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Dimensions of well-being

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Abstract

The notion of well-being is relative to the needs of organisms, both non-human and human. I argue that what we have learned about development, animal consciousness and ecological interrelations requires an evolution-informed extension of the way we think about well- and ill-being. Studies of epigenetic inheritance, mostly in animals, but also in humans, show that the effects of both stress and well-being go deeper ‘under the skin’ and extend further into the future than we thought. Studies of animals’ consciousness suggest that welfare considerations should be extended to many more animal species than most of us imagined. Technological innovations and ecological studies show that well-being depends critically, far more than we anticipated, on global social and environmental politics, social justice and the uses of technology.

Keywords

animal welfare, Anthropocene, environmental enrichment, epigenetic inheritance, evolution of consciousness, symbolic explosion

‘To know and not to act, is not to know’. (Wang-Ming)

Short introduction

My scientific interest in well-being stems from the two major research projects in which I have been engaged: my work with Marion Lamb on the different routes of transmission of information between generations, especially, but not solely, epigenetic inheritance, and my work with Simona Ginsburg on the evolutionary origins of consciousness. Evolutionary biology is the intellectual framework within which all my studies have been set. It informs my discussion of well-being. Since I am going to apply the term ‘well-being’ within this very broad framework, I will first clarify how I use it.

Well-being, welfare and quality of life are overlapping terms that are used interchangeably in the welfare literature (McMillan 2020). Quality of life and well-being *as* quality of life are terms applied by definition to living organisms, humans and animals, and in a much more restricted sense to non-

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sentient living organisms, mainly plants. Good welfare is identified with health, security, sustainable and functional social and ecological interactions and a good mental state (when mentality is assumed to exist), while bad welfare is associated with disease, deterioration and suffering. Well-being is also attributed to ecological systems (Grouzet et al. 2014) and to communities to which social welfare services are extended. Since this notion of welfare is a system property that cannot be described solely in terms of the welfare of the individuals comprising the system, I call it second-order well-being. The global ecological and social facets of such second-order well-being are necessary for the health and thriving of individual living organisms. Indeed, the concept of ‘ecosystem services’ – the outputs, conditions and processes of natural systems that directly or indirectly benefit (sentient) humans – is usually used within the context of sustainability, the long-term persistence and thriving of ecosystems that include and ‘serve’ humans, as opposed to short-term exploitation that leads to the ecosystems’ deterioration and destruction. Within the human, deeply symbolic sphere of life, well-being refers to highly variable, culturally constructed ways of life which satisfy the fundamental needs that humans share and that provide the space for the realization of human capabilities (Nussbaum 2011). The shared needs that I have in mind are those expounded by the Chilean ‘barefoot economist’ Max-Neef: subsistence, protection, affection, understanding, participation, idleness, creation, identity and freedom (Max-Neef et al. 1989).¹

In the following sections I discuss trans-generational effects of developmentally acquired physiological phenomena, the scope of animal consciousness and a few aspects of the human symbolic mode of being that point to global ecological-political issues. All have direct bearing on the entangled dimensions – physiological, social and moral – of well-being.

On being sick in four dimensions, on extended animal ethics and on global worries

In my 2005 book with Marion Lamb, *Evolution in 4 Dimensions*, we discussed the transmission of heritable genetic, epigenetic, behavioural and symbol-mediated information and its effects on evolution. Shortly afterwards, a young Brazilian immunologist, physician, actor and now also psychiatrist, Vitor Alexandre Pordeus da Silva, contacted me. We met in a café near the Tel-Aviv University campus. Vitor, then in his 20s, started talking with great enthusiasm about stress, the relation between the immune system and the brain, the complicated notion of mental disease, epigenetics, meaning-making and drama-therapy – all in the context of his work with patients in Rio de Janeiro, many of whom came from the poorest favelas. He said he wanted to write a book with me: ‘To be Sick in Four Dimensions’. I laughed and said it is a brilliant idea, but that he must write this book himself.

The book never materialized, but it was clear that Vitor and I had a lot of interests in common and should go on talking. I liked his passion, intelligence and love of theatre. I was already looking at epidemiological research that incorporated epigenetic factors and reviewed some of the literature on the epigenetic mechanisms and trans-generational effects of nutritional, toxicological and psychological stress in animals and humans (Jablonka 2004). Vitor and I have kept in touch ever since. I visited him in Rio in 2013, where he worked with psychiatric patients in Nise da Silveira’s mental health institution, (formerly Pedro II National Asylum). In 1946 Nise established the Museum of Images of the Unconscious in the Asylum, which now houses more than 350,000 pictures and sculptures by psychiatric patients. In 1956 she also founded outside the Tijuca community a cultural psychiatric day-clinic, the Casa das Palmeiras (Palms House). Nise was a Jungian who had worked with Jung for 2 years in Zürich and was inspired by the philosophy of Baruch Spinoza. She interpreted the mandala-like images drawn by her patients in Spinozian terms, as simultaneous expressions of patterns in the

mind and the body. She believed they were an expression of innate, archetypal, unconscious representations that become related to each individual's specific historical and cultural background (Pordeus 2017). Vitor followed in Nise's footsteps but used drama therapy, staging plays, both original and classical, that have been performed by the patients in the clinic grounds and all over Brazil, including during or after scientific meetings. Central to his concept of ill- and well-being are the social-cultural-political factors that undermine physical-mental well-being: poverty, drug abuse, physical abuse and social exploitation, ideologies such as neo-liberalism and extreme anthropocentrism.

My interest in mental trauma, and especially in the possible trans-generational effects of mental trauma, is strongly related to my private life-history. As a daughter of Holocaust survivors I had first-hand experience of the mental scars these traumas left, and so came to wonder whether the effects of psychological stress have trans-generational effects that go beyond the attachment-based, emotionally and behaviourally mediated effects of stress. I therefore read what was then available about the trans-generational effects of war, genocide and torture on both the victims and their descendants. The human molecular studies were few in number and inconclusive, but the animal studies did provide very strong evidence of the long-term, trans-generational effects of psychological trauma.

