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In search for evolutionary roots of a mindful cognition: A Darwinian view on sustained intentional awareness

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ABSTRACT

The attention system underwent important evolutionary changes and specializations in the human genus. In fact, our outstanding social and technological complexity strictly depends on our attentional ability, which is sustained, intentional, and conscious. Attention, intention, and awareness are key features for what can be defined a *mindful cognition*, and we may wonder whether a specific combination of these cognitive traits may be the result of a natural selective process, or else an accidental by-product of mental complexity. In this article, basic concepts in evolutionary anthropology are reviewed, to consider whether positive, neutral, or negative selective forces might have influenced the evolution of a mindful cognitive ability. At present, all these alternatives are potentially supported by different kinds of evidence. Hybrid hypotheses, considering stabilizing mechanisms or distinct social roles and intra-specific variation, are also likely. An evolutionary approach to the cognitive abilities involved in attention and awareness can reveal potentialities, limitations, and drawbacks of our individual and collective natural behaviors, especially when dealing with the evolution of the human consciousness.

And crawling on the planet's face, some insects called "the human race", lost in time, and lost in space. And meaning.
(The Rocky Horror Picture Show)

1. Attention, awareness, and human evolution

Attention is the ability to sustain a cognitive process, independently from conflicting or competing stimuli (Rueda et al., 2023). In this sense, it is a limiting factor of all the other cognitive skills and, as such, we can suppose that it underwent profound changes through the course of human evolution (Bruner and Colom, 2022). Awareness, instead, is the conscious part of a perceptual or psychological experience, and it is strongly rooted into the self and the body (Blakemore and Frith, 2003). Although the relationships between attention and awareness are still to be clarified (mostly because of problems with general and consensual definitions), it is likely that they represent mutual processes that are necessary – albeit not necessarily sufficient– to consciousness[1] (Posner, 1994; Posner and Rothbart, 1998; Cohen et al., 2012). Awareness and attention are, indeed, key abilities to the evolution of personal, ecological, chronological, social, and abstract levels of consciousness (Leary and Buttermore, 2003). In modern humans, we may speculate that these skills were integrated with a powerful capacity of mental imaging, increasing the extension (range) and details (amount of information) of a personal storyline which is, eventually, the very foundation of self-perception in time and space (Bruner, 2023). Nonetheless, attention is a general term, useful to define a wider and more heterogeneous group of cognitive abilities, based on different cerebral regions and distinct neural networks. One of the most acknowledged and

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[1] Many of these terms and concepts, despite the vast literature devoted to their analysis, suffer from a lack of clear definitions, and disagreements on their actual meanings. This confusion is probably due their implicit complexity, but also to the fact that their mechanisms are the integrative result of many independent factors, generating blurred frontiers between causes and consequences, and between the different cognitive skills involved. In many Latin-derived languages, the same word or similar terms are used for *consciousness* and *awareness*, which introduces further conceptual and linguistic problems. Additionally, the same terms are also used when dealing with moral or ethical aspects, increasing the confusion in the use and common interpretation of these concepts. Beyond the conceptual and terminological problems associated with attention, awareness, and consciousness, we should also remind that this latter term is further intermingled with other concepts which, all too often, are employed without a proper definition, like "self" and "ego".

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accepted models recognizes at least three distinct attentional circuits, based on different patterns of connections and neurotransmitters (Petersen and Posner, 2012). A first network mainly deals with an alerting system, based on the *locus coeruleus* and its projections throughout the brain, with special involvement of the fronto-parietal cortex. A second network concerns attentional orientation and filtering, with a dorsal pathway (superior parietal lobule and frontal eye field) involved in top-down focus (active screening of specific stimuli) and a ventral pathway (temporo-parietal junction and the posterior regions of the inferior and middle frontal gyrus) involved in bottom-up responses (detection of disruptive stimuli of the environment). A third network, mainly based on fronto-parietal feedbacks, concerns executive functions. These three networks necessarily display reciprocal influences, although we must suppose that they can have undergone independent evolutionary changes.

Homo sapiens displays an outstanding degree of social and technological complexity, which can be achieved only thank to an enhanced attention system, most of all when dealing with top-down selection, focused attention, and executive functions (Bruner and Colom, 2022). Recently, I have proposed that, when compared with non-human primates (and probably with extinct hominids too), our attention is in fact sustained, intentional, and conscious (Bruner, 2024). *Sustained* means that we can maintain the focus of attention for more time, and more firmly. This probably involves endurance (the energy to maintain the effort), but most of all the ability to contrast internal and external distractors. *Intentional* refers to the fact that we can decide, at least to some degree, to turn on and turn off our attention system through volitional mechanisms. *Conscious* deals with the awareness of paying attention, a meta-cognitive aspect for which we know that we are in an attentive state or, conversely, that we have lost it. Indeed, such definitions should not be taken as a rigid and categorical scheme. These three qualities have mutual influences and common bases, and exert a reciprocal reinforcement. Neither should they be intended as discrete (presence/absence) skills because, in fact, they probably display an exceptional individual (within-species) variability. We cannot even be sure that these three qualities are a matter of exclusive (derived) human traits, or else part of cognitive networks shared with other primates (see Sherwood et al., 2008). Namely, it remains to be evaluated to what extent our sustained, intentional, and conscious attentional skills are a matter of enhanced (primitive) abilities or brand-new (derived) cognitive characters. Nonetheless, even if only by degree, the difference between humans and any other animal species is, in this sense, remarkable. There is little doubt that these three qualities and their degree of expression are mandatory to support the level of social and technological complexity of *Homo sapiens*, a species which ecological, cultural, and cognitive niches are embedded and dependent on attention-based mechanisms, like problem-solving, decision-making, or cultural transmission.

