

Review



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# Computational animal welfare: towards cognitive architecture models of animal sentience, emotion and wellbeing

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To understand animal wellbeing, we need to consider subjective phenomena and sentience. This is challenging, since these properties are private and cannot be observed directly. Certain motivations, emotions and related internal states can be inferred in animals through experiments that involve choice, learning, generalization and decision-making. Yet, even though there is significant progress in elucidating the neurobiology of human consciousness, animal consciousness is still a mystery. We propose that computational animal welfare science emerges at the intersection of animal behaviour, welfare and computational cognition. By using ideas from cognitive science, we develop a functional and generic definition of subjective phenomena as any process or state of the organism that exists from the first-person perspective and cannot be isolated from the animal subject. We then outline a general cognitive architecture to model simple forms of subjective processes and sentience. This includes evolutionary adaptation which contains top-down attention modulation, predictive processing and subjective simulation by re-entrant (recursive) computations. Thereafter, we show how this approach uses major characteristics of the subjective experience: elementary self-awareness, global workspace and qualia with unity and continuity. This provides a formal framework for process-based modelling of animal needs, subjective states, sentience and wellbeing.

# 1. Introduction

Animal welfare has grown into an important interdisciplinary area involving significant public concern and societal influence [1–5]. Nonetheless, there are still controversies over the application of the well-being and welfare (the state of wellbeing [2]) concepts to animals [3,6–8]. Indeed, much-used definitions of wellbeing emphasize its multi-faceted nature and link it with subjective feelings, emotions and sentience (see glossary) [6,9–11]. Animal (including human) wellbeing is most naturally understood from the first-person perspective [10]. This makes analyses of subjective phenomena (see glossary) nearly unavoidable in this field [6,10,12,13].

Subjective feeling-based definitions of welfare are sometimes criticized for not being compatible with ‘objective science’. Critiques claim that physical health, naturalness and similar elements deemed easily measurable should define what welfare really is [6,12]. Folk judgements of animal welfare seem to support this to some extent [14,15]. If animals cannot communicate their subjective experience, a sceptic view is to remain agnostic. This entails ignoring their existence, resulting in a utilitarian approach to animal welfare: the main reason why animals matter is what they provide to us as farm or companion animals [16]. Then, the study of subjective feeling can divert us in the wrong direction [16]. But deliberately stripping complex cognitive abilities and subjectivity out sets an unnecessary ceiling on our understanding of welfare in healthy animals and fails to address the concerns for the animal suffering that were at the inception of animal welfare science [6,11].

Further, strong agnosticism can be ungrounded [17–20]. There is growing evidence for fascinating cognitive capacities in animals, including intentionality [21], components of conscious experience [13,18,22–24], planning and thinking [25–27], episodic memory [28,29] and meta-cognition [30,31]. It can therefore be fruitful to analyse complex cognitive abilities and subjective phenomena if we want to understand animal behaviour [32] and welfare [6,13]. There are still significant controversies over whether subjective phenomena, self-awareness and consciousness are just epiphenomena [20,33], or have adaptive significance [34–37] and whether they can be used to account for human and animal behaviour. However, as they are the essence of animal feelings and suffering, they are critical for understanding wellbeing [6,11].

This view justifies the development of theoretical approaches to animal sentience and subjective processes beyond general philosophical and metaphysical thinking. A better understanding of the core concepts of wellbeing requires formal models for standardized assessment (e.g. [38,39]) and quantitative models [40] that reflect how physiological, cognitive and behavioural needs relate to subjective states, emotions, suffering and stress.