My concerns about the effects of trauma also had a more immediate political facet. I live in Israel, where chronic mental stress is imposed on both the Israeli population and more so on the Palestinians living in the occupied territories in the West Bank and Gaza. In summer 2014, when Israel relentlessly bombed Gaza, I felt helpless rage, and wrote, with Marion Lamb, a short commentary about the potential long-term effects of chronic warfare on the cognitive and emotional dispositions of the victims. We started our commentary with Philip Larkin's famous words from 'Be this the verse' (1971), 'Man hands on misery to man'. Larkin's poem focuses on the faults and miseries parents transmit to their offspring but we looked at the more general miseries brought about by wars and their traumas. We suggested that acute and persistent armed-conflicts affect, via epigenetic mechanisms, not only the physiology and psychology of the traumatized individuals but also that of their descendants – children, grandchildren, and possibly great-grandchildren – and hence may contribute to social and domestic conflicts in later generations. After summarizing the data available to us then, we outlined a research project that could test the hypothesis that these stresses have trans-generational deleterious effects, taking the effects of the continuing political conflict in the Middle East on the civilian populations in Gaza and southern Israel as our case study. The paper, which was submitted to the *Lancet*, was promptly and politely rejected by the editor, but I did lecture about the subject in various venues, with the vain hope of influencing policy makers.

A lot of the work on the trans-generational epigenetic effects of psychological trauma has been based on animal studies, mainly in rodents, which were assumed to have mental states. This assumption, however, has not stopped the execution of some awful experiments and the horrendous practices of mainstream meat industry on domestic animals. (I stopped eating meat after a meeting in Brussels on the food industry to which I was invited as an epigeneticist.)

My ethical concerns about the mental well-being of animals have been broadened by my second major research project, on the evolutionary origins of consciousness, with Simona Ginsburg. Since only sentient/conscious animals can be said to have *mental* well-being, the question 'who is conscious' is not ethically neutral (within most current ethical systems). If we have reasons to believe that non-human animals are sentient, our moral duties towards them are different from those we have if we have reasons to believe that they are non-sentient beings. To some extent the history of the welfare laws in countries like the UK reflects changes in reasoned beliefs about the distribution of sentience in animals. I have been associated for the last three years with the Foundations of Animal Sentience project led by Jonathan Birch (Birch et al. 2021), whose team prepared the scientific document on the basis of which extension of welfare laws in the UK to some invertebrate groups is now applied.

Finally, like most people today I am extremely worried about our species' extensive, short-sighted and brutal exploitation of resources affecting the present and future of all living beings. A notion of well-being must therefore be embedded within the global, political-ecological-technological discussions and concerns in this century. These must include a good understanding of humans' evolutionary history. I will point only to a very few aspects of these huge and urgent topics here. We ignore them at the peril of our planet and ourselves.

The long-term effects of ancestral adversity

The effects of traumatized parents and groups on future generations through attachment relations and collective memory constructions have been studied for decades and are topics of intense medical and social interest (van der Kolk 2015). These investigations focus on the long-term effects of stress in victims and on the altered physiological and psychological dispositions in their offspring or associates, rendering them more susceptible or more resilient to physical and mental illness. Such psychological studies preceded by many decades the molecular studies of the cellular mechanisms that underlie the long-term effects of trauma and chronic stress. The molecular studies have reinforced the conclusions of the traditional psychological investigations and uncovered novel ways in which the effects of trauma, and lifestyle more generally, can affect future generations. They have shown that history goes deeper 'under the skin' than conventional wisdom has assumed.

The molecular processes underlying the maintenance and transmission of changes that have been induced during ontogeny are known as epigenetic mechanisms. These mechanisms can maintain altered patterns of gene expression and modified cellular structures in both non-dividing cells, such as most mature neurons, and dividing cells, such as stem cells. When changes in information are transmitted vertically in cell lineages, or horizontally between cells in different lineages through migrating molecules (such as small RNAs), epigenetic inheritance is said to occur. Today most scholars are aware of epigenetics and of epigenetic inheritance. Epigenetic research is booming. Here I provide a very general outline of what these mechanisms are – the picture I want to paint does not require more. A detailed account of the mechanisms underlying epigenetic inheritance, the evolutionary effects of this mode of inheritance and the evolution by natural selection of this inheritance system is given in Jablonka and Lamb (2014, 2020).

The major types of epigenetic inheritance systems that have been recognized are:

- (i) self-sustaining loops involving, for example, positive feedback regulation of a gene's activity by its products, which cause the same state of gene activity to be reconstructed in daughter cells when the products are transmitted following cell division;
- (ii) structural templating, in which three-dimensional cellular variant structures (e.g. prions, some membranous structures) act as templates for the production of similar structures, which then become components of daughter cells;
- (iii) chromatin-marking, in which patterns of DNA modifications such as attached methyl group (CH₃), and modifications in the histone proteins around which DNA is wrapped are reconstructed during cell division;
- (iv) RNA-mediated systems, in which small or long regulatory RNA molecules interact with the mRNA or the DNA sequences to which they are complementary, altering patterns of cellular activity. The resulting cellular patterns are maintained and reconstructed through mechanisms including autocatalytic RNA loops, RNA-mediated chromatin marking and cell-to-cell transmission of regulatory RNAs within and between cell lineages.

These epigenetic mechanisms operate and interact in all cells, including cells of the nervous system. The chromatin-marking and RNA-mediated systems have been shown to be central to the nervous system's

development, and to animal and human behaviour and learning. These discoveries have led to the establishment of a new discipline, Behavioural Epigenetics, a field of study that investigates both the role of behaviour in shaping developmental epigenetic states and the role of epigenetic factors and mechanisms in shaping behaviour (Champagne and Rissman 2011). There are many sub-disciplines of epigenetics today, including for example cancer epigenetics, epigenetic epidemiology, environmental epigenetics, epigenetics of aging and psychiatric epigenetics. The latter studies the epigenetic correlates, some of which seem causal, as well as the epigenetic outcomes of mental disorders such as autism, bipolar disorder and schizophrenia (see e.g. Nestler et al. 2016).

