead to founder effects, whereby the small number of individuals who initiate new populations do not encompass the full genetic complement of the parent population. As a result, the subset of genetic variants from the parent population that were carried by individuals who established new populations are expected to be more frequent in the child population" (Kirch 2021 p477). A "directionality index" was created by Ioannides et al (2021) which showed the amount of retained gene variants.

This genetic model showed some difference to archaeological evidence and historical linguistics (Kirch 2021).

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2. LAUGHTER

2.1. INTRODUCTION

"Laughter affects conversational schemes, supports speech production, establishes social bonds and is connected to playfulness" (Caruana et al 2022 p1). This is the focus on the socio-emotional nature rather than cognitive underpinnings of laughter.

Laughter can be seen as having three social purposes (Robson 2021):

i) Reward - "it shows appreciation of a particular behaviour and reinforces the interaction, so that we are more likely to act in the same way in the future" (Robson 2021 p73).

ii) To signal connection (affiliation) (appendix 2A).

iii) To signal dominance.

Wood et al (2017) found different acoustic properties for each of the three "types" of laughter when 50 short audio clips presented to 762 online participants. A "reward laugh" was louder and longer, an "affiliation laugh" quieter, shorter and mellower, and "dominance laughs" "uglier and noisier" (Robson 2021).

"Play vocalisations" (the equivalent to laughter) have been documented in 65 species, mostly mammals (Winkler and Bryant 2021).

2.2. EVOLUTION OF LAUGHTER FROM PLAY

Vocal and facial expressions of play are common in primates, and this suggests an evolutionary basis to human laughter. Davila Ross and Palagi (2022) were interested in reconstructing laughter and laugh face evolution.

For example, "great apes produce play vocalisations that show similarities with human laughter. Often, these vocalisations involve a series of low-frequency staccato grunts that can be easily induced by tickling in infants and juveniles. These vocalisations predominantly accompany open-mouth faces (play faces), facial expressions of play that often occur on their own, ie: as silent expressions" (Davila Ross and Palagi 2022 p2). The open-mouth face in play has also been observed in other mammals (eg: lions; African wild dogs) (Davila Ross and Palagi 2022).

Faces and vocalisations during play have a social function - ie: "to signal 'this is play', which helps to co-ordinate actions among playmates. Probably most importantly, such signalling is likely to help avoid escalation into real fights during rougher play and, consequently, to prevent getting hurt, especially when the playmates are dissimilar in strength and do not have close social relationships" (Davila Ross and Palagi 2022 p4). Also mimicry of expression of the playmate is evident (Davila Ross and Palagi 2022).

One area of research is facial muscle movements. The ChimpFACS (Facial Action Coding System) (Vick et al 2007) was developed for this purpose. It was found that chimpanzees "part their lips while dropping/stretching their jaws and often they would also pull both lip corners back and upwards and raise their upper lips (revealing their upper teeth) as well as their cheeks (causing wrinkles around the eyes, ie: crow's feet). These facial movements of the apes matched those of laughing humans that were measured with FACS" (Davila Ross and Palagi 2022 p2).

Davila Ross and Palagi (2022) felt that the evidence supported the "Complexity and Continuity Hypothesis" (Davila Ross and Dezacache 2021). "According to this hypothesis, both human laughter and laugh faces of positive affect most likely evolved within the context of play in pre-human times and were already complex in both form and function when produced by ancestral species" (Davila Ross and Palagi 2022 p3).

2.3. EVOLUTION AS LAUGHTER AS SOCIAL BONDING

Although great apes show a form of laughter in play, for humans it is a very different thing "in the fine detail of both its structure and its physiological characteristics" (Dunbar 2022 p1). Another kind difference is the social element of laughter, and humans are much more likely to laugh at the same comedy video while in a group watching compared to alone (Dunbar 2022) [2] [3].

This contagious and involuntary form of laughter is known as Duchenne laughter, and its evolution has a central role in social bonding [4]. "As such, it seems "like a plausible candidate to fill the gap between primate social grooming and other evolutionarily more recent social bonding behaviours such as singing, dancing, feasting and storytelling. There are good grounds for supposing that laughter evolved before these other bonding behaviours: first, only laughter is shared with the great apes and, second, laughter has a strongly involuntary component to it whereas all these other behaviours are under explicitly voluntary control (and/or depend on language). This suggests that laughter has very deep evolutionary roots whereas the other bonding behaviours are of much more recent origin" (Dunbar 2022 pp1-2).

Dunbar's (2022) hypothesis is that laughter appeared because mutual social grooming as means of social bonding is limited at a certain group size, and that it appeared in hominin evolution around 2.4 million years ago (ie: early Homo species).

Primates tend to live in relatively small stable social groups. "These require considerable investment in behavioural processes that create bonded relationships so as to maintain their stability and cohesion through time" (Dunbar 2022 p2). Mutual social grooming is a key process here, where another individual sweeps through the fur searching for parasites. The sweeping movement has been observed to result in the release of endorphins in human neuroimaging studies (eg: Nummenmaa et al 2011).

The amount of time in the day in social grooming increases with group size, but Dunbar (2022) argued for a ceiling of around 20% with the demands of foraging and

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[2] For example, a diary study (Provine and Fischer 1989) with adults, and a study of 3-4 year-olds (Addyman et al 2018).

[3] Provine (1993) observed that laughter is less associated with jokes than in interactions with comments that do not have obvious humorous intent. So, laughter is "used to mark (or seek) affiliation, affection, agreement, understanding
and recognition, in conversational settings" (Scott et al 2022 p4).

[4] Provine (1992) noted that "laughter is highly behaviourally contagious, with many laughter episodes occurring simply because someone else has laughed. These contagious laughs are also highly social — people are much more likely to catch a laugh from someone they know than from a stranger" (Scott et al 2022 p4).

sleep in particular. This equates to a group size of less than fifty (Dunbar 2022). So, how to maintain the stability of larger groups where mutual social grooming of all members is time constrained?

One answer is "chain grooming", where A grooms B, who grooms C, and c grooms A, say. Dunbar (2022) rejected this answer as still time constrained, and argued for laughter as the evolutionary solution. Laughter as a form of chorusing releases endorphins similar to social grooming (Dunbar 2022).

In experiments, strangers who laugh together in a brief interaction (eg: watching a comedy video) score higher on self-rated perception of bonding measures than strangers who do not laugh together (eg: watching a factual documentary) (eg: Dunbar et al 2021).

Dunbar's (2022) estimate of the evolution of laughter with early Homo species (rather than early humans at 600 000 years ago) was based on the calculation of group size of different hominin species. The group size was estimated on a continuum from chimpanzees (at the lower end) to modern humans (mean group size of 154; Dunbar 2021). Put simply, Homo erectus started to live in groups too large for mutual (or chain) grooming, and so there was evolutionary pressure for a social bonding mechanism, which was Duchenne laughter.

Encryption theory (Flamson and Barrett 2008) made a similar argument for humour. It proposed that "humour is a special case of ostensive communication (ie: the signalling of an intention to communicate) in which meaning is encrypted (ie: hidden) such that only receivers with certain information will be able to decrypt it" (Bryant and Bainbridge 2022 p2). Only those who share beliefs and knowledge can decrypt, so humour is a means to maintain bonds. Laughter is the spontaneous signal of shared knowledge. It is rewarding to be in on the joke.

2.4. LAUGHTER WITHIN SPEECH

Considering laughter from a cross-cultural perspective, Bryant and Bainbridge (2022) argued that "laughter occurs in highly similar ways across all documented languages studied to date, and that listeners around the world hear laughter similarly, and are able to make accurate judgements about laughers from very brief exposures (eg: approx 1 s), providing initial evidence for cognitive adaptations that extract rich social information from laughter" (p2).

A common method of study is to play recordings of laughter to individuals from different cultures to see if it is recognised as laughter. Bryant et al (2016), for example, played recordings of "conversational co-laughter" (laughter within interactive speech) to 966 participants from 24 different societies. There were six pairs of speakers - two male friends (M-M), two female friends (F-F), and male/female friends (M-F), and the same combinations for strangers. The task was to say whether the pair of speakers were friends or strangers, and how much the speakers liked each other. All societies were similar in correctly classifying friends and strangers significantly above chance, and there was agreement on ratings of liking. "Laughs with shorter duration, less regular pitch and intensity cycles, and less variation in pitch cycle regularity were more likely to be judged as between friends" (Bryant and Bainbridge 2022 p3). Accuracy of judgment was best for F-F friends.

Building on this research, Bryant et al (2018) created conversational co-laughter recordings containing genuine or fake laughter, and played 36 extracts to 884 listeners from 21 societies. All societies were able to tell the difference to an accuracy significantly above chance.

These two studies showed "universals in basic identification of laughter as a signal of amusement, as well as widely shared intuitions about the relationships between people laughing together..." (Bryant and Bainbridge 2022 pp4-5).

Another method of study is to make recordings from real-life interactions and analyse them. For example, Gavioli (2009) compared encounters between staff and customers in bookshops in England and Italy. Focusing on the shop assistants, "[W]hile both used laughter in the context of a dispreferred response (eg: a desired book being unavailable), in the English corpus, laughter was turn-initial and prefacing an excuse or other account. In the Italian corpus, the laughter occurred at the end of their conversational turn, leaving open discussion for resolution of the situation" (Bryant and Bainbridge 2022 p6).

A relatively new method of study is the use of machine learning algorithms. "Algorithms are typically 'trained' on a set of tokens, and then, based on any detectable information structure in that set, can be used to perform classification on novel databases. An interesting, though at times frustrating, aspect of the technique is that it can be impossible to know exactly how the algorithms learn the classification" (Bryant and Bainbridge 2022 p6).

2.4.1. Round-Robin Conversation Method

Social interactions containing laughter are reported as more enjoyable than when there is no laughter. Wood et al (2021) recruited sixty-six US undergraduates to interact with strangers in same-sex pairs for ten minutes. The interactions were video recorded, and scored for "laughter bouts". There was an overall average of 8.88 laughter bouts per ten-minute interaction. After each interaction, each participant individually rated their partner on eight scales (eg: "have a lot in common"; "like to be friends with"), and the conversation enjoyment.

More laughter was associated with higher ratings of perceived similarity between partners, but less with conversation enjoyment.

The frequency of laughter only was measured, which ignored other aspects (eg: duration).