Our main aim is to develop new computational technology for animal welfare. We bring together ideas from animal behaviour, neurobiology and computational cognitive science. First, we outline a general organization of adaptive behaviour in animals focusing on subjective state and predictive cognition (§2). We then provide a brief review of the wellbeing concept and its links with subjective state and predictive cognition (§3). Next, in §4, we describe the essence of the computational modelling approach to cognition with a focus on cognitive architecture. We then provide a natural framework for process-based modelling of both subjective wellbeing, sentience and consciousness evolving through natural selection and bounded by the ecological conditions in §5. Finally, in §6, we propose a way forward towards the computational animal welfare science and outline several implications (§7). While our computational framework has been used in evolutionary ecology (e.g. [41,42]), this proposal for animal welfare is currently at an early stage. We think it is rich enough to inspire empirical and modelling work as well as a critique that will help to refine it in this area. We also believe that it may become an effective tool in the current era of digitalization and precision livestock farming [43,44].

## 2. How adaptive behaviour is produced

### 2.1. Animals as autonomous predictive decision-making agents

Animals live in complex and unpredictably changing natural landscapes, where making adaptive decisions require trading priorities among various needs related to survival, growth and reproduction [45–47]. This is a computationally complex task [48–50]. Rather than having automated responses to any immediate signal, animals have evolved to be ‘autonomous agents’ (see glossary) [51–53]. Their behaviour is generated endogenously [51], driven by the internal state [54] and follows from

expectations and goals set by the organism [52,53,55]. This has been long realized in ethology and animal welfare. The classical models of motivation [53,56,57] recognize the importance of internal causation. Similarly, the notion of behavioural needs in animal welfare was originally defined in terms of internal motivations [58,59].

There is a growing recognition of intrinsic spontaneity and indeterminacy of behaviour [60,61]. This spontaneity requires a capacity for predictive modelling in the nervous system that considers an animal's internal state [62–64]. Such predictive modelling is found even in insects [65,66]. Making predictions for the future is central to the adaptive functioning of the nervous [67,68] as well as hormonal system [69]. Thus, there is a growing realization that a stimulus–response paradigm is insufficient to account for complex behaviour [70,71]. Letting animals express their agency and cognitive complexity has therefore become an important animal welfare priority [55].

## 2.2. The link between decision-making and integrated self

Adaptive behaviour involves arbitration between alternative stimuli, responses and choices. A key mechanism for this is competition and negotiation among multiple neural ensembles and cognitive modules in brain function [72–74], learning [75], cognition [76,77] and decision-making [78–80]. The need to make goal-driven decisions with top-down behavioural control in dynamically changing environments requires the organism to maintain a view of itself and its surroundings through an internal (and hence, subjective) model [67,81,82]. This model may contain both evolved and learned components [50], should detect discrepancies from the reality [62,83,84] and monitor stress the state of wellbeing.

An animal can potentially produce a wide range of responses (including ignorance) to any given stimulus depending on its subjective model of its current state and its surroundings. Signs, like the smell of a predator or prey, are stimuli that signify something other than itself [85]. A multitude of signs can be found in the environment, some are also sent from the animal to other organisms voluntarily or involuntarily, and all organisms live in a 'semiosphere' of signs (and noise falsely interpreted as signs). Recognition of the meaning of important signs among the complex sensory input is essential for learning and prediction of the future. This recognition or interpretation capacity (semiotic freedom) is therefore also essential for how rich the animal's phenomenal world is and how well an animal copes with its environment. It will directly impact welfare in both positive and negative ways [85]. From a welfare perspective, we are most concerned with situations that pose a challenge to the animal. For instance, while wildebeest spot predators regularly and still keep on with their normal activity, there are combinations of signs that set the animal in alarm mode. When this occurs, cognitive, physiological and behavioural systems are focused in a single, unified defensive state often called 'fear'. Such global emotional and motivational states are of central importance for what is considered important (or irrelevant) for appropriate behavioural response [86–89]. Threat imminence is instrumental in fear: low-risk anxiety requires wide information integration governed by conscious feeling while panic at high risk substitutes consciousness with rapid innate automatic responses [90].