In non-human mammals, stressful or traumatic experiences, such as social defeat, physical and emotional abuse or deprivation of early parental care, can have long-term, trans-generational effects on learning ability and mental health, mediated by molecular epigenetic mechanisms (Blaze and Roth 2013; McGowan 2013; for one of many recent reviews see Schiele, Gottschalk, and Domschke 2020). There are two main routes through which the effects in the parents can be transmitted to descendants. Epigenetic states can be constructed in the next generation somatically through the direct effects of altered parental characters on their offspring's development, as occurs, for example, in rats when poor maternal care reduces the offspring's ability to withstand stress, leads to poor maternal care in daughters and is thus perpetuated in the lineage (Szyf 2011).² Alternatively (and sometimes additionally) epigenetic changes in the parents can be transmitted through the gametes. For example, depression-like behaviour and anxiety in male mice that had been deprived of normal maternal care for a few hours each day during the first 2 weeks of their life is transmitted to their male offspring through modified RNA in their sperm (Franklin et al. 2010; Gapp et al. 2014). Similarly, the fearfulness of mice to a particular odorant that had been paired with a shock was found to be mediated by epigenetic mechanisms, and the fear reaction was transmitted through the males' sperm to their offspring, although the way that sperm methylation affects brain development is as yet unclear (Dias and Ressler 2014). Since gametic epigenetic transmission is investigated in these studies, paternal rather than maternal effects are the focus of research because sperm is a major (though not the sole) contribution of the male to the next generation.³ Females have multiple contributions, affecting the next generation not only by contributing gametic epigenetic marks or factors but also through the effects of the uterine conditions and maternal mental state (e.g. anxiety) during both pregnancy and early maternal care (e.g. Schmidt et al. 2018). Hence, maternally transmitted trans-generational effects require the study of gametic modifications as well as the study of effects that are mediated through multiple somatic reconstruction mechanisms (McGowan 2022). The number of studies showing adverse effects of psychological stress on offspring, grand-offspring, and great grand-offspring in mammals (mainly, but not exclusively, in rodents) is growing rapidly. The research on epigenetics inheritance is beyond a scope of a single review; for a large handbook on the topic see Tollefsbol (2019) and for a review focusing on environmental epigenetic epidemiology, mainly in humans, see Vaiserman, Lushchak, and Koliada (2021).

Generally, acute early psychological stress in humans is known to increase the risk of later psychological disorders (including major depression and suicidal behaviour), and in some cases this has been found to be correlated with altered molecular epigenetic states (Rahman and McGowan 2022). A well-known case is that of the effects of the acute 6 months' famine in the German-occupied part of the Netherlands during the winter of 1944–1945 that led to the death by starvation of about 22,000 people. Babies born to women who were exposed to the famine during the second trimester of pregnancy had increased incidence of obesity, type II diabetes and schizophrenia. Their rate of mortality was 10% higher than that of individuals who were not exposed to this adversity in utero. The epigenetic profile of the affected individuals, 67 years after the event, was also altered – their DNA methylation profile was different from that of unaffected people (Tobi et al. 2018).

Although the effects of starvation were the focus in the Dutch winter study, war-related starvation cannot be separated from psychological stresses. However, even when starvation is not involved, the effects of mental war stress have long-term, epigenetic effects. There are indications, for example, that war-related mental stress can affect descendants' disposition to develop trauma-related vulnerabilities. Children of Vietnam veterans had an increased risk of post-traumatic stress disorder (PTSD) of 5-fold for sons and 3-fold for daughters (O'Toole et al. 2017), the children of Holocaust survivors are more prone to develop PTSD than control groups (Yehuda et al. 2014; Yehuda and Lehrner 2018), and even the short stress of the September 11th attack seems to have led to behavioural changes in the children of the pregnant women who became acutely stressed while witnessing it (Sarapas et al. 2011). A genome-wide study of DNA methylation patterns in the sperm of trauma-exposed Vietnam veterans showed changes in DNA methylation in regions that have been previously implicated in PTSD, and some of these epigenetically altered sites were significantly associated with a reported history of a diagnosed mental health condition in the children of these veterans. Hence, unique sperm-specific DNA methylation patterns in trauma-exposed veterans are associated with PTSD and are correlated with vulnerability to mental disorders in their offspring (Mehta et al. 2019). However, there is also evidence that trauma-exposed veterans with PTSD have *less* accelerated epigenetic aging (based on Horvath's 'epigenetic clock') compared to combat trauma-exposed veterans that did not develop PTSD. Although this somewhat counter-intuitive association may be partly due to the extensive antidepressant use by PTSD patients, it may also point to a mechanism of compensatory resilience in these individuals (Verhoeven et al. 2018). We must be aware of limitations in our current understanding of the effect of mental stress on humans and the difficulty of teasing apart different aspects, such as the physiological stress of malnutrition and the stress of acute anxiety or mental pain, which often go together during war. Furthermore, the possible effects of stress on the development of resilience and tolerance to stress must be also considered.

In spite these caveats, the overall picture painted by studies of the trans-generational effects of severe mental stress is grim. It may lead to dire conclusions. It can lead to environmental determinism and to the substitution of genetic racial, gender or class stigma with a corresponding epigenetic stigma. Have we replaced genetic determinism with environmental, epigenetically-induced determinism? Worries are warranted (Meloni et al. 2022), but fortunately, just as epigenetic defects can be induced so can they be reversed – under the right conditions: a mere return to the unstressed default state is not sufficient. There are studies showing that effects of environmental enrichment (EE) on the epigenome of nerve cells in the mouse brain are profound and wide-spread (reviewed in Espeso-Gil et al. 2021).

Moreover, epigenetic patterns induced through EE that provides complex, safe and rich opportunities and challenges can affect not just the lucky individuals but also their descendants. There is also evidence pointing to the mechanisms underlying this effect: EE leads to enhancement of synaptic plasticity and cognition not only in the enriched mice but also in their offspring; this effect is mediated through sperm RNA (Benito et al. 2018). Furthermore, *transmitted effects of trauma* can be reversed by EE: Gapp and her colleagues (2016) showed that transmission of the effects of paternal trauma induced in baby male mice by unpredictable maternal separation during the first 14 days of their life can be prevented if, following the trauma, the traumatized mice are reared in an enriched environment. This allows them to have social partners, safe places to hide, opportunities for exercise and cognitive challenges. The behavioural effects of stress, which were accompanied by changes in DNA methylation in both brain and sperm, were reversed both in the traumatized fathers and in offspring that lived in the regular dull environment of the lab cage. Another study in mice shows that adverse effects that have both behavioural and epigenetic manifestations can be reversed by the extinction of the learned fear (Aoued et al. 2018). Although the number of studies on the trans-generational transmission of the positive epigenetic effects of EE is smaller than that published on the transmissible effects of adversity, the research on the effects of EE is rapidly growing.