The attention system also takes part in the wider frame of the evolution of modern human working memory, in which a central executive system coordinates visual and phonological resources (Coolidge and Wynn, 2005). Selective attention probably represents a crucial factor behind the noticeable correspondence between working memory and general intelligence (Conway et al., 2003; Matzel and Kolata, 2010) and, as such, its enhancement is compulsory for consistent technological development. In this sense, humans have been "obligatory" tool users in the last 300,000 years (Shea, 2017), and we can suppose that this is the chronological frame in which technological and social extensions became integrative parts of our cognitive and evolutionary dynamics (Iriki and Taoka, 2012). Both modern humans and Neandertals concurrently evolved large brains and complex cultures in this same period, although the behavioral complexity displayed by our species is, from what we know at present, definitely outstanding when compared with any extinct species of our genus (Wynn et al., 2016). This may suggest that a substantial enhancement of the attention system is particularly associated with our own lineage (Bruner and Colom, 2022).

Evolution has, however, its drawbacks. Genes and biological traits are integrated into complex networks based on reciprocal influences, scaling rules, multiple linkages, and environmental effects. Within these networks, therefore, natural selection does not pick single features but instead blocks of features, constituting evolutionary "modules" that are transmitted according to their global effect on reproductive success. Therefore, in such "packages", some good features (the ones increasing fitness) can be associated with some bad ones (decreasing fitness), because of the overall good advantage of the assortment (antagonistic pleiotropy; see below). A second kind of drawback concerns the fact that the interests of evolution are not the same as those of the individuals. Evolution is focused at maintaining and distributing the species, while individuals should be more interested (at least since "suffering" has been introduced as a conscious and chronic element of our mental landscape) in a healthy, fulfilled, and satisfactory life. And the two kinds of interests can be, sometimes, in conflict. A third kind of drawback is associated with the fact that genetics and evolution do operate on a long chronology, while environmental changes can be faster, mostly when dealing with human culture. Therefore, a specific adaptation, advantageous in a given environmental condition, can rapidly become counterproductive. In this last case, the term "evolutionary mismatch" is often employed in psychology to describe a dissociation between our biological background and our current behavioral or environmental models (Li et al., 2018).

In the case of attention, it has been hypothesized that the extraordinary specialization of our frontoparietal system could have generated a sort of imbalance within the working memory system, in which the attentional capacity has not kept the pace with the visuospatial and phonological abilities (Bruner, 2023). Consequently, the attentional system is not able to cope with the extraordinary imaging and linguistic production, and this leads to an excess of mind wandering and rumination that can seriously affect the individual well-being (Killingsworth and Gilbert, 2010; Brewer et al., 2011). Accordingly, the *ontological anxiety* described worldwide in many philosophical traditions should be intended as a phylogenetic feature, rooted in the recent natural history of our lineage. Following the principles of human ethology (Eibl-Eibesfeldt, 1989), the human tendency to suffer for imagined occurrences (past and future projections, inner dialogues, ruminations, imagination, and so on) could be a *human universal*, namely a behavioral character that is independent by culture and hence associated with natural selection. It remains to be evaluated to what extent this is a condition only associated with our species or, even to a different degree, shared with other (extinct) species of the human genus. With a broad evolutionary scenario in mind, it is not even clear whether we can label this specific condition as "evolutionary unbalance", because we ignore whether or not such a condition decreases our fitness, although it might severely harm our mental welfare. Hence, we can only mention that this condition (the ontological stress of the human mind) might have an evolutionary foundation.

In a seminal book on the main principles of Buddhism, Robert Wright (2017) interpreted this ontological stress into the frame of natural selection, evidencing how the interests of evolution (i.e., the reproductive success and the distribution of the species) shaped a human cognition profoundly based on self-centered feelings, emotions, and reasoning, which, albeit increasing genes transmission, generated a deformed view of reality, triggering a constant state of psychological distress.

Wright developed his perspective within the secularized version of the Buddhist philosophy, because it gives special importance to a mindful integration of our cognitive abilities. Beyond a robust theoretical and conceptual background, Buddhism (like other philosophical and religious traditions) relies on meditation as a practice aimed at training and developing our cognitive resources. In very different cultural and historical contexts, meditation has been repeatedly proposed as a way to enhance the balance between attention and mind wandering. In fact, meditation is often associated with an iterative shift between the attention system and the default mode network, which is a crucial component of ruminations[2] (Hasenkamp and Barsalou, 2012; Hasenkamp et al., 2012). Part of the meditative practice is therefore a sort of training to improve our capacity to recognize a disconnection from the present (default mode) and move back our cognitive resources to perception and present moment (attention system). Of course, the default mode network is not only associated with negative mental states, but also with positive skills like creativity and daydreaming (Christoff et al., 2016; Vago and Zeidan, 2016). Therefore, the problem is not associated with those neural circuits or behaviors *per se*, but with their common excesses and disorders. Despite meditation is a heterogeneous term used to identify different kinds of practices and psychological approaches (Brandmeyer et al., 2019), attention is generally a common factor of most contemplative processes, as a set of skills trained and developed through different but complementary principles (e.g., Lutz et al., 2008; Dahl et al., 2015; Dahl et al., 2015; Raffone et al., 2019; Sumantry and Stewart, 2021). Also in terms of neural circuitry, meditation (in particular mindfulness meditation) involves many cerebral components associated with the attention network, like the precuneus, the cingulate cortex, the insula, and the prefrontal regions (Josipovic, 2014; Tang et al., 2015).

Within this cognitive frame, the term "mindfulness" is currently employed with different meanings, which are of course intermingled and based on reciprocal effects. In either personal or clinical context, it is generally defined as the awareness that arises through paying attention to the present moment, on purpose, and non-judgementally (Kabat-Zinn, 2013). It can refer to a practice (formal meditation), an attitude (a way to behave), or a skill (a psychological ability). This latter meaning is particularly relevant for considering possible evolutionary influences on these aspects, and it can labelled as "dispositional mindfulness", a cognitive trait that can be tentatively investigated in psychometrics (Rau and Williams 2016; Karl and Fischer 2022). Attention and intention are central elements of such a mindful ability, namely the capacity (or even the possibility) to attend the present moment and the current perceptual horizon, limiting random fluctuations associated with inner imaging and speech. Hence, a mindful ability strongly depends on the kit of attentional resources mentioned previously, namely focus endurance, intentionality, and awareness. At least, these aspects are mandatory (although not sufficient) to develop a mindful capacity.