Emotion or affect represents a combined behavioural, physiological and cognitive state that primarily carries an individual organism's value of stimuli or context [91–93]. Emotion is closely linked with the assessment of rewards and punishments [89,94] and functions to focus the animal to avoid harm and obtain valuable resources [93–95]. Affective states come in degrees, which translates to the concept of arousal: an elementary neuronal process that activates many cognitive processes, emotions and behaviours. It affects both ascending and descending brain pathways and brings about alertness to a range of sensory stimuli, reactivity and motor activity [96,97]. This leads to the circumplex model of affect in two dimensions: positive versus negative valence and low versus high arousal [89,98,99]. While initially developed in the context of human psychology, this view is supported by evolutionary models [100] and has been applied to animals [89,101–103].

Historically, the global state of the organism was introduced to neurobiology at the beginning of the twentieth century by Ukhtomsky [104,105] as the principle of the dominant. The dominant was thought of as the prevailing source of excitability in the nervous system that greatly influences responses of the organism to a wide range of stimuli at a particular time. The dominant was conceptualized as the basic mechanism for focusing attention, subjective model and anticipation of the near future [105]. In modern terms, the global emotional and motivational state reflects the arbitrated primary need state of the organism that defines its current behavioural goals and predicted future [50,106]. If the organism anticipates that it cannot satisfy its needs, it may become stressed [89,107].

Given a particular dominant state, the animal selects the appropriate action. Organisms of many species (at least those with motility and complex behaviour) have evolved the ability to make

predictions of their near future based on their internal model and use this to decide its next behaviour [50,89]. In the process, the internal model is challenged and updated with new information that appeared as a consequence of the behaviour. Prediction error—the mismatch between the expected and perceived information—is central for cognition based on prediction. New information resulting from the behaviour can modify the internal model, bringing about a continuous flow of goal-driven computations for predicting the best behavioural action onwards. Alternatively, the animal can try to keep the outside world to agree with the subjective predictions as much as possible, as in the active inference paradigm [64,68,108]. In this perspective, animals can be viewed as prediction machines [62,64,109] that have the ability to consider and forecast future ‘bodily feelings’ (emotions, tastes) that result from potential actions [89,91]. Examples come from associative learning [84,110,111], goal-oriented cognition [62,83] and sensorimotor control of action and behaviour [67,83,112]. In this view, motivation, emotion and wellbeing can be central components and provide the common currencies for prediction-based cognition [89,113].

The mechanisms in the pathways from genes to development, physiology and behaviour [114–116], and from perception to decision and action [117–119], are to a large degree modular throughout the Tree of Life. This means that the whole system can be decomposed into discrete functional and/or structural components. This can apply to emotions and motivations. For example, there are certain core types of affect [86,93]. Threat imminence is also thought to evoke distinct modules of fear [90]. There are still debates in what respect and to what degree human cognitive architecture is modular (e.g. [120–123]). Modularity can increase the functional efficiency of large networks [124], especially when we consider connection costs [115]. Modularity can significantly increase the efficiency and the ability of both the living organism and the evolving gene pool to cope with environmental change [125,126]. It allows components to be modified, duplicated, replaced or deleted without catastrophic loss of function to the whole organism [127]. In this way, modularity creates a potential for individual variation [42,128], facilitates adaptive evolution and increases evolvability [41,115,127].

Many animal brains have a mechanism ensuring widespread information access across multiple processes working in parallel [129]. General components that link numerous modules are crucial for the cognitive function. For example, broad neuronal communication across encapsulated modules provides a computational advantage [130]. In humans, awareness counteracts modularity through the maintenance of widespread, almost global, connectivity [131]. For consciousness, this mechanism has been called the dynamic global workspace: a functional hub that binds and propagates neural signals across a wide range of specific networks [132,133]. This workspace is likely to have evolved gradually, so that many animals have ‘not-so-global’ dynamic workspaces [134]. We will still call them global in this article, in the sense that they represent all that is connected. In vertebrates, convergent neuronal pathways integrating several projections are often found outside of the cortex [135]. For example, the habenula links many diverse circuits [136], and there are links integrating telencephalon with the cerebellum [137]. Converging connections are common not only in vertebrates but also in animals with small nervous systems [138,139].