There are many studies in humans which show that epigenetic changes in relevant genomic regions accompany beneficial changes in lifestyle, such as exercise, cognitive therapies and meditation. Furthermore, epigenetic changes have been found to be useful markers that predict the clinical response to psychotherapeutic interventions and of the chances of psychotherapy to alter, even reverse, epigenetic risk patterns (Roberts et al., 2015; Schiele, Gottschalk, and Domschke 2020). Studies that explore the gametic epigenetic effects of EE on the next generations in humans are still relatively few in number. However, what we do know is encouraging: trans-generational effects of EE that reverse adverse effects and transmit the effects of well-being to subsequent generations are likely to be found in our species even after chronic, multi-generational conditions of ongoing stress.

In spite of the limitations of the research on inherited epigenetic effects in humans and the caution that biologists must exercise – precisely because the authority of biological research is so great today⁴ – we cannot ignore the social, educational and political implications of the studies I described. The miseries that humans hand on to the next generation contribute to cumulative pathological effects, to self-sustaining vicious cycles of deprivation, war, psychosis and depression. However, as these studies also show, these effects can be reversed by the right kinds of lifestyle interventions. Beneficial effects can be transmitted to future generations. We did not need epigenetics to tell us that poverty, disease and brutal wars are bad, nor did we need epigenetic research to appreciate what a good human life is, although the aspects of well-being that are considered central and the ways well-being is realized are culturally dependent. What the epigenetic research does tell us is that the effects of misery and well-being (in the sense described by Max-Neef’s fulfillment or deprivation of fundamental human needs) have deeper roots and can radiate further into the future than we assumed. As I’ve stressed, these studies also tell us that we can reverse the pathologies we generate, and that our acts can promote the flourishing of future generations. Our moral obligations to our fellow humans are, we find, more far-reaching than we ever imagined.

To which animals should we extend moral considerations?

It is a common affair for mules to be imprisoned for years in the limitless night of the mines. ... Usually when brought to the surface, the mules tremble at the earth radiant in the sunshine. Later, they go almost mad with fantastic joy. The full splendor of the heavens, the grass, the trees, the breezes, breaks upon them suddenly. They caper and career with extravagant mulish glee. A miner told me of a mule that had spent some delirious months upon the surface after years of labor in the mines. (Crane 1894; <https://ehistory.osu.edu/exhibitions/gildedage/content/CraneDepths>)

Most people believe that they have a moral obligation to reduce suffering and to enhance well-being among fellow humans. This moral commitment is accepted with varying applicability by all human societies, with the scope of its applicability being largely determined by whether or not one considers these ‘other’ human beings – from different communities, sexes and ages – as moral patients like oneself. The views on the moral status of ‘others’, which have changed during human history and are differently understood in different cultures, are less universally extended to animals, mainly to animals on which our actions impinge. The animals which are at the centre of this moral concern are the domestic animals we consume and the wild animals whom we hunt, otherwise use and, more recently, those whose habitats we destroy.

The notion of animal welfare is intimately connected with the assumption that animals are sentient or conscious beings (I use the two terms interchangeably) that experience feelings which can be described in terms of joy and suffering. Marian Dawkins (1998) notes that ‘when people express a concern about animal welfare, it is conscious experience of suffering that worries them most’ (p. 306). Jeff Sebo asserts

that ‘you have moral status, i.e. you are a subject of moral concern, if and only if you are sentient, i.e. if and only if you are capable of phenomenally consciously experiencing pleasure or pain’ (Sebo 2018, 4).

The animal welfare literature offers three welfare notions, which emphasize different aspects of welfare (Fraser et al. 1997, Mellor and Stafford 2008 and McMillan 2020, discussed by Browning 2020):

- A functional and health-based notion of well-being that is agnostic about mentality and can be applied to any living organism. Plants or corals that are considered to be non-sentient can be nevertheless said to have good or bad welfare because these living organisms can be healthy or sick, flourish or deteriorate. However, when an organism has mental states, these states affect physical health and vice versa. Although we do not have the health data on the imprisoned mules, on the basis of what we know about the effect of sensory deprivation on neurological health in imprisoned humans, in Guantanamo Bay for example (Kaye 2009 and references therein), most people would infer that the imprisoned mules suffered from anxiety, hallucinations, memory malfunction and were more prone to various diseases.
- A notion of well-being based on ‘natural living’, which usually means the typical life of animals in the wild and the preferences they display in their typical, natural habitats. The mental aspect of well-being is not always explicit, although very often ‘preference’ is used in a context that implies that the animal has mental states. The habitat of the dark mines in which mules were imprisoned was clearly unnatural, and hence the mule can be considered to have had reduced welfare in this case (one has to remember, however, that many natural conditions are enormously stressful).
- A notion of well-being based on feelings. The subjective experiencing of the subject, its pleasures and displeasures, joys and sorrows, are central to this notion. The joy of the sensory-deprived mule when exposed to the spring field is an expression of its improved welfare.

Heather Browning (2020) convincingly argued that for animals that are assumed to have mental states, physical well-being, natural-living welfare and preferences provide instrumental conditions for the realization of subjectively experienced well-being and are important *only* with regard to their effects on subjective experiencing. Indeed, the Five Domains model, which is the one used by most welfare scientists with respect to domestic and wild animals (Mellor 2017; discussed in Browning 2020), highlights these domains: (1) nutrition; (2) physical environment, including comfort and safety; (3) health and (4) behavioural interactions with other animals. All these four domains feed into (5) subjective feelings, which determines the welfare of the animal.

The question is *which* animals are sentient and can be said to have mental welfare and so to be moral patients. This is a very loaded question. Opinions differ widely, spanning the whole spectrum from those who claim that only humans are sentient to those who assert that all living organisms are sentient. A fuzzy consensus, encompassing many scholars engaged in consciousness studies, is expressed by the 2012 Cambridge Declaration:

Convergent evidence indicates that non-human animals have the neuroanatomical, neurochemical, and neurophysiological substrates of conscious states along with the capacity to exhibit intentional behaviors. Consequently, the weight of evidence indicates that humans are not unique in possessing the neurological substrates that generate consciousness. Nonhuman animals, including all mammals and birds, and many other creatures, including octopuses, also possess these neurological substrates. <http://fcmconference.org/img/CambridgeDeclarationOnConsciousness.pdf>

Which creatures other than octopuses are included is not clear. Since I have my own opinion on the topic and have been working on it from an evolutionary perspective with Simona Ginsburg for nearly

two decades, I present our view and discuss its implications for the extension of welfare considerations to non-human animals. (For a detailed discussion see Ginsburg and Jablonka 2019; for an alternative view, attributing consciousness only to birds and mammals, see Humphrey 2022.)