Buddhist philosophy has traditionally investigated these skills under two distinct (and somehow opposite) assumptions: that these abilities need to be trained and developed, or else that they are part of a "natural" condition, that should be simply revealed and restored by a proper perceptual cleanse and psychological decontamination (see Williams and Kabat-Zinn, 2013). The difference is not subtle, and the term "natural" should be properly interpreted, mostly when dealing with evolution. As with most biological or cognitive traits, these features display their own variation within the human population and, beyond crucial environmental effects (Pepping and Duvenage 2016), they are hence susceptible, in the long run, of natural selection. We can therefore wonder whether the ability to express or cultivate a mindful cognition is the result of specific selective processes, or else the spontaneous by-product of complex neural mechanisms.

[2] The ontological nature of this state is peculiarly remarked by the fact that such a rambling agitation of the mind has been labelled as a "default" condition for our species.

2. Human evolution, and the principles of natural selection

Evolution is a fascinating history, and even more if we are dealing with our own chronicle, namely the story of *Homo sapiens*. As well as the individual *ego* is formed by a storyline of past and future projections, our evolutionary *ego* is nourished by our past and future phylogenetic narrative. From where did we come? Where are we going? And, as in the case of individual history, this evolutionary storyline often generates a narrative that is more based on expectations and emotions than on real facts. Indeed, although more than 150 years have passed since "The Origin of Species" of Charles Darwin, some basic concepts in evolution are still hard to integrate into the current human culture. For example, we are still used to interpreting every biological feature as an enhancement, an adaptation to ameliorate our capacities and conditions. However, such a generalization may be deeply misleading, and it requires at least four comments.

First, evolution is still frequently interpreted as linear (a straight line), gradual (through intermediate steps), and progressive (from less to more skillful species), although most theories in paleontology have rejected this perspective since the 70s (e.g., Gould, 1977). Instead, phylogeny is formed by many independent lineages, each with its own specializations and derived characters (Fig. 1). These independent lineages underwent selection primarily because of their changing environments, and environmental changes are neither directional nor gradual or progressive. Therefore, it is definitely a mistake to think that whatever living species (for example, a fish, a reptile, or a monkey) could be a sort of "ancestral form" when compared with another living one (for example, us). Unfortunately, chimpanzees are still often used as models for the biology or behavior of archaic human species, forgetting that all living apes are specialized taxa, independent from the human natural history (Bruner, 2019). After a phylogenetic split some 5–10 million years ago, humans kept on changing, and chimps too. And their changes reflected adaptations to an environment (rainforest) that was much different from the one in which we evolved (savannah). Of course, comparative approaches are always necessary to investigate evolution in terms of its process and products, but must be interpreted within wide taxonomic scenarios, acknowledging the limitations of their principles when applied to single species. Namely, for many biological and cognitive aspects, it is not very reliable to use chimps as a model for human evolution, the same way it would not be reliable to use humans to understand chimps' evolution. The same can be said for those situations in which two species, even if extinct, are not in an

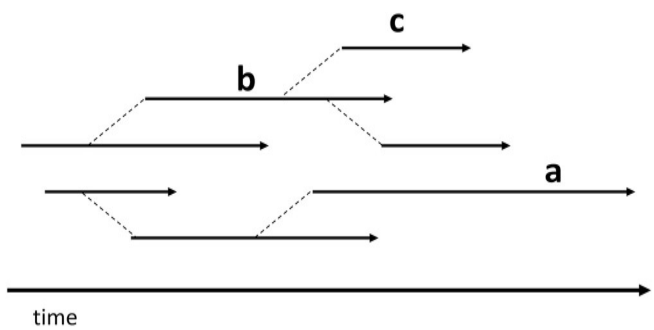

Fig. 1. The evolutionary process generates multiple independent lineages, each with a set of specialized and derived features. There is no reason to think that, even within a single zoological group, a given species (a) is an enhanced version of an older one (b) just because its origin is more recent. The two species will probably display shared and distinctive features, and each group will have a peculiar combination of traits, mixing quantitative (the degree of expression of a character) and qualitative (specific characters) differences. Also when there is a direct evolutionary linkage (b and c) it is unlikely that the latter species is simply a progressive version of its ancestor, and will probably be associated with a distinctive set of traits. Namely, in evolution, species are never "better" or "worst", but simply "different".

ancestral-descendant relationship, like for example modern humans and Neandertals.[3] Therefore, different lineages (like modern humans, chimps, and Neandertals) should not be interpreted as forming a sequence of increasing abilities, being "more" or "less" of the same pattern, but instead they must be interpreted, simply speaking, as "different". Something diverse. Different biology, different brain adaptations, different cognitive skills. It should be considered, hence, that other species (like chimps, Neandertals, or any other primate) might have evolved cognitive abilities that we have lost, or never developed (Bruner, 2024).

The second point deals with the transmission of characters. Superficially, it is generally given for granted that characters (genes, traits, behaviors, etc.) can be transmitted individually, one by one, and hence promoted or discarded by natural selection. However, this is not the case for most situations (e.g., Gould, 1966; Cheverud, 1996; Klingenberg, 2008; Fagny and Austerlitz, 2021). Genes are reciprocally integrated, and biological features (physiological or anatomical) are integrated too. Furthermore, a single gene can influence many features (*pleiotropy*), and a single feature can be influenced by many genes (*polygeny*). Then, there are scaling rules that constrain the architectonic structure of the biological elements, and, finally, we must consider the effect of the environment, that can channel a genetic configuration toward different outputs (*phenotypic plasticity*). Taking into account all these issues, it is too simplistic to conclude that a specific trait (the shape of the ear, some biochemical components, or a cognitive skill) is surely the result of a targeted selection. Instead, all those genes and traits are arranged in a modular way, so that what can be promoted or demoted by selection is a "package" of features, linked together by complicated and unknown networks or causes and consequences. Selection will hence promote or demote a group of features depending on their global effect on evolutionary success. In these evolutionary packages, there will be positive traits (features that enhance the evolutionary success) as well as neutral traits (features that have no impact on the evolutionary success) and even negative traits (features that are harmful for the species or for the individual, but are compensated by the advantages of the positive ones). Namely, if we observe a specific or derived trait in a species, there is no reason *a priori* to think that it is an adaptation for the sake of the species itself. Therefore, before stating that a specific trait is adaptive, we must wonder whether it is a primary change (selected by evolution for some functional reason) or else a secondary consequence of a wider selective array.