Wood et al (2021) were also interested in whether the tendency to laugh was a stable characteristic of an individual. Because each participant engaged in ten social interactions (round-robin conversation method), it was possible to compare the individual's behaviour across the different interactions. Three possibilities were tested:

i) "Actor effect" - An individual laughs the same amount in every interaction.

ii) "Partner effect" - The amount of laughter by an individual is always dependent on the amount of laughter by the partner.

iii) "Relationship effect" - The amount of laughter is unique to an interaction.

Statistical analysis supported the "actor effect" in the main, "providing strong evidence that the tendency to laugh is a stable individual difference" (Wood et al 2021).

2.5. APPENDIX 2A - CLICK FRIENDSHIP

"Click friendships" (CFs) are non-romantic (usually same-sex) relationships that "form almost instantaneously" (Ravreby et al 2022 p1). Based on the work on body odour among non-human mammals, Ravreby et al (2022) investigated whether "click friends indeed smell alike" (p1). It is already known among humans that "a friend's body odour and one's own body odour induce similar patterns of brain activity, yet exposure to a stranger's body odour induces a very different limbic fear–type brain response" (Ravreby et al 2022 p1).

Ravreby et al (2022) performed five studies:

Study 1 - 225 online participants were asked to define "click friendship" in their own words. Most of the participants had a clear notion of the concept, and common terms used included "matching", "friendship that is formed immediately when meeting", and "chemistry" (p1). This suggested to the researchers that CF is "a real social event, despite the lack of formal definition" (Ravreby et al 2022 p1).

Study 2 - Twenty pairs of click friends each wore a new cotton T-shirt for two consecutive nights to capture their body odour. An "eNose" was used to detect similarities between friends. The body odours of CF were more similar in terms of "chemical fingerprint" than expected by chance.

Study 3 - Twenty-four new participants smelled the T-shirts from the previous study, and stated which two of three choices were a CF. This study found that "at the group level, participants failed to explicitly classify dyads based on body odour" (Ravreby et al 2022 p3).

Study 4 - Twenty-five more participants were presented with two of the above T-shirts from a CF and two of the above T-shirts from random individuals, and had to say which pair was the CF. The body odour of the CF was rated as significantly more similar than the random pairs.

Study 5 - Seventeen participants were randomly paired a number of times to play the "Mirror Game" (ie: copying the other person's movements), and to say afterwards who they clicked with. The similarity of body odour was measured by the "eNose" for CFs and non-CFs.

The pairs who rated themselves as a CF after the two-minute interaction had more chemically similar body odours than pairs that did not click.

In summary, the studies, in the main, showed that "the body odours of same-sex click friends are more similar to each other than the body odours of of same-sex random dyads" (Ravreby et al 2022 p6). Put more catchily, "there is indeed chemistry in social chemistry" (Ravreby et al 2022 p7).

The study, however, did not investigate the brain mechanism that may explain these findings. The "eNose" showed the chemical similarity in body odour, which not be the same as human perception.

The idea of body odour similarity fits with the general view that individuals form relationships with people who are similar to themselves (eg: age, education, religion, attitudes, physical appearance).

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3. INTER-GROUP CONFLICT ACROSS THE ANIMAL KINGDOM

3.1. OVERVIEW

For a long time it was assumed that war and conflict were unique to large human societies, but in the last few years it has become evident that early humans were involved in inter-group violence, as well as non-human primates (eg: chimpanzees, baboons), and other animals (eg: meerkats, wolves, certain group-living birds, social fishes) (De Dreu and Triki 2022).

De Dreu and Triki (2022) commented that "inter-group conflict [IC] can be exceedingly costly to the involved individuals, their groups and the population at large. In humans, political revolts, civil wars and inter-state conflict since 1946 resulted in over 40 million people killed. Chimpanzees kill and die from battle-related injuries, and inter-colony warfare among social insects such as ants and bees can kill tens of thousands. Moreover, and in addition to battle-related trauma, inter-group conflict has, across species, been linked to environmental degradation and famine, migration and forced relocation and the spreading of infectious diseases" (p2).

So, how to explain costly IC across the animal kingdom? A simple answer is that many animals "require access to territories and resources that are shared with and also demanded by other species, conspecifics included. This can create competition and conflict both within and between groups of individuals" (De Dreu and Triki 2022 p2). IC can thus be seen as "a two-level 'game of strategy' in which (i) individuals within groups co-operate at a personal cost to (ii) generate a group-level 'fighting capacity' to compete against (groups of) outsiders. Accordingly, groups need to ensure that (enough of) their members participate — groups need to overcome problems of co-operation that emerge from individual temptations to free-ride on others' co-operative efforts and avoid the opportunity costs and injuries associated with joining intergroup conflict" (De Dreu and Triki 2022 p2).

There is a case for a "win-lose" conflict where the victors take all and the losers are left empty-handed. "However, not all inter-group conflicts result in win-lose outcomes. In many cases, for example, when rivalling groups are of equal strength and invest equally in conflict, conflict settlement can take the form of a 'lose-lose' conflict" (De Dreu and Triki 2022 p3). Humans also can have a "win-win" conflict where post-conflict co-operation benefits all (De Dreu and Triki 2022).

IC in this light tends to be analysed in "economic" terms - the gains versus the costs. For example, Mathew (2022) found that the promise of more cattle motivated individuals of the Turkana in East Africa to join a raid on neighbouring communities. The "spoils of war" are important to encourage "reluctant" community members to join the fight. Female vervet monkeys have been seen to offer males mating opportunities as an incentive to engage in IC (Bshary et al 2022).

Also there can be non-material benefits like status and reputation for participation in IC, which later lead to material benefits. "Conversely, groups can sanction free-riders through peer punishment, effectively reducing the individual's social and material benefits from free-riding, something seen in various mammalian species, in social fishes and insect societies. At least in humans, punishing members who did not fight increases their conflict participation" (De Dreu and Triki 2022 p4). Furthermore, in humans "past conflicts perpetuate in spiteful desire for revenge, prejudicial misperceptions and feelings of in-group superiority and thwarted entitlements" (De Dreu et al 2022 p1).

Humans have sharing rules to aid co-ordination in the collective conflict. There is "evidence that such a mechanism generalises beyond humans — collective grooming and food sharing in chimpanzees prior to intergroup encounters can increase social ties among group members [Lemoine et al 2022]" (De Dreu and Triki 2022 p4) (appendix 3A).

Furthermore, "[T]o solve problems of co-ordination — who contributes what and when — individuals within groups can specialise in some tasks and not others" (De Dreu and Triki 2022 p4). Task specialisation can be horizontal ("fighters" and "producers") and vertical ("leaders" and "followers") (De Dreu and Triki 2022).

If IC is about scarce resources, then the availability of resources in the environment is crucial. While groups that prosper (ie: increase in size) require more resources, and create their own "carrying-capacity stress" which increases the potential of co-operation and conflict (De Dreu and Triki 2022).

3.2. FITNESS CONSEQUENCES

In terms of the consequences of IC, those can be proximate, distal or ultimate. Proximate consequences may include in-group bonding and co-operation, or suffering for those not involved (eg: human refugees) (De Dreu and Triki 2022).

The longer term consequences (distal and ultimate) include the reproductive success of victors, and even impact the evolution of a species (De Dreu and Triki 2022).

"Individual contests can also lead to later knock-on consequences for non-participating group members. For instance, a breeding vacancy created by contest-related mortality of the incumbent can be filled by another group member. An outsider taking over a breeding position can generate reproductive opportunities for unrelated opposite-sex individuals, but can also cause feticide, infanticide and eviction" (Morris-Drake et al 2022 p2).

Morris-Drake et al (2022) reviewed the fitness consequences of IC at two levels:

i) Between species - Species vary in the physical or ritualised nature of IC, as well as whether the fights are lethal. For example, one study of banded mongooses estimated that one-tenth of adult deaths was due to lethal IC (Morris-Drake et al 2022).

ii) Within species - The amount of IC within a species can vary at different levels:

a) Population - Populations in high population density areas will face more ICs. For example, Heinsohn (1997) simulated territorial intrusions in two different areas of Tanzania, finding that female African lions were more likely to respond if living in a high than low population density area.

Diana monkeys in forests with high population density show "nasty neighbour" behaviour (ie: more aggressive) towards neighbours than in low density areas, where "dear-enemy" behaviour is shown (Decellieres et al 2021).

b) Group - "Within a population, each group experiences a particular level of outsider pressure over a given time frame, leading to variation in the consequences of out-group conflict. For instance, groups probably have different numbers of neighbours and differ in their spatial positioning relative to others. In general, a group with more neighbours and/or a more central territory has a greater likelihood of an IGI [inter-group interaction] arising than a group with fewer neighbours or that is located on the edge of a population..." (Morris-Drake et al 2022 p6).

While the death rate from IC among nine well-studied chimpanzees communities varied between 69 and 287 per 100 000 individuals per year (Lemoine et al 2022).

c) Individual - Individuals vary in their involvement in and risk with IC. This may be due to individual differences (eg: some individuals are more aggressive than others), the position in the dominance hierarchy, body condition and health, and involvement of kin in conflicts, for instance (Morris-Drake et al 2022).

3.3. FACTORS IN WINNING

Winning IC (or between-group conflict (BGC)) is influenced firstly by group size (ie: larger groups), but also on home territory (ie: "familiarity and knowledge of an area's value are assumed to increase the group members' willingness to fight. The resulting increased probability of winning is called the 'Bourgeois effect' [Smith 1979]; in contrast, individuals are expected to behave cautiously in unfamiliar or unknown terrain and hence the group becomes less likely to win"; Garcia et al 2022 p2). Availability of food resources at that time is another factor (Garcia et al 2022).

To investigate these ideas, Garcia et al (2022) used data from 515 BCGs observed between January 2016 and October 2019 in four groups of wild vervet monkeys in the Mawana Game Reserve in South Africa. The food availability in an area of 50 m^2 was scored by the "Normalised Differentiation Vegetation Index" (NDVI), and BCG was defined as waves of chases and counter-chases until one of the two groups left the area.

The probability of winning was influenced by being in home territory with a high NDVI in its core area (ie:

good resources as a motivation to defence). But "larger groups with a larger number of adult females were more likely to lose" (Garcia et al 2022 p6). This was different to previous research, and one explanation was that larger groups can include more free-riders (ie: non-fighters) than smaller groups do. These are group members who gain the group benefits without contributing (also known as the "public goods problem"; Lewis et al 2020).

3.4. ENVIRONMENTAL STRESS

De Dreu et al (20220 assessed the role of environmental unpredictability with experimental contests ("inter-group attacker-defender contests"; IADC), and archival data on militarised disputes between neighbouring states.