Our evolutionary approach is inspired by the methodology that the Hungarian chemist Tibor Gánti has developed for the study of minimal life. Although there is no consensus about how life should be defined, there is a broad consensus around a list of capacities that are jointly sufficient for minimal life. Gánti listed these hallmarks of minimal life,⁵ built a model, the chemoton, which implements these capacities through functional and structural couplings, and identified an evolutionary marker of the transition to minimal life (Gánti 2003). An evolutionary transition marker is a property that when we find evidence of it we have evidence that the major evolutionary transition in which we are interested has been completed. The transition marker allows us to reverse-engineer to the system that enables it (Ginsburg and Jablonka 2015, 2019; Birch, Ginsburg, and Jablonka 2020, 2021). For the case of minimal life, the evolutionary transition marker is the capacity for unlimited (open-ended) heredity.

Following Gánti, we started with a characterization (*not* a definition) of minimal consciousness or minimal subjective experiencing. A being having the functionally overlapping capacities listed below would be considered as minimally conscious by most scholars:

- *Perceptual Binding/unification as well as differentiation*: e.g. see the apple as a composite whole, as red, round, smooth, but also able to discern different aspects, combine them and discriminate between different apples.
- *Global accessibility and broadcast*: the ability to bring together percepts memories, values, action-plans and broadcast the outcomes in order to execute actions, form beliefs, generalizations, etc.
- *Exploration and differential stabilization*: the ability for spontaneous and induced exploratory activity followed by selection; e.g. by exercising *attentional skills* enabling one to select objects of attention, switch attention, and maintain attention.
- *Intentionality (aboutness)*: the ability to form representations or mappings of body, world, action, value and their relations.
- *Integration over time*: having working memory, a specious present, an ability to experience duration.
- *Flexible evaluative capacity*: the ability to evaluate and prioritize categorized inputs, responses and predictors of valued actions according to their overall physiological effects in varied contexts.
- *Agency*, including the ability to control and predict environmental contingencies; possession of object-oriented spatial cognition that requires many degrees of freedom of movement and allows many motor-affordances leading to voluntary, goal-directed behaviour.
- *Registration of self/ other* and a stable perspective; a sense of body ownership; an ‘ego-centre’.

We have suggested that the evolutionary transition marker of minimal consciousness, which requires that all these capacities are in place, is unlimited associative learning (UAL): a domain-general, open-ended, generative, recursive and representational type of associative learning. It enables goal-directed behaviour that involves representation and recognition of predictive relations between sensory inputs, actions, outcomes and rewards.

Operationally, UAL requires that the animal is able to:

- (i) Discriminate among novel compound patterns of stimuli and actions and attribute differing values to them. For example: discriminate between perceptual patterns or between action-patterns, and learn about the adaptive value of new associations. The learned represented patterns are novel:

they are not reflex-eliciting, nor have they been learned in the past. This requires mapping, perceptual and action unification and global accessibility and broadcast.

- (ii) Learn about predictive cues or actions even if there is a time gap between the ‘neutral’ complex stimulus and the reinforcement (the reward or punishment). The formation of such representations requires working memory and temporal integration.
- (iii) Learn to flexibly alter the value of a learned pattern of activity following changes in action-outcome and outcome-value representations. Learn that action-outcomes and outcome-values can re-valued. For such learning to occur the reward or punishment value of a particular stimulus or a particular action cannot be fixed. There must be context-dependent evaluation and prioritization of action-representations from a point of view (a sense of self is needed) requiring evaluative flexibility.
- (iv) Manifests ‘second-order’ (cumulative) learning. Once the animal learns a new complex image or a new pattern of action, these patterns can become themselves associated with new compound patterns, allowing the building up chains of associative links, performing modality transfers, and generalizing. Cumulative learning requires modifiable, flexible perceptual unification and evaluative flexibility.

UAL representations instantiate all the capacities in the consensus list and get as close as one can get (from a third person perspective) to consciousness, which is always first person and private. UAL points to the function of consciousness. It enables reaching goals that are based on learned representations of composite perceptions, action-outcomes, motivations and past and present affects/values, all. In press from a point of view (Ginsburg and Jablonka 2019; Jablonka and Ginsburg 2022, 2023). This is in line with William James’ suggestion in 1890 that consciousness is ‘*a fighter for ends*, of which many, but for its presence, would not be ends at all’ (James 1890, 141, his emphasis); this goes along with Dickinson’s and Balleine’s view that ‘It is only with the evolution of intentional control of goal-directed action that there is a function for the feelings and affective reactions elicited by motivationally significant events, that of grounding the assignment of value to the outcomes of action in biologically relevant processes’ (Dickinson and Balleine 2000, 200).

The capacity for UAL is testable in extant organisms. A hundred and fifty years of studying animal learning suggests that *some* mollusks, *some* arthropods and *most* vertebrates⁶ have the capacity for UAL. (We have, meagre information about learning capacity in most other animal phyla, and within all phyla only a minority of species were tested.) UAL probably evolved independently in these 3 phyla and was probably lost in certain groups such as some parasitic arthropods. Since animals exhibiting UAL have dedicated brain structures that support the capacity for integration, action representation, memory for composites and prioritization of values, and since these structures can be identified in extant and (sometimes) fossil organisms, we can get an idea not only which additional animals have UAL, but also when UAL, and by implication minimal consciousness, first appeared. The fossil record suggests that two of the three animal groups that show the brain structures supporting UAL first appeared in the Cambrian, 542 MYA: the arthropods and vertebrates, and that 250 MYA later, UAL and the brain structures instantiating it appeared in the coleoid cephalopods (octopus, squid cuttlefish).