Subjective experience cannot be found in a neural system based on reactive, feed-forward circuit organization alone [140–142]. Neither is compositional and computational complexity in itself sufficient for the subjective experience [140]. Subjective experience and consciousness arise in systems that are able to (i) integrate information, (ii) monitor itself, and (iii) generate and process virtual (hypothetical, possible) rather than actual information [141–143]. The simulation theory of cognition [144] accounts for the emergence of the subjective world through the development of integrated sensory-motor circuits. The whole circuit is activated when producing the next behavioural or physiological action. But it is also engaged (subjectively simulated) when the same action is planned, anticipated or even observed [145–148]. In humans, reactivated sensorimotor circuits are involved in conceptual processing, declarative knowledge and understanding [145,149]. Thus, the first-person conscious subjective experience involves the acquisition and re-entrant activation of linked sensorimotor and affective circuits [145]. Re-entrant here means repeated, recursive, activation of the same neuronal ensembles and circuits [132,150].

Emotions and personality are closely associated with subjective phenomena and self [88,93,120]. Consistent personality variation, linked with affect, exists in many taxonomic groups and can originate from shared genetic, physiological, developmental, neurobiological and cognitive mechanisms as well as an evolutionary adaptation [151–153]. Personality in humans can significantly depend on cognitive architecture [154]. From this, we can see that a unitary understanding of the integrated cognitive and behavioural phenotype—the self—emerges. It includes subjective processes as well as externally observable traits, personality. In this perspective is subjective wellbeing a crucial component of the system, because it links with information integration and self-monitoring.

### 3. Wellbeing and suffering: objective and subjective

Wellbeing describes what is good for the individual [10]. The notion of ‘good’ is here intimately linked to Darwinian fitness. Evolutionary forces have formed sensitivity to stimuli, emotions and availability of response mechanisms for the organism through random mutations and selective survival and reproduction. Thus, wellbeing is about how life is going on for the organism from its own perspective. There is, however, a range of views on how animal wellbeing can be defined scientifically. Some schools tend to focus on the healthy, stress-free physiological functioning of the organism, its ability to cope with the current environment, and satisfy its basic motivational and behavioural needs [155–157]. Naturalness, i.e. ability to perform natural, ecologically adaptive behaviour, is also crucial [15,16,158]. For others, welfare largely involves subjective cognitive needs [55,159] and feelings (e.g. ‘Let us not mince words: animal welfare involves the subjective feelings of animals’ [160, p. 1]). This view depends on the assumption that many animals are capable of various degrees of sentience: the capacity to experience feelings such as pain and suffering [6,12,13,161]. The common position in the field has become to understand animal wellbeing as a complex set of phenomena involving cognitive constructs, subjective awareness and desires in contrast to simple physiological and health status [6,12,162].