The IADC involved six individuals randomly divided into a three-person "attacker" group or "defender" group. Individuals could share as much of their endowment (20 "Experimental Euros") with their group, and the group with more money in their pool is the winner and they gain the total amount. The researchers varied the risks in the game to simulate environmental unpredictability. The participants were over 450 students in the Netherlands.

In Experiment 1, participants in the unpredictability treatment were told that they would randomly lose a part of their non-shared endowment. This increased the sharing of the endowment compared to a predictable environment (mean: 82% vs 53%). Experiment 2 varied the risk for each player, but still found the same results (mean of 75% of endowment shared in the unpredictability condition).

From the archival data on 1447 militarised disputes, it was found that "in the decade prior to conflict onset, aggressors compared to their defenders experienced more climatic variability" (De Dreu et al 2022 p6).

The conclusion, for De Dreu et al (2022) was that "[W]hen environmental unpredictability increased, individuals contributed more to their group's efforts to exploit other groups through co-ordinated out-group attacks and were more victorious" (p7).

3.5. DRAWS AND LOSER BENEFITS

Brown et al (2022) noted that "it is generally assumed that only winners experience benefits (such as access to food, shelter or mates). This perspective stems partly from the way in which a 'win' is defined: after the separation of the two groups, the winner is the contestant that remains in the encounter location with continued access to local resources, while the loser is the group that departs first. If the groups depart simultaneously, the winner is the group that continues moving in its pre-contest direction, while the loser moves away at a larger turning angle. In both cases, the underlying assumption is that losers experience costs, but no benefits" (pp1-2).

But losers can gain the same benefits as winners. For example, "when conflicts occur over a resource that neither contestant can deplete or monopolise for long periods" (Brown et al 2022 p2). Bands of feral horses, for instance, show a "respect for ownership" convention where the first group at a water hole in the dry season is allowed to drink their fill undisturbed, and then the other group can have access (Stevens 1988). The first group is typically scored as the loser in research studies (Brown et al 2022).

The "loser" may leave a resource patch because they are satiated, and so not motivated to defend it. So, this situation is closer to a draw. Brown et al (2022) noted the limited research on this situation. They investigated this with data on six groups of red-tailed monkeys in Kibale National Park, Uganda (collected between January 2012 and June 2015).

Two-four observers tracked each group from dawn until dusk, and recorded details of inter-group encounters (eg: length; location; physical contact or chases). Four types of encounter were defined - "displacement" (the winner stays in the encounter location) (n = 34 cases observed), "deflection" (both groups move, but the loser shows a retreat to their home territory) (n = 7), "mutual avoid" (both groups retreat before conflict) (n = 38), and "mutual ignore" (both groups continue on their way) (n = 1). The latter two categories were classed as a "draw". Fresh urine samples were collected to indirectly measure the energy balance of individuals.

The findings showed evidence of conflicts (with "winner benefits") and draws (with "everybody benefits"). The amount of time at a site seemed to be key. If a group had just arrived, they were more likely to win a contest (ie: motivated to defend because hungry), but if they had been at the site for thirty minutes or more, they were more likely to lose (ie: withdraw because satiated). We could call this the "graceful loser". "In short, groups in poor energetic condition win whereas groups in better condition lose" (Brown et al 2022 p5).

3.6. SIMULTANEOUS COMPETITION

IC may occur over multiple resources (simultaneously), like food and shelter, so animals "may need to prioritise which resource to compete over when their competitive effort is limited" (Neumann and Pinter-Wollman 2022 p1). Large groups have the advantage of being able to allocate members to compete for particular resources in a form of specialisation.

Neumann and Pinter-Wollman (2022) investigated simultaneous competition for multiple resources in two species of ants in North America - the invasive Argentine ant (Linepithema humile) and the native odorous house ant (Tapinoma sessile). "In one-on-one interactions, T. sessile generally outcompete L. humile, but when entire colonies compete, L. humile is typically the dominant species" (Neumann and Pinter-Wollman 2022 p2).

For their experiments the researchers collected 3000 workers from each species in California. In a specially designed apparatus, there were three separate areas, one each for the two species ("home area") and an area for competition. Fifty workers from each species were used in each condition. This was the situation for testing competition for a single resource - either food (removing the supply hitherto provided by the experimenters) or shelter (removing the tinfoil covering the home area). When competition over multiple resources was tested, there were two separate competition areas. So three conditions were tested - only food, only shelter, or both. The number of aggressive interactions in five-minute periods were counted.

In the single resource conditions the Argentine ants were more likely to control the shelter resource and the odorous house ants the food resource. But when there were multiple resources, both species preferred the shelter resource area (ie: more aggressive interactions here compared to the food resource area).

This suggested an "allocation-control trade-off" - ie: "groups either allocate a small number of workers to all resources at the risk of not being able to control any single resource, or allocate many workers to a single resource and control it, at the risk of not obtaining enough of the other resource(s)" (Neumann and Pinter-Wollman 2022 p7). Both species showed the latter. So, the researchers concluded, the "result of a competitive scenario over one resource might not necessarily indicate how competitors will behave in the presence of other resources, other species, or on different temporal or spatial scales" (Neumann and Pinter-Wollman 2022 p8).

Neumann and Pinter-Wollman (2022) admitted that the workers were "competing in the absence of a queen or brood. It is possible that the presence of queens or brood would have resulted in different outcomes that could be examined in future work. For example, it is possible that the presence of queen and brood would lead to more aggressive behaviour by workers, especially when competing over shelter, because of their importance for reproductive success" (p8).

3.7. APPENDIX 3A - PAROCHIAL ALTRUISM

The "parochial altruism hypothesis" (Choi and Bowles 2007) suggests that "out-group conflicts drive in-group cohesion and co-operation. The hypothesis postulates that groups with more individuals to favour the in-group over the out-group (parochialism) are more co-operative during an out-group conflict (ie: those that confer benefits on others at an immediate cost to self)" (Lemoine et al 2022 p1). Human parochial altruism is believed to have evolved through joint hunting and gathering, and co-operative breeding (ie: shared care of infants or alloparenting) (Lemoine et al 2022).

The pre-requisites for human parochial altruism were "probably present in the last common ancestor between Pan and Homo" (p1), according to work with well-studied wild chimpanzee populations in Africa (Lemoine et al 2022).

Studied with playback or simulated intrusion experiments, which involve an audio recording of long-distance vocalisations of an out-group male, and the reaction of the in-group is observed (eg: joint chorus of loud vocalisations; co-ordinated approaches to the playback speaker) (Lemoine et al 2022).

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4. GENOMICS AND POST-GENOMICS

4.1. GENOMIC DATA

Large amounts of genomic data has allowed the calculation of "polygenic scores", "which provide a measure of the degree to which an individual is genetically predisposed to developing... disease" (McCarthy and Birney 2021 p175). These findings are important, but McCarthy and Birney (2021) argued for more holistic measures of individual risk that includes both genetic and non-genetic factors. These authors emphasised three issues about over-reliance on genetic risk only:

i) The source of the genomic data - Polygenic scores "leave out many sources of relevant data, and work best for the predominantly white, wealthy populations in which most genetic studies have been performed" (McCarthy and Birney 2021 p176).

ii) Diverting attention away from non-genetic risk factors - For example, the risk of type II (or late-onset) diabetes is mostly linked to factors "collectively labelled as environmental", like diet, socio-economic status, access to health care, personal relationship status, and gut-microbiome diversity (McCarthy and Birney 2021). "Genetic and non-genetic risk factors often interact in ways that can be hard to disentangle" (McCarthy and Birney 2021 p176) (appendix 4A).

iii) Assessing risk as degrees rather than either/or categories - "Rather than classifying an individual as imply being an average or high risk for a condition such as coronary artery disease, researchers and clinicians should consider graduation of risk. And instead of trying to categorise people into discrete sub-types of disease, we should appreciate that common disease typically involves several processes running in parallel" (McCarthy and Birney 2021 p176).

4.1.1. Working with Indigenous Populations

Tsosie et al (2020) observed: "For decades, scientists have collected genomic information from Indigenous peoples and their ancestors with the goal of elucidating human migration events, understanding ancestral origins, and identifying ancestral variants contributing to disease. However, such studies may not have offered much benefit to the Indigenous groups who contributed DNA, and many have instead perpetuated stereotypes and other harms" (p91).

A number of issues arise from studies of current and especially ancient DNA (aDNA) and the mapping of ancestors for Indigenous groups. These include challenging the beliefs that Indigenous people are not originally from their ancestral lands, but are part of the broader dispersal of Homo sapiens out of Africa, or, on the other hand, "past sampling portrayed Indigenous peoples as isolated groups, leading to problematic notions of racial purity... and conflations of biological classifications of race with socio-cultural and political designations of Indigeneity" (Tsosie et al 2020 p92).

How to build trust with Indigenous communities in aDNA research? Tsosie et al (2020) offered some reflections in relation to the Americas.

Concern has been raised by Indigenous groups about the open accessibility of their collected and sequenced genomic data. "Much of the apprehension stems from concerns about bio-colonialism [Faye 2004], or the commodification of Indigenous peoples' biological information. Additionally, there is considerable pluralism in the ability of Indigenous people to exercise autonomy in governing their genomic data. In the US, for example, some tribes exert their sovereign authority by instituting their own research regulations" (Tsosie et al 2020 p93). Empowering Indigenous communities to become "data stewards themselves to enforce safeguards around the use of data" is recommended (Tsosie et al 2020).

Another area is the treatment of ancestors from which the aDNA was extracted. "Many Indigenous peoples assert that their ancestors should remain in ancestral lands near kin to maintain their connections to land and relatives, which is essential for ancestors' spirits to rest" (Tsosie et al 2020 p94). But Tsosie et al (2020) had a word of warning: "We caution that repatriation should not be oversold as a benefit to Indigenous communities as each community has its own unique cultural history and diaspora" (p94).

An over-riding issue is the categories of "race" or "ethnicity" used. These are not neutral. "The politics of what constitutes Indigenous identity and ancestry are complex, and the issue is further complicated when lay individuals falsely equate biological constructs with Indigeneity" (Tsosie et al 2020 p95). Tsosie et al (2020) continued: "Furthermore, scientists must be careful not to 'equate those who are more admixed as being less Indigenous than ''non-admixed'' Indigenous people' [Leroux 2018] because Indigeneity and kinship are socially and politically determined, and Indigenous people retain the right to define them for themselves" (p95).