If one accepts this view, the animals belonging to these groups have to be considered as moral patients, and welfare-affect considerations, minimally the minimization of pain, should be applied to them. The recent document written by Birch et al. (2021), which offers partially overlapping criteria that are focused on the ability to experience pain, goes in this direction. According to this document and the act it is now based on it, welfare considerations, which at present are confined to vertebrates, should be extended to decapod crustaceans (an order of invertebrate animals of the crustacean subphylum containing around 15,000 species, including the true crabs, lobsters, crayfish, and true shrimps) and

to the cephalopods (a class of around 750 species in the mollusk phylum, including all species of octopus, squid, cuttlefish and nautilus). It is important to stress that we lack information about other animal groups, so all the current suggestions are open to changes. It should also be noted that if UAL rather than Birch's pain-focused list is chosen as a criterion of sentience, species from additional arthropods groups (such as the hymenoptera, which include bees, and the blattodea, which include cockroaches) should be included in the extended welfare bill.⁷

If UAL is accepted as a positive marker of sentience, it can tell us which biological organisms are sentient but it cannot tell us which are not sentient. Nevertheless, if an organism lacks most UAL capacities it is unlikely to be sentient in any sense we can recognize and understand. Organisms like bacteria, fungi and plants are unlikely to be sentient because there is no indication that they have anything like UAL and the sentience-indicating capacities that underlie it (Ginsburg and Jablonka 2020a). Similarly, ecosystems, institutions, groups and even super-organisms like termitaries are not sentient according to this view (although individual termites may well be sentient in some very limited sense).⁸ This does not mean that we have no moral obligations towards ecosystems and their non-sentient inhabitants. But the well-being of these systems, is, as I see it, second-order well-being, which depends both on their network structure which includes sentient beings, and on our symbolic, human, moral and aesthetic judgments.

Extended welfare and extended ethics

How our practices – at the personal, institutional and political level – need to change once we recognize the sentience of an increasing number of species is a hotly debated question and its discussion is beyond the scope of this paper. What is clear is that just as research on epigenetic inheritance has extended our moral duties, so do animal consciousness studies. They extend our first-order, welfare-based moral duties further than we thought into the animal realm. It is not enough for the science of welfare to recognize that many animals are sentient beings. It is obvious that the consciousness/sentience of a crab, a roach, an octopus, a dog and a human are different and that these differences have welfare implications. The social needs of these animals are very different. Only for the human animal is the denial of the right to access higher education (something the Taliban denies girls) devastating.

We clearly need qualifications. Birch, Schnell, and Clayton (2020) suggest that consciousness varies and each species has its own unique consciousness profile. They list five dimensions of consciousness:

- (i) *Perceptual richness*: the modality specific degree of perceptual discrimination that depends on the amount of content, fineness of discrimination, and categorization-levels of percepts;
- (ii) *Evaluative richness*: the varieties of positively and negatively valenced, motivating states associated with emotions and drives, which can have different levels of richness and fineness;
- (iii) *Integration at a time*: the unity of experience at any single moment, including the perceptual unity within and between modalities (a unimodal or multimodal gestalt rather than a perceptual mosaic) and perspectival unity or disunity (as in split-brain humans, and possibly octopuses);
- (iv) *Integration across time*: the ability to perceive continuous movement rather than snapshots, judge duration, realize when events happened and in what temporal sequence, and perform mental time travel into the past and the future;
- (v) *Self-consciousness*: The ability to register the distinction between self and the world, realizing the continuity of one's bodily and experiential self in time and space, and the ability for reflective consciousness.

These five consciousness dimensions correspond to some of the minimal consciousness-characterizing capacities that we suggested. We would like to add an additional dimension, which we believe is as fundamental, that of agency:

- (vi) *Agency*: How many action-affordances are there? How much motor, attentional and emotional control does the animal require and have over its actions and over the active choice of its conditions of life?

All these aspects of sentience and cognition are functionally related. But let us focus here on agency: we believe that already in minimally conscious animals will it be possible to recognize an inherent affective value of the need for agency, an emotion that Jaak Panksepp called the basic emotion of seeking, of what we recognize as curiosity (Panksepp 2011). It is based on the inherent and intrinsic variability-creating activity apparent at all levels of life, such as biochemical reactions within the cell (including mutations, and epimutations), exploratory behaviour of roots searching for water, the motor behaviour of all animals, the imaginative roaming of some animals and of humans. There is a fundamental difference between living, exploring organisms and human-designed abiotic machines: only living organisms that are made of ‘soft’, highly sensitive and responsive materials, which make their existence precarious, have intrinsic, open-ended plasticity that enable their survival. The variations generated by the flux of material and energy in living organisms are shaped through processes of differential stabilization that either return the system to a previous state of stability (homeostasis), or shift development onto alternative developmental trajectories that lead to a new stable state. All living beings can be described as dynamic networks with a default inner turbulent state, which is necessary for the generation of patterns and structures that can undergo selection-evolution at different levels (genetic and epigenetic in all organisms, behavioural in some and symbolic-cultural in humans). The prevalent ascription of the machine metaphor to non-sentient living organisms is deeply flawed and misleading.⁹ The difference between the living mode of being and the non-living mode of being is as great as that between non-sentient living beings and sentient ones (Ginsburg and Jablonka 2019, 2020*b*).

In neural organisms, especially animals with UAL, developmental plasticity is closely linked with learning, and in many animals it is linked with play (which involves learning). Animals never cease learning. The capacity for learning is itself positively selected: the more you can learn (anything and everything) the fitter you are because knowledge and fitness are related. Aristotle pointed this out long ago: ‘All men by nature desire to know. An indication of this is the delight we take in our senses; for even apart from their usefulness they are loved for themselves; and above all others the sense of sight. [...] The reason is that this, most of all the senses, makes us know and brings to light many differences between things’ (Aristotle 1984, *Metaphysics* 1.1-6). Nicholas Humphrey has likewise highlighted the pleasurable feeling of the animal’s active, exploring, living body, making the animal desire to care for its survival, do everything it takes to go on living (Humphrey 2011, 2022).

The positive emotive value of knowledge and agency is beginning to receive more attention in animal welfare science (Browning and Veit 2021). The need for agency is most apparent when animals are deprived of exploration and a sense of agency, as the case of imprisoned mules and imprisoned humans, and as many experimental studies on the humble rat show. But there is more to the need for agency than the need to play and be liberated from deprivation. Agency includes the need for control. Rats prefer signalled (preceded by a predicted cue) rather than un-signalled (and hence non-predictable) electric shocks, even when the predicted shock is four to nine times longer and two to three times stronger than the unpredictable shock (Badia, Culbertson, and Harsh 1973; these and similar experiments are discussed in Bassett and Buchanan-Smith 2007). The inherent affective value of the sense of control that often includes exploration is contextualized as a sense of agency and self-efficacy, and can take extremes forms in cultures like the Wari’ and the Jivaro (discussed by Taylor and Vilaça in this issue), overwhelming other fundamental needs such as the need for personal safety.