While the role of positive emotional states and pleasure has been emphasized in animal welfare [163–165], wellbeing is elusive and multi-faceted and difficult to define precisely. It is especially hard in species that do not frequently display positive emotional states, social and play behaviour. However, deficit in wellbeing—physiological and psychological stress and suffering—may be easier to define, detect and measure [3,166,167]. Stress is understood as an organism’s response to the actual or predicted threat, challenge or disruption of the organism’s homeostasis. Usually it involves an increase of the general arousal, activation of the autonomic nervous system: hypothalamic–pituitary–adrenal axis [168–170] in mammals or hypothalamic–pituitary–interrenal in fish [171,172]. Incidentally, invertebrates have specific stress hormones [173], e.g. hyperglycaemic hormone in crustaceans [174]. Stress is also a subjective state of perceiving potentially adverse changes [170]. Theoretical discussions emphasize complex cognitive and behavioural aspects of the stress involving the animal’s inability to anticipate the kind of challenge (unpredictability), its extent and possible avoiding strategies (uncontrollability) in addition to simple physiological responses [107,170,175]. Thus, stress is intrinsically linked with the emerging predictive cognition paradigm where the organism is depicted as a prediction machine [62–64]. Stress as a response is closely associated with a range of negative internal emotional states. In the animal wellbeing literature, such states have traditionally been subsumed under suffering. Suffering is defined as ‘intensely and/or enduring unpleasant subjective feeling’ [59, p. 210] or a ‘wide range of unpleasant emotional states’ [160 p. 1] or ‘unpleasant feeling, which is prolonged or severe’ [176, p. 374]. Thus, wellbeing is a combination of both objective and subjective aspects of the organism and reflects not just its current state, but also the anticipated change for better or for worse [9,159,177]. The needs of the animal (whether objective, such as adequate food and health, or subjective), its current state and anticipation of the near future are central for understanding wellbeing.

### 4. Computational models of cognition and cognitive architecture

Many biological and especially brain processes are computational, at least in the generic term [178,179]. Computation generally means manipulation of specific elementary units (e.g. digits, strings, neural spikes, continuous physical processes, variables, etc.) that are defined according to rules independently of the physical media that implement them [180]. Computation describes inherent functional and ‘algorithmic’ processes at the level of molecules and reaction networks [181,182], neural networks, the whole brain [183,184] and up to higher forms of cognition [185,186]. In this perspective, cognition and even the human mind (see glossary) are to a significant degree accounted for by computation [185,187,188]. Computational modelling and simulation of perception, cognition, learning, motivation, emotion and mind are therefore among the most natural ways of understanding the brain function and behaviour [70,183,185].

Complex computational models of the human mind are often implemented in the form of cognitive architecture [189–191]. This is a general framework that can be used through building more detailed computational models of cognition and behaviour focusing on particular problems [192,193]. It refers to algorithmic models of brain functioning rather than structural descriptions of neuronal wiring and brain morphology. It also differs from simple elegant mathematical equations, such as a function linking reinforcement rate and the response rate. Typically architectural models work through

building a virtual agent mechanistically implementing cognitive and behavioural functions that can just ‘run’ [194]. This is a thriving research field integrating psychology, neurobiology, artificial intelligence, computer science and philosophy of mind [189,190]. Cognitive architecture also provides a valuable tool for building quantitative models of animal cognition, sentience and welfare [50,106].

## 5. A modelling framework for subjective wellbeing and behaviour

Over the years, we have developed a model of an adaptive architecture for decision-making [41,42,45,128,195–198]. It currently contains a general framework and computer software components [199,200] for building simulation models that integrate cognition and behaviour in a phenotype that includes genome, physiology, hormonal system, perception, emotions, motivation and cognition. It also includes a virtual environment where the agents live and the gene pool evolves. This *adapted heuristics and architecture* (AHA) [50,106] provides a methodology for computational simulation of various internal subjective states and processes that account for animal wellbeing. Characteristics of the AHA cognitive architecture evolve through natural selection: the genetic algorithm leads to evolutionary adaptation of individuals and the gene pool [197,201,202]. This aligns well with the common view that all the mechanisms that account for animal wellbeing, including subjective feelings, are Darwinian fitness adaptations [176,177,203]. The AHA modelling framework can tackle elementary computational mechanisms thought to underlie subjective experience in different animals. We argue that our common evolutionary history suggests a continuity in neural, computational and evolutionary mechanisms that underlie subjective phenomena [91,134,204]. We are therefore concerned with functionally defined concepts in the same way that founders of ethology [205] and comparative psychology [206] used various human-derived terms without anthropomorphizing them.