Jackson et al (2021) argued that "to demolish genetic racism. geneticists must defer to communities to self-define their 'belongingness'" (p475). Current categories have their origins in eighteenth century colonial thinking (Jackson et al 2021).

Tsosie et al (2020) ended with this advice: "First, researchers should consult with the community about important questions that can be answered using genomic techniques, then proceed with permission to carry out respectful methods while maintaining transparency, and finally collaboratively work to interpret the results with culturally-appropriate viewpoints" (p96).

4.1.2. Mixed Race

In Latin America the idea of individuals as a mixture of different ancestors (eg: "mestizos" in Mexico: Indigenous peoples and Spanish colonisers) has been taught. "But like all other race-based labels, the mestizo is a social construct, not a well-defined scientific category of people who share similar genetic characteristics. And many researchers have started to challenge the mestizo ideology, which they see as a source of pain for many people - and an obfuscating, sometimes troubling, influence in science" (Mega 2021 p375).

It has been argued that the "mestizo myth" means that individuals with Indigenous and African ancestries have been misrepresented or ignored in science (Mega 2021).

Meanwhile there is the search for "risk alleles" and the linking to certain ancestral groups. Social anthropologist Peter Ward noted the suggestion that diabetes and obesity in Mexico are linked to genes inherited from Indigenous ancestors - "It's kind of [implying] these health problems are somehow the fault of the Indigenous people or Indigenous ancestry" (quoted in Mega 2021).

4.2. PREGNANCY IN THE POST-GENOMIC ERA

Valdez (2021) advocated the position that "while science and society may frame pregnant people as uniquely and totally responsible for the welfare of growing foetuses and children, pregnancy and reproduction are not individual processes. We all encompass the maternal environment. We all collectively participate in reproduction, regardless of sex, race, gender, orientation, ability, or fertility. We all contribute to the social, institutional, and environmental circumstances that shape each pregnancy, birth, and child" (p4).

This includes how the "maternal environment" is "constructed", whether it includes poverty and racism and their influence on the growing foetus, say, or epigenetics and the "developmental origins of health and development" (DOHaD). The latter "frames pregnancy as a critical period of development because it encompasses multiple generations in one: the pregnant body is the first generation, the foetus is the second generation, and the reproductive cells in the foetus represent the third generation" (Valdez 2021 p5). Note the inclusion of a third generation that will be impacted by the current pregnancy.

The risk, argued Valdez (2021), is that "scientific and media interpretations of epigenetics and DOHaD theories individualise the health risks of future generations onto pregnant bodies alone" (p5) (eg: headlines like "diet permanently influences baby's DNA"). Valdez (2021) continued: "Denying our collective participation in reproduction and continuing to promote individual lifestyle interventions draws resources away from much needed systemic and institutional change" (p6).

Valdez (2021) used the concept of "epistemic environments" to describe how scientific knowledge (specifically "post-genomics" [5]) is involved in the individualisation of environmental risks.

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[5] "Post-genomics represents a significant shift in approaches and scientific content, including 'research on gene-expression, population-level genetic variation, and gene-environment interactions" (Ackerman et al 2016) or (GEI) research" (Valdez 2021 p209) (appendix 4B).

4.2.1. "CRISPR Babies"

In 2018 He Jiankwi announced the use of CRISPR technology to "genetically engineer" three embryos who grew to be the children known as "Amy", "Lulu" and "Nana" (twins). The genetic engineering was an attempt to prevent the children contracting HIV from their fathers (Gutierrez C 2022).

CRISPR is a molecular technology that can delete a specific portion of a gene (in this case on gene "CCR5"). But there are problems with the technology. Kiran Musunuru (at the University of Pennsylvania) pointed out: "CRISPR is often referred to as molecular scissors, but this implies a level of precision that it does not have... rather than cutting a precise point in a page like scissors would do, it is more like tearing through the page" (quoted in Gutierrez C 2022).

A key concern is "off-target" edits where uncontrolled cuts have occurred elsewhere in the genome. While "mosaicism" is another problem, where the edits in the gene are different from one cell to another (Gutierrez C 2022).

4.3. APPENDIX 4A - EXPOSOMICS

"Exposomics" is the term for the measurement of environmental exposures and their impact on health, or more specifically, to "measure lifetime exposures to everything in our environment and link these to disease risks" (Lawton 2022 p44).

It is estimated that twelve million deaths globally per year are due to "the cumulative effect of potentially harmful environmental exposures, or 'insults'" (Lawton 2022 p44).

Toxicology is interested in short-term exposures to individual toxic substances, but exposomics seeks to understand to understand the long-term interaction of multiple insults (Lawton 2022).

Peters et al (2021) outlined eight ways that environmental exposures impact health (Lawton 2022):

i) Oxidative stress and inflammation - the immune response to environmental chemicals.

ii) Genomic alterations and mutations - pollutants damaging DNA.

iii) Epigenetic alterations - pollutants change the expression of genes.

iv) Mitochondrial dysfunction - pollutants damage mitochondria, which powers cells.

v) Endocrine disruption - hormones affected by pollutants.

vi) Altered cell communication - the ability of cells to communicate changed by environmental chemicals.

vii) Altered microbiome communities - the effect on the gut bacteria.

ix) Impaired nervous system function - eg: noise pollution disrupts the nervous system.

4.4. APPENDIX 4B - THE REALITY OF GEI RESEARCH

In the 21st century "the lure of genetic determinism is loosening its grip as new understandings of developmental and aetiological complexity undermine 'the pre-ordained genetic body' (Lock 2005...) and displace the gene as the prime mover of health and illness" (Ackerman et al 2016 p195) [6]. Despite the acceptance of a role for the environment, Krieger (2013) has argued that a "gene-centric" approach persists, and "that a move away from genetic determinism in the life sciences has nonetheless been accompanied by a 'neo-reductionism in which virtually everything external to the material body remains black-boxed' (Lock 2005...)" (Ackerman et al 2016 p196).

Ackerman et al (2016) found from their interviews that among GEI researchers, the emerging 'interactionist consensus' (Kitcher 2000 cited in Landecker and Panofsky 2012) co-exists with significant uncertainty about how best to study aetiologically complex diseases. Questions of proper measurement are a particular source of anxiety among scientists involved in GEI studies, and our findings suggest that measurement and other forms of quantification do not operate simply as value-neutral techniques of knowledge production. Rather, quantification is a field of social activity that is

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[6] For example, the association between genes and lung cancer is much stronger when smoking (the environment) is included in the analysis (Ackerman et al 2016).

simultaneously moral and technical [7]. As scientists collectively struggle to define what counts as 'genes' and 'environments' and how to count them, they debate which procedures and standards constitute the proper conduct of science, and who and what constitutes a 'good' GEI scientist" (p197).

These researchers interviewed thirty-two genetic epidemiologists and other scientists engaged in GEI research on heart disease, type 2 diabetes, or cancer between 2010 and 2014.

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[7] "Although measurement is commonly understood simply as description, historians of science remind us that it is a strategy of quantification, which, along with other scientific values such as empiricism and objectivity, has a contingent and altogether social history" (Ackerman et al 2016 pp199-200). Daston (1995) described quantification "as a kind of 'moral economy' of science" (Ackerman et al 2016 p200).

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5. INTERACTION ENGINE

5.1. OVERVIEW

One explanation of the evolution of human language is the "interaction engine" (InEn) hypothesis (Levinson 2006a). Language use evolved for face-to-face interactions, and to co-ordinate collaborative action. "From this viewpoint, the advent of language was preceded by the evolution of unique interactional ethology, or a 'cognition-for-interaction' [Levinson 2006b], enabling communication through a distinct set of cognitive and behavioural capacities, metaphorically described as the 'interaction engine'" (Heesen and Frohlich 2022 p1).

The InEn has four major components (Heesen and Frohlich 2022):

i) Multi-modality - Communication through different sensory channels (eg: visual, auditory) and organs (eg: mouth, hands). Also the "orchestration of multi-modal signals" (ie: gesture, facial displays and vocalisations together) (Levinson 2022).

ii) Sequence organisation - "communicative acts that have a contingent relationship with the previous and following act, presuming a normative obligation to deliver appropriate responses at the next best occasion" (Heesen and Frohlich 2022 p2) (eg: question and answer).

iii) Turn-taking (ie: timing).

iv) Intentionality - Communication of and response to intentions. "Humans not only communicate ostensibly, via 'Gricean intentions' (Grice 1957) (speakers wanting to have their intentions recognised) [8], but also infer intentions from others' utterances against the background of pragmatic information on context, previous

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[8] Communication is "intention recognition": "It is not sufficient for signaller S to have a goal or desire and produce a signal aimed at inducing a response in the recipient, R. It is critical for S that R recognises S's intention and acts accordingly" (Melis and Rossano 2022 p1).

interactions, and relationships. Humans constantly establish and mutually refer to common ground — a platform of common beliefs and knowledge that stacks up through repeated interaction and builds the foundation against which signals and actions are being interpreted" (Heesen and Frohlich 2022 p4) [9].

Intentionality has different levels, including first-order (communications that get the receiver to do something; eg: "pass me the bottle of water"), and second-order (getting the receiver to think something; eg: the speaker wants the bottle of water). There is also third-order intentionality (getting the receiver to think something; eg: the receiver thinks the speaker is thirsty and that is why they asked for the bottle of water) (Levinson 2022).

Importantly, the InEn comes before language, and "the interaction engine's ingredients are not some distinct brain modules but describe distinct principles of human interaction that are universally observed across the world's cultures" (Heesen and Frohlich 2022 p2). In reflecting on the research on the evolution of the InEn, Heesen and Frohlich (2022) noted five major aspects:

a) A wide variety of methods have been used to study the topic.

b) The "variability in interaction engine components across primates is a matter of degree rather than an all-or-nothing situation" (Heesen and Frohlich 2022 p7).

c) Communicative performance is modulated by various factors (eg: dominance and kin relationships).

d) Some aspects of the InEn are the consequences of the evolution of language.

e) Many questions remain unanswered about the "different interaction engine ingredients" (Heesen and Frohlich 2022 p7).