When thinking about animals' felt needs, and especially about human needs, what strikes us is the variability not only in how basic needs are satisfied, but also how very context-dependent and plastic is the feeling itself, the trade-offs among felt needs, and in humans, the dominant role of cultural construction. However, in spite of this variability it is possible to categorize types of consciousness in terms of levels. In addition to non-conscious living beings to whom we extend only physiological criteria of welfare (health, flourishing), we recognize three broad levels of consciousness that have implications for welfare:

- (i) *Minimally consciousness*, which is attributed, according to the UAL theory described in the previous section, to many animal species (vertebrates, several groups of arthropods and cephalopods). Welfare considerations based on this notion focus on the avoidance of pain, anxiety and fear, and the satisfaction of basic physiological, nutritional, social and ecological needs that contribute to health and flourishing.
- (ii) *Imaginative consciousness*, the experiencing of the virtual worlds of the past and the future, which is attributed to a smaller number of species such as ravens, elephants, dolphins and apes (Zacks, Ginsburg, and Jablonka 2022). For these animals, welfare considerations have to include the additional dimensions of emotionally-loaded episodic memories and future possibilities, which can lead, when the animals are traumatized, to mental pathologies such as PTSD (McMillan 2020).
- (iii) *Symbolic consciousness*, which as far as we know is specific to humans. Humans were aptly called the symbolic species by Ernst Cassirer (1944) and we (Ginsburg and Jablonka 2022) called the emergence of our species, which is guided by a new set of values and goals (the just, the good, the true, the beautiful), *the symbolic explosion*. Symbolic meanings are entangled with every aspect of human life, from what we eat to where we dwell. They enormously extend and modify the dimensions of human well- and ill-being. Art, science and philosophy, including moral philosophy,¹⁰ are the magnificent expressions of our unique symbolically-saturated life.

The symbolic explosion

Different aspects of human, symbolically embedded well- and ill-being are explored in this volume. I have used a developmental, cultural-evolutionary perspective to discuss the epigenetic underpinnings and long-term effects of some human experiences. This developmental approach can be seen as belonging to the ambitious cultural-historical psychology project that was outlined by Vygotsky and those of his school, who tried to unite the study of the human mind, brain and culture, and to explain human consciousness (del Río and Álvarez 2021). The study of words and linguistic abilities more generally were central to this project: Vygotsky believed that the peculiarities of child development, mental pathologies in children and adults and humans' potential for increased freedom can be best studied by using language-development and usage, although he recognized that meaning and sense-making cannot be fully captured by language. He was, however, aware that humans not only have the ability to enjoy new extended aspects of freedom and well-being but that they also pay a high price for their greatly expanded linguistically-embedded mentality (Zavershneva 2014). Indeed, the Diagnostic and Statistical Manual of Mental Disorders (DSM-5) gives some idea of the enormous, and, it seems, expanding, range of the mental ills of humans, many of which make sense only within the context of our idiosyncratic symbolic, linguistic and consciousness.¹¹

Language shapes human emotions, perceptions and memory. The therapeutic effects of psychoanalysis show the power of symbolic language to alter the neurophysiology of the brain. In a somewhat counter-intuitive way this may be related to the emotional and perceptual-memory price humans pay for

the gift of language. Language, which can be functionally characterized as a technology for the instruction of imagination (Dor 2015), cannot operate without considerable emotional control. We cannot understand, for example, the ubiquity and scope of the human lie, of politeness, and of the ability to listen without acting out exciting and horrible stories, without considering the emotional control interlocutors must exercise. We know that language affects perceptual memory: it leads to ‘verbal overshadowing’, in which events that are linguistically described lead to degraded perceptual memory of these very events. People who describe a burglar in words are, for example, less likely to identify him in a police lineup. It is plausible that encouraging traumatized humans to describe their experience in words, as in therapies such as psychoanalysis, schematizes their rich traumatic experiences and triggers the inhibition of emotions and the perceptual memory of the traumatic event, thus contributing to the positive effects of this ‘speech-therapy’ on mental health.¹² Language also has, of course, emotionally (controllable) exciting effects. It can lead to extended empathetic understanding of others, including sentient animals, but it can also lead to harmful manipulations of both emotions and memory, something that psychopaths and some politicians excel at.

The symbolic dimension also enables ill-being and well-being to be decoupled from some physiological measures. Handicapped people, for example, can live rich, enjoyable and meaningful life, while people who seem to have every material and physiological advantage may be suicidal. We clearly have to be pluralists about humans’ well-being, but we also have to acknowledge the basic needs that we share with other animals. The need for subsistence, social integration, agency and autonomy are basic at the individual and group levels in both humans and non-human social animals, even though individual humans can inhibit some of them in special circumstances (as do hermits who choose to live alone in the desert). Some needs – for education, for political participation, for intellectual and artistic immersion – are unique to us humans. In fact, the contents and the ways of satisfying even our most basic needs involve cultural construction.

Technology, which is one of the material expressions of our symbolic existence, extends the contents of social integration, autonomy and agency of our species far beyond what these needs mean for other tool-using animals. We are natural cyborgs (biological-technological hybrids), as Andy Clark (2004) put it. Since we began to manufacture complex material tools and develop new communication, memory and classification technologies, our mentality has become extended to accommodate the technologies we develop, which amplify and add to our senses, our actions, our emotions and the free play of our imagination (McCarty 2023). However, these technologies can also constrain our imagination and can even suppress certain aspects of emotions and cognition, making us increasingly dependent, even addicted to them.¹³

The machine–human interfaces that are developing at an exponential rate today are redefining our mental needs and self-image (Ishiguro 2020), reshaping our notion of well-being and may generate novel hybrid biological beings to whom we may need to extend moral considerations. The possibility of sentient robots, is, I think, further removed (Bronfman, Ginsburg, and Jablonka 2021), but the possibility cannot be ignored and it raises serious moral concerns (Metzinger 2013). The range and scope of well-being in our age is strongly bound with the technologies we develop. The great worry is that if their development continues to go unchecked these technologies will promote neo-feudalism by creating a symbolic space that will allow new means of subjugation and exploitation. Though we have little idea what future trans-human consciousness may be like, we can already see how these cooperative-technological endeavors may turn against us.