The third point concerns the meaning of the term "evolutionary success". In our culture and narrative, the term *success* may be influenced by factors that have little to do with evolution. In general, in evolutionary biology, the term is much simpler than our common and polysemous use: it refers only to reproductive success, namely the number of offspring. If a feature (or, better, a block of features) increases the number of offspring, it will be probably promoted. If it decreases the number of offspring, it will be probably demoted. If it does not affect the number of offspring, its promotion or demotion will largely depend on stochastic factors. Stochastic factors are anyway always determinant, as the term "probably" in the former sentences suggests. Therefore, before stating that a specific trait is adaptive, we must wonder whether it can increase the reproductive success.

The fourth issue concerns the level at which selection does operate. In general, according to most genetic theories, the key level is neither the individual nor the species, but the population, namely the most inclusive group sharing the same genetic pool and the same environment (that is, undergoing the same selective forces). Although this level is probably the effective one, multiple intermediate levels make this question more difficult to resolve. Primates are incredibly social, and humans are the most social primates ever (Dunbar, 2018). Therefore, the term "population" may have different ranges, mixing biogeographical and cultural boundaries. Accordingly, before stating that a specific trait is adaptive or beneficial, we must wonder whether we are referring to the individual, the social group, or the species. This is important not only because of the following phylogenetic considerations, but also (and more pragmatically) because these three levels might have different (or even conflictive) needs. Very often, the interests of evolution are not the same as the interests of an individual. The first prioritizes the reproductive success and the distribution of the species, in time and space. The latter, instead, should strive for quality of life and well-being. Sometimes the two criteria do match, sometimes it does not.

In sum, before tagging some traits as "adaptive", one should consider whether that feature has been directly selected or not, whether it may influence reproductive success, and whether a supposed effect would concern the individual, social, or species levels. Of course, there is no way to answer conclusively any of these questions. Most of the experiments necessary to validate most hypotheses would be unethical (isolating individuals or populations in controlled artificial conditions) and would require hundreds of generations to be performed. The alternative, however, is not a savage tagging of every biological or cognitive change as "adaptation". The aim should hence be a reasonable dose of speculation, informed and based on the available scientific evidence.

So, back to our initial issue: are mindful skills under the effect of natural selection, or are emerging by-products of a complex cognitive landscape?

3. A mindful mind: adaptation or by-product?

In the previous sections, I have mentioned chimpanzees and Neandertals as examples of species (living and extinct, respectively) that are not ancestral to modern humans, which evolution must be interpreted in terms of derived and independent lineages, and not through a biased perspective supposing linear, gradual, and progressive changes, which superficially align different taxa along a shared primitive-derived axis. The same can be of course applied to any living species, and to most fossil ones (Fig. 2). When dealing with human evolution, chimps are often used as comparison because they are expected to be the living species that is at least more similar to our hypothetical ancestral genus, *Australopithecus*. In contrast, Neandertals are of special interest in paleoanthropology because they share with early *H. sapiens* two relevant features: a similar brain size, and a similar technology.

Therefore, at the beginning of the Late Pleistocene (around 130,000 years ago), we had two large-brained hominids, whose evolution could have generated, at least on average, different cognitive patterns and, at last, different destinies. Neandertals have been hypothesized to lack an enhanced working memory when compared to *Homo sapiens*, and their technological complexity is compatible with procedures that could be instead largely based on long-term memory (Wynn and Coolidge, 2004). In addition, their visuospatial system might have been less specialized than ours (Bruner et al., 2018). Finally, as already mentioned, there are also several evidences associated with brain anatomy, social organization, and cultural complexity, suggesting that modern humans experienced a noticeable enhancement and specialization of the attention system (see Bruner and Gleeson, 2019; Bruner and Colom, 2022). These specializations in our lineage are probably not associated with the early

[3] There is a never-ending debate on the degree of hybridization between modern humans and Neandertals, incautiously developed on small samples and few genetic or anatomical features. This issue might be, anyway, not so crucial as expected. In fact, hybridization in Primates does naturally occur in affine species, or even in close related genera. With this in mind, "independent lineages" must be intended as a group of populations sharing, on an evolutionary chronological scale, the same genetic pool, selective pressure, adaptations, and phylogenetic destiny. A lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies is in fact the basic assumption under the *evolutionary species concept*, introduced by the paleontologist George Gaylord Simpson in the 50s of the past century.