Evidence is emerging from palaeontological data and ancient DNA that other hominin species had "biological adaptations for language including specialist enervation

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[9] Grice (1989) "put forward the notion of a co-operative principle driving human communication, which suggests that all human signals are usually interpreted with the underlying assumption that they have been produced with a co-operative intention, ie:. not to deceive or mislead. This assumption facilitates the inferential process necessary to interpret what a signaller is trying to communicate and what kind of response would be the most appropriate next" (Melis and Rossano 2022 p2).

of the respiratory and vocal tract, tuning of hearing to the bandwidth of speech, the auditory-vocalisation pathways for vocal imitation, neural adaptations like slight extension of the arcuate fasciculus, and genetic adaptations like variants of FOXP2 which facilitate language production through developmental pathways. Yet it is also clear that the great bulk of language complexity, by contrast, must be attributed not to an innate source but to cultural evolution, for languages differ in their construction on every level, from the sounds to the syntax" (Levinson 2022 p1). Darwin (1871) had remarked that "language is an art made possible by an instinct to learn" (quoted in Levinson 2022).

Intense social interactions by humans may have been a pre-requisite of language as it has been established that humans spend around one-third of their waking time in such interactions compared to about one-fifth among chimpanzees (Levinson 2022).

5.2. GESTURES

The role of gestures in the evolution of human language is viewed from two broad camps: "those arguing for 'gesture-supplanted-by-speech' scenarios of language evolution, where gesture fulfilled a bridging function and its relevance largely withered away once a fully fledged linguistic system had been acquired, eventually leading to the speaking species that we are; and those who argue for language having evolved as a multi-modal system, with the vocal and gestural modalities intertwined from the very beginning, and playing an integral role in communication also in modern human language" (Holler 2022 p1).

Holler (2022) favoured the latter view. Visual bodily signals, like hand gestures, body movements, facial signals, head gestures, and gaze, are "co-ordinated devices in human communication" (Holler 2022 p2). For example, a "palm-up-open-hand gesture" occurs when the speaker is offering or sharing information (Holler 2022).

While comparisons with non-human primates show that, for example, "the use of palm-up gestures in humans, orang-utans and chimpanzees when making requests (eg: food)" (Holler 2022 p8). Multi-modal communication is also seen in facial expressions and vocalisations in chimpanzees, for instance, and with the development of facial behaviour coding systems (eg: ChimpFACS; Vick et al 2007).

Holler (2022) pointed out that a "multi-modal view of human pragmatics and a consideration of visual bodily signals in the co-ordination of minds in interaction makes the gap between humans and non-human primate communication appear smaller than it may seem at first sight" (p10).

5.3. JOINT ATTENTION

One of the underlying processes of language is "joint attention" as seen in infants around 9-10 months old in "showing" and "giving". "Showing involves holding up objects so that others can see them, and giving involves placing and releasing an object into another's hand" (Salter and Carpenter 2022 p1).

Salter and Carpenter (2022) studied twenty-five mother-infant human pairs once a month from six to ten months old. Situations were created for the infants to make use of sharing and giving. For example, the researcher gave the infant a toy while the mother looked away, then the researcher left and the mother looked at the child. Spontaneous showing behaviour was observed at eight months old, and half of the children had shown it by ten months old. Spontaneous giving behaviour was recorded first at nine months old, and one-third of the infants had shown it by ten months old.

The researchers felt that "conventional showing and giving are a product of a series of gradual cognitive and motoric developments that take place in the context of repeated social engagements" (Salter and Carpenter 2022 p7).

The mother-child interaction is key, and great apes "presumably do not engage" in such interactions (Heesen and Frohlich 2022 p3).

5.4. CO-OPERATION AND COMMUNICATION

The differences in intentionality are seen in great ape communications and co-operation. These animals "might be constrained owing to their limited capacity in comprehending helpful intent, insofar as signals are mainly understood as imperative acts (signallers wanting something) rather than as helpful cues (signallers wanting to share helpful information)" (Heesen and Frohlich 2022 p5).

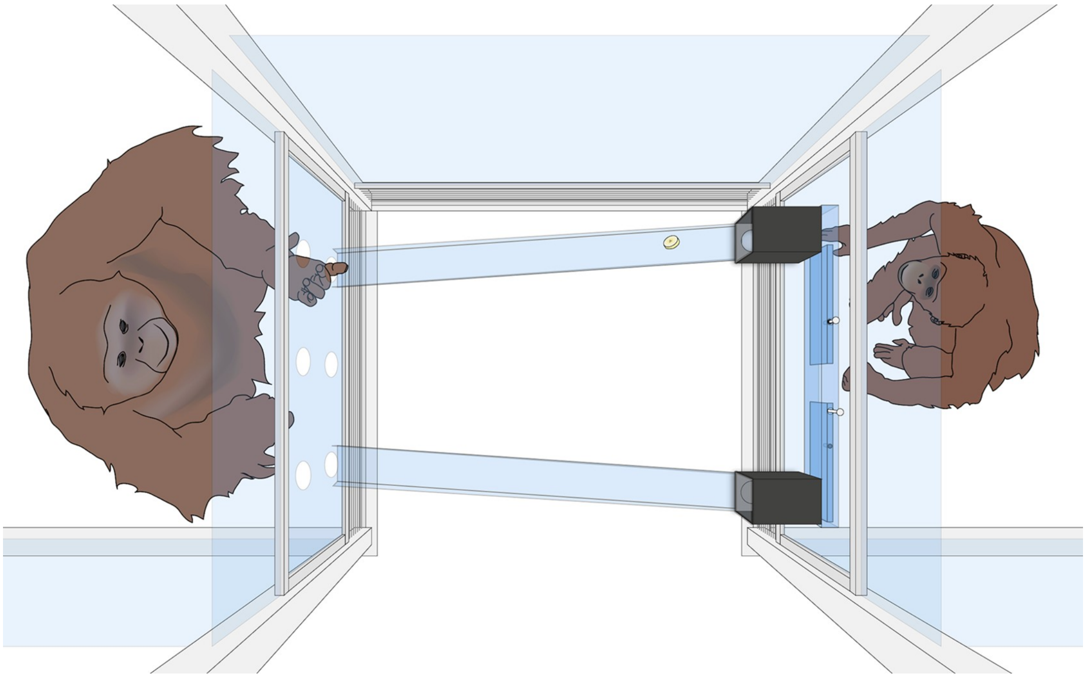
Melis and Rossano (2022) considered this problem and other issues in a review of experimental co-operative tasks. Communication in relation to co-operation has two elements - (i) getting the attention of another ("summons"), and (ii) what assistance is needed ("requests") (Melis and Rossano 2022). Experimental tasks that involve both of these elements are joint actions - ie: the goal cannot be achieved without two or more individuals working together. For example, the "heavy box pulling task" requires both chimpanzees, say, to pull the box containing food to within arm's length (eg: Crawford 1937).

Linked to this task is the "co-ordinated breakdown scenario" where an adult human working with a chimpanzee, say, stops co-operating in order to force the chimpanzee to communicate. Warneken et al (2006), for instance, found that human children did communicate, but not chimpanzees in this situation.

Another type of experimental task involves asymmetrical knowledge. For example, Moore et al (2015) tested pairs of orang-utans "where the communicator could see the location of food but not reach it, and the potential helper could not see where the food was but could release it to the partner. They found that one male orang-utan pointed regularly to the food location, but helpers almost never reacted and when they did, not always correctly. However, it is important to note that because recipients didn't get any food, this is a helping task rather than a mutually beneficial joint action task, so the study is not only measuring their comprehension and co-ordination abilities but also their altruistic motivation" (Melis and Rossano 2022 p6) (figure 5.1).

Experimental tasks often use animals raised by humans, and, as Melis and Rossano (2022) pointed out, "[A]pes raised in a rich social-communicative environment perform significantly better than other apes" (p7).

Melis and Rossano (2022) made the "tentative suggestion... that what differs in the human 'interaction engine' when compared to non-human great apes are the following recipients' features: (i) a generalised motivation to pay attention to communicative signals produced by all conspecifics, ie: also non-kin and non-bonded partners; (ii) trust that communication will be honest and co-operative (ie: not competitive and/or deceptive); and (iii) higher motivation to produce responses to communicative signals produced by non-kin and non-bonded partners" (p8).



(Source: Moore et al 2015)

(The individual on the left can see which box has the food (communicator) while the individual on the right controls the lever for release of the food without being able to see into the boxes (receiver))

Figure 5.1 - Experimental set-up used by Moore et al (2015).

5.5. UNIVERSAL GRAMMAR

Evans and Levinson (2009) argued against the idea of "Universal Grammar" because "languages differ so fundamentally from one another at every level of description (sound, grammar, lexicon, meaning) that it is very hard to find any single structural property they share" (p429). They rejected the idea that the "differences between languages are merely superficial, and that they can be resolved by postulating a more abstract formal level at which individual language differences disappear..." (Evans and Levinson 2009 p429).

But a challenge to Evans and Levinson (2009) is that diverse languages are the product of one cognitive system. There are two possible resolutions of this problem. "Either the innate cognitive system has a narrow core, which is then augmented by general cognition and general learning principles to accommodate the additional structures of a specific language..., or it is actually a 'machine tool', pre-built to specialise and construct a machine appropriate to indefinitely variable local conditions" (Evans and Levinson 2009 pp445-446).

Evans and Levinson (2009) offered a number of theses:

a) "The diversity of language is, from a biological point of view, its most remarkable property - there is no other animal whose communication system varies both in form and content. It presupposes an extraordinary plasticity and powerful learning abilities able to cope with variation at every level of the language system" (Evans and Levinson 2009 p446).

b) Linguistic diversity is linked to cultural-historical and geographical diversity.

c) Linguistic diversity is characterised by "clusters around alternative architectural solutions, by prototypes (like 'subject') with unexpected outliers, and by family-resemblance relations between structures ('words', 'noun phrases') and inventories ('adjectives')" (Evans and Levinson 2009 p446).

d) A co-evolution model of human language (ie: biology and culture together).

e) Language is an evolutionary recent development, so it "must exploit pre-existing brain machinery, which continues to do other things to this day" (Evans and Levinson 2009 p446).

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6. LEWONTIN 50 YEARS

Fifty years ago Lewontin (1972) pointed out that "85% of human genetic variation resides within populations" (table 6.1) [10]. The article and this "sound bite" provide "an important response to the misappropriation of descriptions of human biological variation in support of racism" (Edge et al 2022 p1) [11].

- "The results are quite remarkable... Less than 15% of all human diversity is accounted for by differences between human groups!" (p396).
- "It is clear that our perception of relatively large differences between human races and sub-groups, as compared to the variation within these groups, is indeed a biased perception and that, based on randonly [sic] chosen genetic differences, human races and populations are remarkably similar to each other, with the largest part by far of human variation being accounted for by the differences between individuals. Human racial classifcation [sic] is of no social value and is positively destructive of social and human relations. Since such racial classification is now seen to be of virtually no genetic or taxonomic significance either, no justification can be offered for its continuance" (p397).