Second-order well-being

The trans-generational epigenetic aspects of well-being and the realization that the physical and mental well-being of non-human animals is a moral issue, depend on both local and global political decisions,

which so far have been relentlessly leading, in spite of mounting protests, to increasing ecological and moral devastation. The second-order well-being of our ecosystem is acknowledged to be the most urgent and burning issue (metaphorically and non-metaphorically) of the twenty-first century. Hundreds of millions of people on the planet suffer malnutrition, water, food and soil poisoning, climate extremities, physical and mental brutality, wars and many types of subjugation, which result from perverted use of planetary support systems that are treated as resources. In addition, billions of sentient, helpless animals are suffering unimaginably through the practices of mainstream food industries, and billions of others are dying as a result of unprecedented, human-made ecological habitat destruction. Our geological era which is shaped by the effects of the symbolic explosion is aptly called the 'Anthropocene'. There is a scientific consensus that we are in the midst of a sixth mass extinction leading to an ecological and social apocalypse (<https://ipbes.net/news/special-report>).

The physical and mental well-being of humans and animals is bound to the second-order welfare of the entire planet. There is a huge body of theoretical and empirical work that explores the interrelation of the parts or elements to the functioning of the global planetary system. The analysis of these interrelations, their history and the pathological power-dynamics that have led to the present dire state of the planet and its inhabitants is far beyond the scope of this paper. Kate Raworth's 'doughnut of social and planetary boundaries' (Raworth 2018 is a useful visual depiction of the interactions between human needs and planetary parameters that define spaces of well- and ill-being) (see <https://www.kateraworth.com/doughnut/>). I end with her simple and wise words:

'Humanity's 21st century challenge is to meet the needs of all within the means of the planet. In other words, to ensure that no one falls short on life's essentials (from food and housing to healthcare and political voice), while ensuring that collectively we do not overshoot our pressure on Earth's life-supporting systems, on which we fundamentally depend – such as a stable climate, fertile soils, and a protective ozone layer. The Doughnut of social and planetary boundaries is a playfully serious approach to framing that challenge, and it acts as a compass for human progress this century.

The environmental ceiling consists of nine planetary boundaries, as set out by Rockstrom et al.,¹⁴ beyond which lie unacceptable environmental degradation and potential tipping points in Earth systems. The twelve dimensions of the social foundation are derived from internationally agreed minimum social standards, as identified by the world's governments in the Sustainable Development Goals in 2015. Between social and planetary boundaries lies an environmentally safe and socially just space in which humanity can thrive'. (Kate Raworth Exploring doughnut economic <https://www.kateraworth.com/doughnut/>)

The doughnut image triggers some interrelated questions: How did the cultural evolution of humans lead to the current, ecologically and socially ever-increasing vicious circles? What currently prevents our symbolic cooperative species from entering into the just space in which humanity can thrive? How can we accommodate, in a global world, where people interact and mingle, different types of thriving that are based on different views and experiences of the world and of well-being? How can we escape the vicious circles that recruit our enormous cooperative potential to benefit only a thin layer of society and condemn most humans and other sentient beings to misery?

What is clear is that it is not lack of resources that is preventing solutions. The economical-political ideology that regards economic growth as an ultimate value is at the core of the problem. Strathern (this issue) discusses the valorization of life and the disastrous notion that identifies life itself with growth that is so prevalent that it seems self-evident. She presents an alternative notion, that of regeneration, which highlights perpetuation and sustainability and requires the coupling of individual, lineage and group life-cycles, where trade-offs, restrictions of growth, decline and death, are all inherent. This is an aspect of a

systems-view of the planetary system that resonates with notions of well-being that envisage humans as elements and nodes in a global web of life, and that needs to be developed within the framework of the global, human-dominated planetary system of the twenty-first century.

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Notes

1. See also https://en.wikipedia.org/wiki/Manfred_Max-Neef%27s_Fundamental_human_needs.
2. There are many additional, often interacting routes of this mode of transmission that do not involve modifications in the germ line. Marion Lamb and I called this mode of transmission ‘soma-to-soma transmission’ and it is also known as ‘intergenerational inheritance’ to distinguish it from transgenerational inheritance that does involve gametic modification (for reviews and discussion see Jablonka and Raz 2009; Perez and Lehner 2019). The transmission of the microbiome is one such route that is now receiving a lot of attention. In all cases transmission involves ontogenetically-reconstructed epigenetic modifications in the somatic cells of the receiver.
3. Other male contribution includes factors transmitted through the seminal fluid in the ejaculate. The contribution of these factors to the offspring phenotypes can be evaluated by using IVF (for a review see Evans et al. 2019).
4. I thank Marilyn Strathern for gently raising this concern.
5. The characterizing hallmarks of life according to Gánti are: maintenance of a boundary separating the entity from its environment; metabolism; dynamic persistence; information storage; regulation of the internal milieu; growth; reproduction; death. If we meet a being with these characteristics on another planet, most scientists would agree that it is alive.
6. Mollusks: a phylum that includes snails, slugs, octopuses; arthropods: a phylum that includes insects, crustaceans, spiders and myriapods; vertebrates: a phylum that includes fish, frogs, reptiles, birds and mammals.
7. I expect these groups will be included in the bill once the relevant pain-related aspects are investigated.
8. The level of cohesion and coordination in a termitary is amazing and has been described in compelling manner by Eugène Marais, in ‘The soul of the white ant’, which was first published in English in 1937. The level of cohesion of this superorganism may be described in cognitive terms (Turner 2011), though not in terms of sentience. I am grateful to Piers Vitebsky for suggesting that I read Marais’ book and address this question.
9. For detailed discussion of the machine metaphor see Nicholson (2013). Riskin (2016) discusses a living-like notion of machine.
10. Morality and virtue are symbolic notions, and a discussion of the origins of human morality within an evolutionary, cultural and historical context should be part of a comprehensive discussion of well-being. This subject has received massive scholarly attention. Unfortunately I cannot discuss it within the scope of this article.
11. The DSM categorizations are not without problems, as Hacking (1995) shows. It should be noted that many of the pathologies described in DSM-5 are shared by non-verbal humans and by some animals.
12. I am grateful to Aparecida Vilaça for leading, through a good question, to this suggestion.

13. The effects of current AI-based technologies on imagination and the sense of self and agency is a vast area of research and speculation, which goes beyond the scope of this paper. On internet addiction see: <https://web.archive.org/web/20220708213948/https://www.psychom.net/iadcriteria.html>.
14. Steffen et al. (2015); see also <https://stockholmresilience.org/research/planetary-boundaries.html> (27/8/23).

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