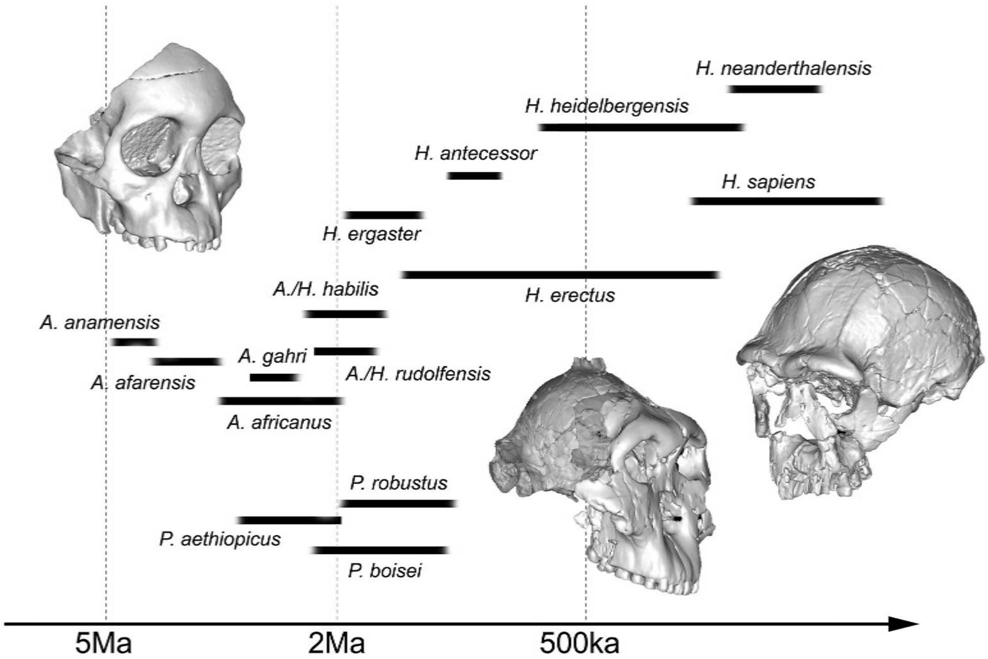

Fig. 2. The human genus (*Homo*; *H.*) probably evolved in Africa 2 million years ago (Ma), within an evolutionary radiation that includes the genera *Australopithecus* (*A.*) and *Paranthropus* (*P.*). Its most encephalized species evolved in the last 500,000 years (ka).

origin of our species, around 200–300 thousand years ago, but with a later stage, including the last 50–100 thousand years. At present, it is not possible to establish whether these changes have been gradual or punctuated, and to what extent they are the result of genetic factors or environmental feedback (Bruner and Iriki, 2016). Also the archaeological evidence does not support either linear or gradual changes in the early behavior of our species, but instead a mosaic of cultural patterns probably associated with the integration of multiple local components, influenced by diverse ecological conditions and selective forces (Scerri and Will, 2023).

Following principles employed in Mindfulness-Based Cognitive Therapy, John Teasdale (2022) proposed that human reasoning could depend on two cognitive subsystems, somehow in competition: holistic procedures relying on perceptual inputs (visual, acoustic, somatic), and conceptual procedures relying on words and images. Interestingly, words and images are the two main elements of both present-moment reasoning (working memory) and past/future projections (default mode network), and are settled on visual (images) and acoustic (words) information. Consequently, only the somatic inputs are (almost) exclusive of the holistic subsystem, and that is why body perception (proprioception, exteroception, enteroception, space and movements, etc.) is central to any mindfulness-based practice or protocol, generally aimed at decreasing the level of pain or emotional imbalance associated with an excess of ruminations. The conceptual system is supposed to be a recent evolutionary acquisition, and its hypertrophy might be responsible for stress and anxiety associated with excessive mind wandering. Speculatively, I have proposed that Neandertals and modern humans, the two more encephalized species that ever evolved, might have invested their reasoning ability in the two opposite directions: more holistic (based on perception and online information) for the former, more conceptual (based on words and images, and offline information) for the latter (Bruner, 2024).

If this were the case, the extinct human species would have been more protected against the stress and anxiety typical of modern humans. Nonetheless, this does not mean that they had a "more mindful" cognition, because, at the same time, they would have lacked, to a certain degree, the sustained, intentional, and aware ability of *Homo sapiens*. Their "present moment" attentional state could have been more unstable (more sensitive to bottom-up distractions), unintentional (more influenced by random conditions than by volition), and unaware (reduced meta-cognitive ability). Of course, such a difference might not have been a discrete one (different kinds of minds), but simply a matter of degree, with a certain overlapping when individual variation is considered. Our intraspecific variability for these traits is indeed remarkable too, so it remains to be evaluated to what extent possible cognitive differences between modern humans and extinct human species are a matter of diverse psychological models (different abilities or combinations of abilities) or just a matter of average values.

In sum, it appears that our modern cognition (enhanced conceptual subsystem, default mode network, attentional capacity) is at the same time the source of the ontological suffering but also mandatory for developing conscious and mindful responses. So the question is whether dispositional mindfulness (the ability to intentionally sustain an attentional awareness to the present moment without judgments) could have been positively selected for a functional effect on reproductive success, or is an unexpected emergent consequence of our peculiar cognitive development.

4. Mindful cognition and natural selection

Before considering different hypotheses on sustained intentional awareness and natural selection, we should introduce some basic terms in evolutionary biology. When a trait (or a package of traits) does increase the reproductive success, we can conventionally say that there is a *positive* selection for this trait, in the sense that individuals with those features are advantaged, in terms of evolutionary fitness. Consequently, the trait will progressively increase in frequency, as to increase evolutionary fitness. In contrast, when a trait does decrease the evolutionary success, we can say that there is a *negative* selection, in the sense that individuals with that trait will have a genetic or biological disadvantage for what concerns reproduction. Consequently, the trait will progressively decrease in frequency, as to increase evolutionary fitness. In both cases, the expression of that character in a given population will (gradually or rapidly) change, shifting the distribution in one direction (increasing the frequency of the trait) or another (decreasing the frequency of the trait). Both cases are examples of *directional selection*, namely a progressive shift of the expression and distribution of this feature. Of course, the terms "positive" and "negative" can introduce some conceptual misinterpretations. Firstly, because they are reciprocal processes: promoting a trait does mean, at the same time, demoting its opposite, or at least its absence. And vice-versa. So, any positive selection is also negative, if we invert the polarity of the features we are interested in. Secondly, because "positive" and "negative" are often linguistically embedded in moral or finalistic interpretations, which, in evolution, are definitely not applicable. Hence, these terms are just conventionally employed to stress whether natural selection does increment (positive selection) or decrement (negative selection) the expression of the trait under discussion. In the case of quantitative features (in our case, a cognitive skill), the terms are used to refer to those conditions in which selection increases (positive) or decreases (negative) the expression or complexity of the ability. In most cases, however, the expression of a trait will have an optimal value, and natural selection will demote those subjects with scarce or with excessive expression of the feature. This mechanism is generally termed *stabilizing selection*. In some way, we can say that stabilizing selection is an admixture of positive and negative selection.