(Source: Edge et al 2022)

Table 6.1 - Key quotes from Lewontin (1972).

Lewontin's (1972) work should be seen in the context of the approach of "hereditarian biological racism", which is based on three claims: "(1) the claim that human diversity is structured racially, with pronounced genetic differences between 'races'; (2) the claim that differences across populations in distributions of meaningful complex traits trace straightforwardly to genetic differences between populations; (3) the claim that such differences in distribution have a simple basis in past adaptation of different populations to different environments" (Edge et al 2022 p5).

On the downside, "ignoring differences among populations can lead to challenges in addressing effects of genetic variation in biomedical problems... Lewontin's

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[10] Subsequent work has shown that the difference between individuals rather than populations is because "there simply has not been enough time for substantial differentiation between groups to emerge" (Novembre 2022 p5).

[11] The sound bite has been taken up by others in the "no biological basis to race" (Fullerton 2007) position (Novembre 2022).

paper [1972] has been referenced beyond the field of human evolutionary genetics as supporting an over-simplified view of human variation, in which population structure is completely ignored even in situations in which it might be relevant, such as matching problems in forensics or transplantation, where population variation in match probabilities affects the societal use of population-genetic computations" (Edge et al 2022 p4).

Lewontin (1972) was interested in a key question, which is still important today, namely, "at a 'typical' genetic locus, how does the amount of genetic variation within populations compare with the amount of genetic variation between populations?" (Edge et al 2022 p1). Lewontin's (1972) analysis of data from seventeen genetic markers ("systems") was the best of that time. Subsequently, more detailed analysis has confirmed that "the bulk of the genetic variation is within populations" (eg: Bowcock et al 1994), even before the advent of the Human Genome Project (Shen and Feldman 2022).

Other studies at the time, however, did not all agree (eg: Mitton 1977) and disputes emerged. Neel (1981) suggested that different questions were being asked by both sides - "What proportion of all the genetic variation within some large group can be attributed to differences among sub-groups and among individuals, on average, over all known loci?" (Lewontin) versus "Are the levels of allelic frequency variation found between human populations sufficient to generate a useful taxonomy?" (Mitton) (Shen and Feldman 2022).

Lewontin, over his life, "fought against the trend of using biology to justify and strengthen the existing structural inequality among races, classes and sexes" (Shen and Feldman 2022 p1). For example, Lewontin et al (1984) particularly challenged sociobiology (ie: "the theory that there exist universal aspects of human nature, which are genetically determined, and which were established by natural selection during evolutionary history"; Shen and Feldman 2022 p1). Biological determinism and reductionism were especially criticised by Lewontin (Shen and Feldman 2022).

Note that "races" in genetics (ie: genetic populations) is different to the social-based "races" (using skin colour, for example). "Lewontin's focus is not on whether one can do classification, but on what a racial classification conveys about genotype. Repeatedly in his writings and interviews, he conceded the human ability to build classification systems using biological traits like skin pigmentation, hair colour and stature that have genetic components that vary across human groups substantially: 'No one would mistake a Chinese for a West African or a Finn for an Australian aborigine' [Lewontin 1982]. The question is whether such race groupings have taxonomic value in the sense that they are predictive of meaningful differentiation at a typical genetic locus" (Novembre 2022 p6). This makes, in Novembre's (2022) view, many of the critiques of Lewontin (1972) "tangential to Lewontin's central question" (p6).

Lewontin was aware that "his [1972] result is not a silver bullet that defeats all possible racist positions, but it does set an important prior expectation. On a scientific basis, one can safely expect that the average variant is not substantially differentiated across race groups, and in turn that race is a poor proxy for genotype at any one locus of interest. For any discussion of human variation, this is an important 'understanding of the situation'" (Novembre 2022 p8). For example, Lewontin gave the "Hitchcock lecture" at Berkeley in 2003. "In the lecture, he acknowledges that his work 'does not prove... that there isn't a gene some place' that might be important for affecting behaviour and that varies across populations. While admitting this, he stressed defensively that 'nobody's ever found it' and 'there's no reason to think such things exist'. In a frank response to a question about what effect his work may have on those with racial prejudices, he expressed 'it's not clear it has any effect... I have not proved [racially differentiated genes for IQ] don't exist'. He continued, 'I think data like these in large part, predispose one toward an understanding of the situation, but if you're a hardcore racist they're not going to have any effect at all'" (Novembre 2022 p8).

LEWONTIN'S LEGACY

Lewontin (1972) is cited over 3000 times, according to "Google Scholar", with a pattern of many citations soon after publication, then "silence" in the 1980s, and a growth since the 1990s (Carlson and Harris 2022).

In terms of the situation today, Carlson and Harris (2022) surveyed "Twitter" for a nine-month period in 2020-21, and found "a picture of a steady, ongoing conversation about Lewontin's work rather than a flurry of activity surrounding any specific controversies or events" (p8). However, the phrase "Lewontin's fallacy" was common, which originated from Edwards's (2003) critique of Lewontin (1972) [12]. Carlson and Harris (2022) observed that "the Twitter users who vehemently oppose the conclusions of Lewontin (1972) often have significant overlap with extreme far-right political communities, underscoring how rejection of Lewontin's interpretation has become a tenet of white nationalist ideology" (p12).

Several similar papers appeared around the same time as Lewontin (1972), but Carlson and Harris (2022) sought to explain what "propelled Lewontin (1972) to its current iconic status" (p2). They identified four factors:

i) Citation of the work in highly influential books and papers (eg: seven between 1972 and 1982) [13].

ii) Lewontin's discussion of the ideas in the "popular media".

iii) The Human Genome Project (HGP) (announced in 1990 and "completed" in 2001). Carlson and Harris (2022) admitted: "Although we found no evidence that the HGP had a direct bibliographic connection to Lewontin (1972), it likely played a role in popularizing the sound bite 'there is more genetic variation within populations than between populations', which is deeply intertwined with Lewontin's legacy today" (p7).

iv) Influences that occurred around 1994 - For example, with the publication of "The Bell Curve" (Hernstein and Murray 1994), which argued that racial differences in IQ had a genetic basis, its "legion of critics" (Carlson and Harris 2022 p 11) quoted Lewontin.

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[12] Novembre (2022) argued that Edwards (as seen in Edwards 2022) was criticising "the implication taken from Lewontin's [1972] paper that one cannot do classification (including building phylogenies) using genetics" (p7) as a fallacy, not the point about differences between individuals and populations.

[13] A publication was defined as "influential" if it had over 1000 citations (Carlson and Harris 2022).

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7. SOCIAL COMMUNICATIVE COMPLEXITY

7.1. INTRODUCTION

Primates live in complex social groups with the advantages in terms of protection, and finding food, for example, but "both communication and cognitive skills are central in enabling primates to meet the challenges of group living" (Roberts et al 2022a p1).

The demands of group living have been suggested as key drivers in the evolution of the larger brain in primates. The "social complexity hypothesis" (or social complexity hypothesis for communicative complexity; SCHCC) (Freeberg et al 2012) proposed that "the demands of living in complex social groups leads to selection pressure for more complex social communication" (Roberts et al 2022a p2). More specifically, Roberts et al (2022b) argued that "complex communication, and the cognitive skills needed for such communication, may have evolved in both humans and primates to enable more efficient social bonding in conditions of social stress".

7.2. BRAIN EVOLUTION

The challenge of social life in a large, stable group is proposed as key to larger primate brain evolution. Schultz and Dunbar (2022) commented: "Ensuring co-ordinated group travel, mitigating the negative impacts of dominance inequalities, reducing aggression, promoting tolerance, increasing social bonds and forming alliances to increase competitive ability or influence in group-level decisions are cognitively demanding" (p2).

Schultz and Dunbar (2022) outlined the major theories to explain brain evolution:

i) To aid "political strategising" in groups ("the

Machiavellian hypothesis").

ii) To respond to the demands of maintaining social cohesion and stability in groups ("the Social Brain hypothesis").

iii) Large brains are energetically expensive and require large brains to plan foraging and find adequate food ("the Expensive Brain hypothesis").

iv) To cope with unpredictability of resources ("the Cognitive Buffering hypothesis").

Schultz and Dunbar (2022) collected data on social, reproductive and foraging behaviours of primates to see how they related to brain size. Factor analysis produced two behavioural groupings - "socio-ecological complexity" (including social learning, tool use, deception, and coalitions), and "reproductive co-operation" (including reproductive behaviours and caring for offspring). The former positively correlated with brain size measures like absolute brain volume, and neo-cortex volume, but not relative brain size. "Reproductive co-operation" was negatively correlated with measures like neo-cortex volume. Next the researchers introduced diet and foraging behaviours into their analysis.

A sequence appears along these lines: "living in large groups is a solution to the problem of occupying predator-risky habitats, with large brains the solution for the cognitive skills needed to maintain the cohesion and coherence of large groups, while enhanced foraging skills are necessary to maintain these calorie-hungry brains" (Schultz and Dunbar 2022 p9).

One problem is that studies use different measures of brain size, including absolute or relative, and/or different areas (eg: relative size of neo-cortex), and whether to control for body size. Another issue is group size, which is used as a proxy for sociability in many studies, whereas Schultz and Dunbar (2022) felt that group size was a proxy for demands like competitive and co-operation.

Overall, Schultz and Dunbar (2022) argued that "primate cognition has evolved along a continuum resulting in an increasingly flexible, domain-general capacity to solve a range of socio-ecological challenges culminating in a capacity for, and reliance on, innovation and social information use in the great apes and humans" (p1). Thus, it may be possible to combine all the major explanations of brain evolution above.

7.3. APE GESTURES

A case can be made that "understanding ape communication helps in our understanding of the origins of human language" argued Hobaiter et al (2022 p1). But how similar or different are ape gestures to human words? Hobaiter et al (2022) concentrated on three issues:

i) Flexibility and ambiguity - The ability to use the same gestures in different situations, and multiple gestures in the same context. This has been called the "means-end dissociation" (Hobaiter et al 2022).

Many words can be ambiguous (eg: "bark" and dog or tree), and the meaning is deduced from the physical or social context. This has also been observed with bonobo gestures (Graham et al 2020). These are "usually ambiguous in the sense that a single gesture may correspond to several intended meanings. But the goal a bonobo signaller intended was found to be disambiguated almost completely by taking into account two simple aspects of the situational context of production: the activity in which the signaller was engaged, and its age and sex relative to the target audience" (Hobaiter et al 2022 p3).