Two more points merit attention. First, directional selection is likely to act in very specific conditions, for example when a mutation suddenly changes the genetic landscape of a population, or when the environment experiences a consistent change, with a subsequent modification of the selective rules. Probably, most directional changes do approach, sooner or later, optimal values, fading into a stabilizing dynamic. Second, it is once more worth remembering that the Buddhist concept of impermanence does also apply to ecology and evolution: advantages and disadvantages always depend on the context, a context that continuously change in time and that can be different for different species or populations.

With all these premises in mind, if we want to investigate the relationships between a mindful cognition and selective forces, we should consider all the alternatives, and, at present, I propose at least five possible scenarios, associated with the main traditional schemes of directional selection (Fig. 3).

Hypothesis 1. positive selection

This hypothesis posits that the abilities to develop a mindful cognition (namely an intentional and detached awareness of the present moment) are the result of a targeted evolutionary selection. The advantages of a mindful attitude are well known in the literature, prompting biological (hormones, neurotransmitters, metabolism, etc.) and psychological (decreased suffering, emotional stability, resistance and resilience, etc.) well-being (e.g. Brown and Ryan, 2003; Grossman et al., 2004; Davis and Hayes, 2011; Zeidan and Vago, 2016). However, to deal with an evolutionary perspective, these advantages must improve reproductive success, namely the number of offspring. In this case, hence, the hypothesis posits that having a mindful attitude would provide a reproductive advantage. Such reproductive advantage can be the result, for example, of better health conditions (psychological stability, acceptance, mental resilience, etc.) or social/technical achievements associated with those cognitive skills (for example, as result of open-mindedness and creativity). Furthermore, it is also reasonable to think that, once the conceptual mode of reasoning was evolutionarily enhanced, some amount of mindful ability could be necessary to limit its drawbacks (excess of mind wandering and self-referential processing). A mindful capacity would be hence required to downgrade the amount of ruminations, at least to a functional degree, able to optimize the reproductive potential by preventing an excess of anxiety and psychological distress. Overall, we can probably say that the hypothesis of a positive selection is logical, although the precise reproductive advantage may be not sufficiently clear.

Hypothesis 2. neutral selection

This hypothesis interprets mindful cognitive abilities as a by-product of a complex cognitive system, with no effect on reproductive success. There are some disagreements on the magnitude of neutral selection on a molecular scale (see Jensen et al., 2018), but it is reasonable to think that not every change in some biological character has a direct influence on reproductive success. In this case, our enhanced cognitive system could have triggered emergent properties that enable high levels of self-awareness and intentional capacity, although this does not

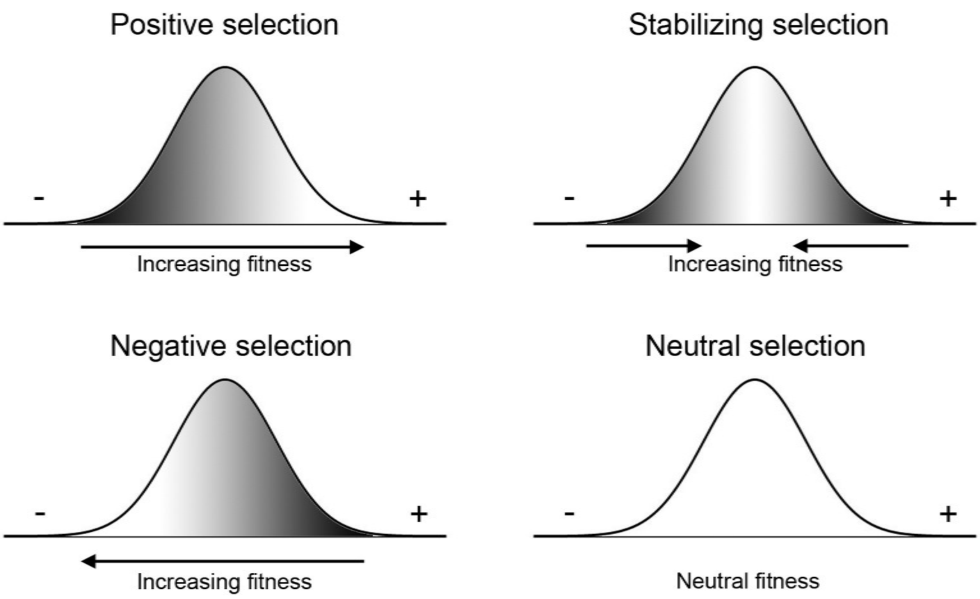

Fig. 3. Natural selection can promote (positive selection), balance (stabilizing selection), or demote (negative selection) the expression of a given trait. Positive and negative patterns are complementary examples of directional selection, in which having a stronger (+) or weaker (−) expression of a genetic or biological trait can influence the reproductive success of an individual, population, or species. Accordingly, the selective process will generate an evolutionary shift in the expression of this trait, increasing fitness. "Positive" and "negative", in this sense, refer to the promotion or demotion of a feature because of its effects on reproduction, and must not intended in terms of "good" and "bad" selective forces. In some cases, the trait has no effect on reproduction (neutral selection). We can consider these different possibilities for any biological or cognitive feature, including specific aspects of attention, awareness, and dispositional mindfulness.

necessarily involve higher reproduction rates. This hypothesis might be supported by the fact that similar meditation practices have been re-invented and re-described multiple times in several societies to respond to the ontological suffering, but never firmly established in any historical cultural context. Meditation, as practice, is designed to improve a mindful cognition, but it is also developed through a mindful cognition. Consequently, the accessibility to the practice probably requires a given degree of intentional and sustained awareness, namely the determination to prompt self-development, and the ability to engage an attentional and metacognitive mental state. It is hence reasonable that the establishment of such practice as "collective habit" (or, conversely, the failure in becoming a consistent element of that culture) would depend on the number of subjects, in a population, that can be able to trigger such cognitive engagement. Instead, contemplative approaches, although efficient, have always been developed and integrated by a restricted percentage of the social group, sporadically becoming "occasional" in some cultures, but never "habitual" or "constitutive" of a particular historical frame. Apparently, the biological and psychological success of the meditative practices is not sufficient to guarantee their cultural spreading to the whole population, suggesting that the contribution of a mindful attitude to fitness (genetic success) might be null or negligible, or even constrained by cognitive limitations for those attentional and intentional abilities. Interestingly, dispositional mindfulness is, as far as we know, not associated with specific personality factors or with standard cognitive skills (e.g., Hanley, 2016; Rau and Williams 2016). This might suggest that what we call "a mindful ability" is a combination of cognitive features, and not a specific variable of the cognitive landscape. Namely, some crucial aspects of intentional awareness can be the result of an admixture of independent traits, whose expression does not depend on their enhancement, but on their proper integration. In general, natural selection has some difficulties in operating with such multifactorial characters, precisely because they are the result of multiple influences and random factors that can be hardly channeled through a directional shift. Inter-individual cognitive differences are frequently based on distinct combinations of traits, they can be the result of different mechanisms, and they can rely on diverse biological backgrounds (Kanai and Rees, 2011). A natural selection for these features is therefore hard to accomplish, because of the unpredictable (or even random) hereditary schemes. All these aspects indeed add strength to the hypothesis of neutral selection.

Hypothesis 3. negative selection

This hypothesis considers the possibility that mindful cognitive skills can decrease reproductive success. Accordingly, such ability (maybe an emergent property of a complex cognitive system) is counter-selected by evolution. The sort of "failure" in the diffusion of the meditation practices described in Hypothesis 2 can also support this third hypothesis, which may explain the limited spreading of the contemplative approaches, when compared to other human habits and attitudes. In evolutionary psychology, a classical explanation of human ontological suffering suggests that a negative emotional attitude (worries, doubts, apprehensions, etc.) can increase survival in a dangerous environment (predation, toxic elements, physical risks, etc.). I would probably add two further factors. First, in a social system in which physical competition is essential (aggression, mating, nutritional resources, etc.), emotional distress and reactive behaviors can add to reproductive success. In contrast, a mindful attitude can reduce the tendency to emotion-based compulsory competition. Second, reproduction is probably the stronger evolutionary impulse of every living animal, including humans. The reproductive instinctual desire has an obsessive and compulsive nature supported by a large set of physiological factors, that cannot be demoted even in those situations in which resources are limited, generating remarkable individual anguish or, at the species level, outstanding problems of overpopulation. It can be hence speculated that emotional imbalance (negative feelings and psychological stress) can promote the search for satisfaction in biological (instinctual) rewards, which includes not only reproduction itself but also the associated social recognition. If this is the case, a mindless mind could be associated with increased reproduction. As a whole, these considerations suggest that also this hypothesis is definitely reasonable, and merits further attention.

Hypothesis 4. stabilizing selection

This hypothesis posits that a mindful ability can increase evolutionary fitness only within a specific functional range. From one side, intentional awareness can increase reproductive success for the reasons mentioned in Hypothesis 1. Nonetheless, at the same time, an excess of intentional awareness can also demote the reproduction rate, as mentioned in Hypothesis 3. Evolution would have therefore favored those individuals with a "given amount" of dispositional mindfulness, stabilizing this figure on a specific mean value and distribution. In this case, selection reduces the tails of the distribution, generating fluctuations around an optimal value. This value can probably vary depending upon the environmental and cultural context, so it may be species-specific or even population-specific or culture-specific.

Hypothesis 5. group (proportional) selection

As already mentioned, primate evolution is strongly based on group selection and social structure (Dunbar, 2012, 2018) and, accordingly, the group reproductive success is probably more relevant than the individual reproductive success. This means that some traits can be selected for the advantage of the whole group, and not according to the reproductive consequences for a specific subject. In this case, therefore, the hypothesis does not concern the reproductive success of the individuals, but of the whole group that, in hominid evolution, can be represented by a hunter-gatherer society (Lee, 2018). A population advantage is in fact particularly interesting taking into account that a cooperative or distributed cognition (Dunne, 2018) can enhance the ecological and economic success of a social system. In this case, the group would benefit from having a given percentage of "mindful individuals" who, independently from their specific reproductive rate, can enhance the reproductive success of the community. Namely, mindful cognitive traits may be advantageous when expressed, to a certain degree, only in a minor percentage of the population. A sort of stabilizing selection would then act not on the character *per se*, but on the percentage of individuals expressing that trait (or a given degree of expression of that trait). In this case, a mindful approach to life does not affect individual reproduction (or it can even be counterproductive, in this sense – see Hypothesis 3), but enhances the group's success. This effect can be associated with the emotional or intellectual contribution of these more mindful individuals, or even to their cultural and technological influence. These individuals can have a special social role (leaders, shamans, etc.; Winkelman, 2002; Singh, 2018), or else be apparently silent elements of the social texture. The reasonability of this hypothesis is motivating, and it opens to many further speculations and research perspectives. The "optimal values" of such parameters should be in fact evaluated, investigating the percentage of individuals, the degree (or range) of differences, and, most of all, the social consequences of such distribution. It must be also taken into account that these "optimal values" are likely to vary depending on environmental and historical factors. Finally, we may wonder whether these parameters are able to adjust in accordance with cultural changes, or have underlying constraints that may generate conflict with specific cultural conditions.

4.1. *Testing hypotheses on the evolution of a mindful cognition*

The hypotheses above are helpful to remind that, while some aspects of a mindful cognition can improve the reproductive success, others can be, in this sense, detrimental. Among the former, there is an increase in well-being and psychological stability, and possibly also in the ability to analyze relationships and contexts, a more open reasoning, and creativity. Among the latter, we can include a possible decrease in danger alert, competition for resources, and emotional reactivity. What is important to take in mind is that, in terms of evolution, “good” or “bad” characters do not refer to the advantage for the individual (or group) comfort or satisfaction, but to the advantage for the individual (or group) reproductive success (that is, the number of offspring).