Hobaiter et al (2022) referred to their own data on chimpanzees in Uganda. For example, the "Big Hard Scratch" gesture can mean "Let's groom" or "Follow me". The context (ie: grooming or travelling) made clear the meaning to others.

ii) First- and second-order intentionality - There is plenty of evidence for ape gestures and first-order intentionality (ie: "the communicator recognises that there is a distinct recipient and aims to change that individual's behaviour in line with a goal they want to achieve"; Hobaiter et al 2022 p4), but second-order intentionality is more difficult to establish (ie: "when we use language, we recognise that the other individual is not only a distinct individual, but that they have their own knowledge, information, and goals"; Hobaiter et al 2022 p4).

Hobaiter et al (2022) admitted: "Intentions are not straightforward to explore; as properties of the underlying cognitive processes of the signaller, they are not something that observers have direct access to. Even with language, it is challenging to access intentions reliably in humans, and in other species we are even more dependent on interpreting patterns of observable behaviour" (p4).

Second-order intentionality may be evident as in studies of orangutans interacting with their human caretakers (eg: Cartmill and Byrne 2007). For example, the orangutans appeared to understand if the recipient had misunderstood a signal given. "In a request for a choice of food items, orangutans adjusted their subsequent gesturing depending on whether the recipient showed signs of incomplete understanding, by giving some but not all of the desirable food, or misunderstanding, by giving the undesirable food" (Hobaiter et al 2022 p5).

iii) Interactive exchanges - Words are used in interactions (ie: back and forth exchanges). There is some evidence for gestural exchanges in ape communication, but again study of the topic is hampered.

Hobaiter et al (2022) favoured an approach to non-human primate communication that focuses on function. They stated: "It may seem like a theoretical stretch at times to ask – how is an ape gesture like a human word, not in its shape or structure, but in its use? But we suggest that this is the approach required to move forward in asking the questions that are key to understanding why human language emerged. Rather than, 'What were the first words like?', we suggest asking, 'What were they used for?'" (Hobaiter et al 2022 p6).

Among chimpanzees, Roberts and Roberts (2022) found that "the use of intentional gestures facilities complex sociality during stress, by enabling understanding of intentionality". Stress was caused by the presence of a weakly bonded dominant individual nearby, and intentional gesturing was more common here.

Roberts and Roberts (2022) commented: "In this study, chimpanzees who received a higher rate of intentional gestures approached a wider range of social partners at a higher rate. Our findings suggest that intentional gestures mediate the transition from less complex to more complex sociality of primates by enabling understanding of intentionality".

The data in this research came from observations over nine months in 2006-2008 of six male and six female well-studied wild chimpanzees in Uganda.

Based on the same observations, Damjanovic et al (2022) found that gestures were more intentional than vocalisations or bimodal signals (combinations of gestures and vocalisations) based on population size, and social bonds. The researchers explained that their data suggested that gestural communication is underpinned by understanding of intentions, whereas vocalisations and bimodal signals are underpinned simply by understanding of behaviour, suggesting that the capacity for intentional signalling in gestures facilitates more complex social dynamics of wild chimpanzees. On this basis we conclude that language as a tool for social bonding has primarily evolved from gestures to facilitate group cohesion in large and complex social groups of hominins" (Damjanovic et al 2022).

"In species with fission-fusion dynamics, where the fluid composition of temporary sub-groups increases the uncertainty with which group members must manage their social relationships, vocal communication must be particularly flexible" (Briseno-Jaramilla et al 2022 p1). Briseno-Jaramilla et al (2022) showed this flexibility among black-handed spider monkeys.

The data were collected in Mexico in 2016-17 on a group of twenty free-living adults (a total of 548 hours of observations). Contact calls (given when individuals join (fusion) and leave (fission) sub-groups) were recorded. Details of the sub-groups were noted (eg: size; sex of members).

The rate of contact calls varied with the size and composition of the sub-group. This showed that "despite their limited repertoire, spider monkeys appear to be skilled at modifying call usage in different social contexts" (Briseno-Jaramilla et al 2022).

Fichtel and Kappeler (2022) commented that the majority of studies "considered only one communicative modality at a time. Investigating one communicative modality only can result in an over- or underestimation of communicative complexity because behavioural traits can be expressed in different modalities. In primates, for example, submission can be expressed either by visual or vocal signals" (p2). So, these researchers studied vocal, olfactory, and visual signals in lemurs in order to see if complexity increased with group size (as compared to other factors like habitat type). Data were collected from a variety of studies:

a) Vocal communication - Data were available on 29 species, and the average vocal repertoire size was ten calls. The repertoire size positively correlated with group size.

b) Olfactory communication - This can occur using saliva, urine or faeces, and different glands in the body produce different scent-marks. Data were found on 37 species, and the number of olfactory sources used increased with group size of a species. "Habitat type influenced the number of olfactory sources with species occurring in semi-open habitats exhibiting a higher number of olfactory sources" (Fichtel and Kappeler 2022 p4).

c) Visual communication - This occurs via body postures, gestures, and facial expressions, and data were available on ten species. The number of visual signals was linked to group size.

Overall, the analysis "revealed that variation in the vocal, olfactory and visual repertoire size of lemurs co-varied with group size, but not with the number of sympatric species with the same activity pattern or from the same genus, or environmental factors such as habitat type, except for the number of olfactory sources" (Fichtel and Kappeler 2022 pp5-6). This supported the social complexity hypothesis. The study was a phylogenetic analysis comparing the different species of lemur for communication behaviours and group size.

7.4. SOCIAL FEEDING

The chimpanzee social environment requires constant monitoring and it is thus stressful. This has been studied with systematic observations, and experiments, and by using observable behavioural markers (like gaze and vocalisation), and by physiological measures (eg: hormones). The latter involve invasive techniques, but do tend to give more objective measures of stress, while observable behaviours are easier to use, but depend on the accuracy of observers. Infra-red thermography, however, combines the best of both approaches. "More precisely, thermal imaging is a contact-free method that can assess the surface temperature of bodies through their wavelength and electromagnetic radiation" (Barrault et al 2022 p2). The upshot is a measure of the animal's level of arousal.

Barrault et al (2022) used this technique in a study of social feeding by chimpanzees (ie: feeding while in the company of others). "In chimpanzees, social feeding carries an elevated risk of aggression owing to resource competition. However, the perceived threat can vary dramatically from one feeding event to the next, in relation to changes in food patch size, monopolisability and desirability of food items, as well as nearby group members" (Barrault et al 2022 p2). Data were collected in Uganda with well-observed chimpanzee populations, which included knowledge of relationships between individuals. The researchers recorded fifty-five occasions of meat and 69 of fig social feeding involving nineteen adults.

Nasal temperature was used as the measure of arousal, and this varied depending on the food resource (meat or fig), audience size (number of males within ten metres), and audience composition (dominance and social partners). Nasal temperature is known to drop in situations perceived as competitive (ie: "reduced temperature in peripheral areas of animals' bodies (such as the nose, or the tail) owing to blood redirection away from areas vulnerable to significant blood loss in social situations likely to be perceived as stressful"; Barrault et al 2022 p5).

Nasal temperature was lower when feeding on meat, when more males were present, and more dominant individuals nearby. The presence of social (co-operative) partners buffered the impact with higher nasal temperatures. The researchers found "the opposite patterns of results for figs, with higher levels of nasal temperature for larger numbers of males present within 10 m, and for lower numbers of social partners present within 10 m. While figs are an important food resource, the small-sized Ficus sur (which accounted for the majority of observations of feeding on figs in our sample) represent a less competed-for and less monopolisable food resource than meat" (Barrault et al 2022 p5).

Overall, the study showed the complexity of the social situation for chimpanzees and the continual need to monitor others "to best prepare oneself for possible intrusion in one's own activities, including potential aggression" (Barrault et al 2022 p5).

The chimpanzees were habituated to human observers who used the thermal camera at an average distance of seven metres away.

7.5. SELECTIVE PRESSURES

Clark et al (2022) stated: "Given the importance of communication for forming and maintaining social bonds, failures in communicative signalling can be costly to the signaller and/or receiver. The potential for fitness costs means that there is selective pressure on communicative signals to be clear and unambiguous" (p1).

But selective pressures may vary between signals. There will be greater selective pressures on signals where communication failure is costly (eg: predator alarms; aggressive interactions).

Clark et al (2022) explored this idea in a study of facial expressions of crested macaques. Low-intensity conflict is common in their multi-male, multi-female groups. It was expected that communication would be "clearer" (ie: less risk of failure) for aggressive than affiliative interactions.

The data came from two well-studied social groups in Indonesia in 2018-19. Facial expressions were categorised, and the intensity scored from video recording. The intensity of facial expression was found to be significantly more intense in aggressive than affiliative interactions. This fitted with the view that "potentially more valuable or costly interactions should involve more exaggerated signals to reduce ambiguity" (Clark et al 2022 p8).

The scoring of facial expression intensity used easy to spot aspects (eg: upper lip raiser; lip corner pulls), but may have missed more subtle changes. Clark et al (2022) admitted that there are a number of ways to define and measure changes in facial expression intensity.

7.6. FLEXIBLE SIGNALLING

Emotional signals can be voluntarily controlled, and strategically displayed by humans, whereas they are assumed to be involuntary in non-humans. But Heesen et al (2022) found that distressed victims in bonobo post-conflict situations could control their emotional signals to influence the outcome of post-conflict events. The flexibility in signalling elicited consolation from others, and reduced the risk of renewed aggression.

The researchers studied sanctuary-living bonobos in the Democratic Republic of Congo, and the use of "baby-like" (paedo-morphic - ie: used by infants to elicit caregiving; eg: "pout face") signals by adults. These signals were greater with a larger audience (ie: more individuals who could console).

The voluntary control of these signals was also seen in the cessation of the signals after having been consoled.

In an evolutionary context, flexibility in emotional communication could facilitate more complex social interactions (Turner 1996). "Language then in turn might have further fuelled the expression of and ability to communicate complex emotions, especially in the face of co-operation, favouring enhancing emotional intelligence in modern humans" (Heesen et al 2022). Whether voluntary control over emotional expressions was present in the last common ancestor of humans and chimpanzees is open to debate. Heesen et al's (2022) findings suggested that it could have been.

7.7. MISCELLANEOUS

7.7.1. Complex Civilisations

The growth of complex civilisations in the past few thousand years has been attributed to agriculture, and the necessary co-operation to manage crop failure (Barras 2022).

An alternative view is that warfare was the driver. Using the "Seshat: Global History Database", Turchin et al (2022) compared different theories. Sashat contains data on the development of societies over the past 10 000 years in 35 natural geographic areas in ten parts of the world (Turchin et al 2022).

Turchin et al (2022) tested seventeen potential predictor variables of socio-political complexity using statistical modelling. Each variable was operationalised. For example, "social complexity" was operationalised in three ways, including the average number of levels of administrative, military, and settlement hierachies.

The variable of "military technology" (ie: new weapons and technology of warfare), and agriculture were significant predictors of social complexity. The two variables also interacted with each other. So, "increasing agricultural productivity is necessary but not sufficient to explain the growth in social complexity... Instead, external (inter-polity) conflict and key technical innovations associated with increasing warfare intensity appear to be the primary drivers of state growth, along with the growing population and resource base provided by increasing agricultural productivity" (Turchin et al 2022 p8).

"David Wengrow (at University College London) questions the idea that societies evolve from simple to complex in a way that can be measured objectively. Roderick Campbell (at New York University) also sees problems with the work, "not least with the starting assumption that complicated variables can be encoded unambiguously in a database" (Barras 2022 p14).

Graeber and Wengrow (2021) argued that "human history at the biggest and longest scales is not a linear process that moves inexorably toward an inevitable present. Nor is it reducible to a set of laws or reliably determinative regularities. Human history, they argue, is composed of a great many small and mutable histories; it is the product of many choices that have gone in a variety of directions" (Burke 2022 p118). For example, the development of agriculture was highly varied in different times and places, and, Graeber and Wengrow (2021) argued, "did not lead to an irreversible dependence upon farming and hence to urbanisation and centralisation" (Burke 2022 p119).

7.7.2. Emojis

Words undergo semantic change over time (eg: "gay" changed from meaning "bright" to "homosexual"). It is possible to analyse semantic change in emojis, as Robertson et al (2021) did on Twitter from 2012 to 2018.

The original context of an emoji was set as the original meaning ("anchor"), and the subsequent contexts were then compared to it. Three hundred and forty-eight of over 500 emojis were established with anchors in 2012.

Five distinct patterns of change were found:

- Cluster A - relatively show change in meaning from the anchor (n = 247) (eg: "skull" emoji [14]).
- Cluster B - mostly unchanged, except for an extreme temporary change in meaning (n = 47) (eg: "frog" emoji).
- Cluster C - similar to B, but the temporary change is less extreme (n = 9) (eg: "diamond ring" emoji).
- Cluster D - only changing at the end of the study period (n = 15) (eg: "maple leaf" emoji).
- Cluster E - changing from the start (n = 30) (eg: "house" emoji).

Contrary to expectations, the more concrete the meaning of the emoji, the more likely it was to change.

Robertson et al (2021) ended: "Most emoji remained stable, and only a small number of emoji appeared to

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[14] Information about potential meanings of emojis at https://emojipedia.org/.

undergo substantive semantic change in our period of analysis" (p8).

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8. GENETICS OF ADAPTATION AND EVOLUTION

8.1. GENETICS OF ADAPTATION

Kitano et al (2022) began: "One of the fundamental goals of evolutionary biology is to understand how organisms and ecosystems have evolved in the past and will respond to changing environments in the future. To this end, we need to know whether evolution proceeds in small steps or large leaps, how repeatable evolution is, and how constrained the evolutionary process is. Understanding the genetic basis of phenotypic diversification and speciation in natural populations is key to properly answering these questions" (p1).

While Perkins et al (2022) commented: "Identifying the general principles by which genotypes are converted into phenotypes remains a challenge in the post-genomic era. We still lack a predictive understanding of how genes shape interactions among cells and tissues in response to signalling and environmental cues, and hence how regulatory networks generate the phenotypic variation required for adaptive evolution" (p1). This has been called "the missing heritability problem" (Perkins et al 2022).

The variety of individuals/traits (phenotypic diversification) in a population can be studied in three main ways (Kitano et al 2022):

i) Quantitative genetic approaches - eg: "reaction norms" (ie: the range of phenotypes produced by a genotype depending on the environment).

ii) Genetic architecture - eg: genome-wide association studies (GWAS) identify particular genes (loci) in a population [15].

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[15] Common variants in the genome associated with disease can be uncovered by GWAS, but rare variants need very large datasets to spot them. Wang et al (2021) were able to find a number of these rare variants by analysing genetic data from the UK Biobank (nearly 270 000 UK participants of European ancestry and nearly 12 000 of non-European ancestry).

iii) Molecular mechanisms - the identification of exact genes and mutations that produce phenotypes.

8.1.1. Butterfly Example

Structural colours, as, for example, in butterflies are produced by the reflection of light from ultra-structures in the wings (Brien et al 2022). The Heliconius genus of butterflies is well studied, and structural colour has evolved multiple times (Brien et al 2022).

Brien et al (2022) used quantitative trait loci (QTL) mapping approach to identify genes involved in structural colours, and cross-breeding of iridescent and non-iridescent Heliconius species. Four phenotypes of the wings were measured in the offspring - blue colour, luminance (overall brightness of the wing span), ridge spacing, and cross-rib spacing.

Tens of thousands of genes were involved in wing development, but it was possible for the researchers to distinguish a small number of genes relevant to structural colours (Brien et al 2022).

8.1.2. Supergenes

The term "supergenes" (Darlington and Mather 1949) has been coined to describe "tightly linked sets of loci that are inherited together and control complex phenotypes" (Berdan et al 2022 p1). The set of alleles are inherited together, thus the term "supergene" [16].

Berdan et al (2022) explained: "The reduced recombination in the genomic region of the supergene splits the evolutionary trajectory of the region into at least two semi-independent branches allowing for distinct multi-trait phenotypes ('polymorphisms') to segregate within a single population or to be easily transmitted across species" (pp1-2).

Berdan et al (2022) highlighted some key issues about "supergenes", including:

i) How do supergenes facilitate adaptation? "While some empirical studies find evidence that the accumulation of mutations inside a supergene over time caused it to establish and persist ('gain' or 'accumulation'), others find that the supergene

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[16] Also called "co-adapted gene complexes" (Dobzhansky 1949).

captured a beneficial combination of locally adapted alleles when it originated ('capture')" (Berdan et al 2022 p3).

ii) Do supergenes repeatedly arise in evolution?

iii) "Many known supergenes are over 1 Million years old, begging the question of how these polymorphisms are maintained over large time scales in the face of drift and selection" (Berdan et al 2022 p4).

One possible answer is a form of "balancing selection" (ie: "sexually antagonistic selection"), "in which an allele that increases the fitness of males decreases the fitness of females, or vice versa" (Berdan et al 2022 p5).

8.1.3. Paradox of Stasis

Luke Harmon commented: "Many of the great mysteries in evolution are not why change occurs, but why it fails to occur" (quoted in Lawton 2022).

Over short time scales micro-evolutionary changes are abundant and rapid. "Yet these micro-evolutionary processes do not appear to accrue to influence inferred evolutionary rates in deep time... This apparent disparity in evolutionary rate across timescales is often referred to as the paradox of macro-evolutionary stasis, where 'stasis' is relative; observed rates of evolution in deep time are low relative to expectations from micro-evolutionary theory and data" (De Lisle et al 2021 p380).

There is evidence that "although evolution can be rapid for a handful of generations, this period of rapid change is followed by a protracted period of relatively slow evolution lasting for over one million years, prior to striking bursts of divergence in deeper time" (De Lisle et al 2021 p381). This suggests that "some process must constrain the accrual of phenotypic change within populations, as well as among closely related populations" (De Lisle et al 2021 p381). Data modelling by De Lisle et al (2021) found that extinction is a constraint.

8.2. PHENOTYPIC PLASTICITY

In 1914 Herman Nilsson-Ehle coined the term "phenotypic plasticity" to describe "the ability of an individual organism (or a single genotype) to produce multiple phenotypes in response to different environmental circumstances" (Pfennig 2022 p95). For example, Mexican spadefoot toad tadpoles tend to eat plankton and algae, but those who by chance eat a fairy shrimp, say, develop differently as carnivorous tadpoles (Pfennig 2022).

Plasticity allows change within generations, whereas evolution occurs between generations, and so "adaptive evolution is always at least one generation behind in responding to a rapidly changing environment" (Pfennig 2022 p96). Scheiner (eg: 1993) offered a series of conditions where high plasticity is an advantage, including the benefits of plasticity outweigh the costs, the environment is changing, no fixed trait is advantageous in all environmental circumstances, and individuals can assess the environment reliably (Pfennig 2022). A flexible trait can evolve to become fixed, and this is "genetic assimilation" (Pfennig 2022).

Plasticity can reduce the risk of a species going extinct in a changing environment, and "it could buy time until a population acquires new genetic variants - for example, by mating with members of another population or even another species - that enable it to adapt to a new environment" (Pfennig 2022 p98). This is the "buying time hypothesis" (Pfennig 2022). There is also "plasticity-led evolution" where genetic variation in a population goes unnoticed until environments change (Pfennig 2022).

But the idea that a parent can pass to its offspring any features it acquired during its lifetime was rejected in the nineteenth century as the "inheritance of acquired characteristics" (as proposed by Lamarck) (or called "trans-generational plasticity" today). However, increasing biological knowledge has shown that "biological information can be conveyed through various non-genetic factors that are not specified by DNA sequence, including factors induced by the environment through plasticity" (Pfennig 2022 p99) (eg: via DNA methylation where the environment can influence the biochemistry of gene expression and this "tag" can be passed to offspring).

West-Eberhard (2003) argued that plasticity is central to evolution. "Adaptive evolution requires heritable changes due to selection; selection requires phenotypic variation; and all phenotypic variation is generated by inputs from genes and environment. Therefore, plasticity - developmental responsiveness to environmental inputs - has long been part of standard evolutionary theory, even if it is not explicitly acknowledged as such" (Pfennig 2022 p100).

Phenotypic plasticity can be helpful in evolutionary theory in a number of ways, including (Pfennig 2022):

a) It can explain the origins of novel, complex features beyond mutations in genes.

b) It can help to explain rapid evolutionary change. "Beneficial mutations are scarce, they initially affect only a single individual and its immediate descendants, and therefore they are often slow to spread through a population. By contrast, features induced by the environment have characteristics that potentially hasten evolution" (Pfennig 2022 p101).

c) It can help explain "convergent evolution", where similar features evolve independently in very different species.

d) Practically, plasticity may help predict which species will "win" and "lose" with anthropogenic climate and environment change.

e) Help in understanding humans (eg: the brain; birth defects; disease).

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