Nonetheless, beyond the conceptual message, these hypotheses can also be useful to consider whether some of the aspects involved could tentatively be tested through quantitative or experimental approaches. For most of those cases, for example, we could test whether individuals who are more mindful display higher or lower reproductive success. This should be tested for different kinds of cultures, although hunter-gatherer societies would be probably more informative, in this sense. In fact, despite modern humans are characterized by an intrinsic ecological plasticity (Roberts and Stewart, 2018), hunter-gathers and foragers still represent the most reasonable model to investigate many aspects of the social and ecological organization of the human genus (Marlowe, 2005; Pontzer and Wood, 2021). The group hypothesis (Hypothesis 5), albeit probably more interesting than the others, is much more difficult to test, dealing with the reproductive success of entire groups, and not of single individuals. In all cases, such paradigms must be necessarily founded on intra-specific variation, which is indeed the rough material of selection and evolution and, in social animals, it is also the target of group selection (Dunbar, 2012; Dunbar and Shultz, 2017).

Beyond scoring dispositional mindfulness, we should also take into consideration some of its key components, namely the ability to sustain a state of mind that is intentional, aware of the present moment, and non-judgmental. These skills are intimately associated with those cognitive features that I proposed as particularly derived in modern humans, and that are the foundation of intentional, sustained, and conscious attentional management.

Most of these cognitive variables (including a mindful ability; Baer, 2019) are difficult to test and quantify, and there are many debates on the actual possibility to score them properly. The need to work with very different cultures adds further problems and limitations to this challenge. Nonetheless, although concluding results may be difficult to achieve, associating psychometrics and reproductive success can help to localize major selective factors or, in contrast, to reject some of those alternatives.

Most of these surveys should concern modern human populations, although additional data can be integrated from other living (apes) and extinct (fossils) species. In fact, taking into account the complexity of these topics, evolutionary theories and hypotheses should be necessarily grounded on multiple and independent source of information. In extinct human species (paleontological and archaeological records), the aim should be looking for whatever sort of cultural, technological, or behavioral discontinuity able to reveal changes in the combination or degree of expression of those cognitive skills. Of course, both evolutionary psychology and cognitive archaeology share a common limitation: the difficulty in separating the influence of gene selection from the influence of cultural channeling (Mesoudi, 2016). These two factors may exert independent effects on the evolutionary shifts but, at the same time, are intimately connected by reciprocal feedback and constraints. Furthermore, the cultural influence is more sensitive to random or local fluctuations, introducing mosaic intraspecific variations whose adaptive role can be difficult to reveal when talking about “species”. This limitation suggests further caution when trying to explain the observed (or hypothetical) differences in terms of causal mechanisms.

Beyond their actual testability, these five hypotheses have nonetheless a wider and more general aim: to remind us that simplistic interpretations concerning the evolution of attention (and in particular of a mindful attentional ability) can be ambiguous and confusing. Statements presenting these cognitive skills as “natural” or as the results of a general progressive enhancement do not fit a proper evolutionary approach, and can be profoundly misleading. In fact, as evidenced by the scenario proposed by Wright (2017), the “natural condition” (i.e., shaped by natural selection) can be precisely the opposite: a low-attentional, continuously judging, and scarcely aware state of mind. Within the Buddhist tradition, there is a debate on whether such qualities must be trained or else are part of an original state that must be simply cleaned by harmful influences (Williams and Kabat-Zinn, 2013). Although the more recent schools point at the latter option, an evolutionary approach is, at best, less optimistic. In the last fifty years, Buddhism encouraged a profound collaboration with neuroscience (Varela et al., 2017). It remains to be evaluated whether it can also interact with evolutionary anthropology, depending on possible conflicts between the interpretation of our natural history and sacred or mythological aspects of this tradition, which is historically embedded in an important religious background.

5. Conclusions

Csikszentmihalyi (1990) proposed that the necessity to constantly reinvent meditation is due at least to three main factors. Firstly, this kind of knowledge is not accumulative, that is, it cannot be simply memorized and transmitted to the next generations. Instead, such a complex form of learning, based on self-consciousness, emotion, and motivation, needs to be obtained through experience, person by person, generation by generation. Secondly, such experience is context-dependent, and cannot be transplanted through different societies. Namely, principles and practices must be reformulated any time there is a substantial change in the social or cultural structure. Thirdly, those principles and practices cannot be institutionalized because, as soon as they become rituals or automatized habits, they inevitably lose their meaning and efficiency. These three reasons explain further why a mindful attitude is difficult to handle for natural selection, when dealing with human societies. Nonetheless, we can probably consider whether specific abilities that are relevant to a conscious behavior can be susceptible to selective pressures. In this sense, attention is a key to a mindful ability, and its components likely underwent important changes during human evolution. Accordingly, investigating the evolutionary dynamics behind attention can supply a comprehensive framework in which distinct aspects of these topics can be explored in the frame of natural sciences. An evolutionary view is necessary to understand the limitations and potentialities of the cognitive skills involved in these processes. This information is crucial not only on theoretical ground, but also when trying to develop a mindful culture, at individual and social level, in the everyday standard conditions or therapeutic contexts.

This perspective article is not aimed at giving any concrete answer on the relationships between mindful cognition and human evolution. Many quantitative approach to attention, awareness, and dispositional mindfulness are still limited by methodological and conceptual disagreements and, therefore, investigating the same factors in human evolution is obviously more problematical. A proper testing of the hypotheses presented here would require psychometric and demographic analyses in large populations of hunter-gatherers which are, at best, very difficult to design. Probably, this is a topic for which concluding statements will hardly be available, and hence what we can do is to develop theories and hypotheses according to a reasonable level of speculation. Such a “reasonable level” would depend on whether these theories and hypotheses can fruitfully add to our interpretation of the concepts and practices behind consciousness and contemplative neurosciences. We should also be aware that probably there is no single answer to this issue, but multiple answers, that can fit different perspectives and different aims. The real scope of this paper is to propose an evolutionary frame in which the debate can be properly developed, offering a comprehensive scenario of the evolutionary possibilities, and supplying a set of concepts and principles that need to be acknowledged when dealing with the dynamics of human phylogeny. Natural selection may not need to consider our personal well-being but, if we want to take care of our psychological prosperity, we inevitably need to consider the rules and constraints of evolution. At last, this means becoming more aware of our natural history.

CRediT authorship contribution statement

Emiliano Bruner: Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of competing interest

The author declares no conflict of interest.

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