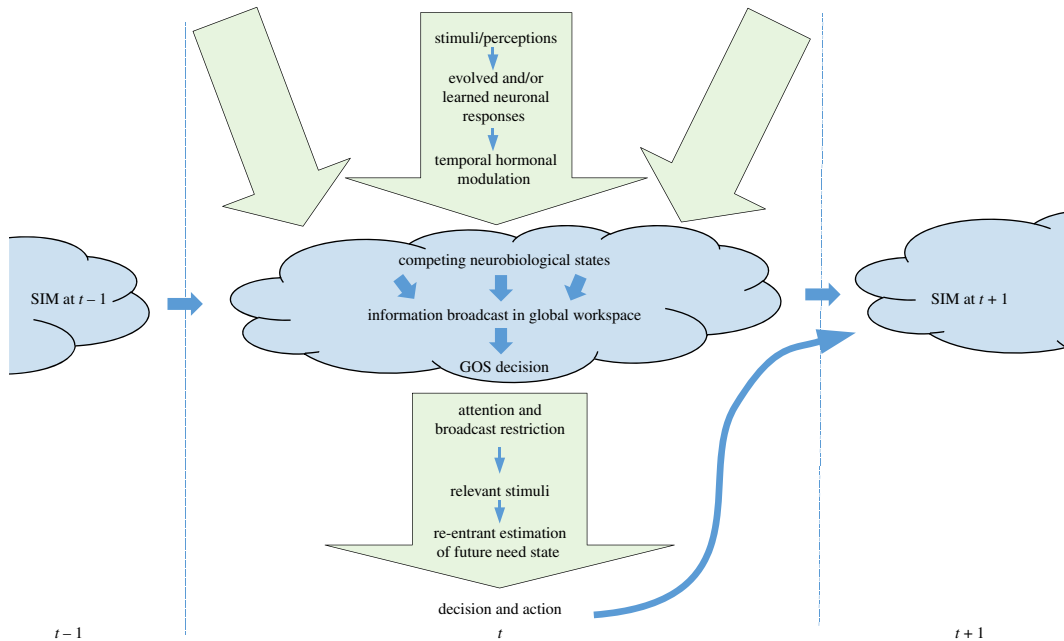
### 5.1. A brief outline of the *adapted heuristics and architecture* cognitive architecture

Analyses of wellbeing take the viewpoint of the individual animal: its individual state, needs and responses [6,160]. Thus, the AHA cognitive architecture [50,106] starts with the needs of the organism. The animal has the basic energetic needs to sustain its life as well as such needs as to avoid predators and secure reproduction, all adapted by the evolution of the gene pool towards a defined (but variable) environment.

The organism is continuously exposed to various signals from the external and the internal environment. How all the numerous sensory stimuli are selected and integrated is defined by the subjective internal model (SIM), which is the animal’s image of itself and its surroundings (figure 1). The strengths of the causal factors that integrate specific classes of sensory input represent the different motivations. For example, perception of stimuli linked to food and the individual’s gut defines hunger, while the perception of stimuli from predators defines fear. As mentioned for the wildebeest earlier, there are many normal situations where no signals from the body or the environment indicate an upcoming urge to the SIM. The animal can then attend to several types of motivations more or less simultaneously, but with lower efficiency, and without evoking wellbeing issues.

Motivational modules will compete for priority if there are more than one of them activated at any time. The strongest becomes the dominant emotional state of the organism, its global organismic state (GOS) [207] (it is a common assumption that the animal performs one major activity at a time [53,86]). This global state reflects how the organism trades priority across its various needs and selects the currently most important one given the state of its SIM. The strength of this dominant need is indicated by the level of the general arousal. It is conceived as one of the main wellbeing indicators, defining the severity of stress and negative feeling. The whole pathway from perception through motivation to the global organismic state, that integrates multiple sources of information, is called the survival circuit [86]. The AHA organisms have several such circuits that encapsulate different emotional states: fear, hunger, thirst, reproductive drive etc. (figure 1). The GOS and the arousal jointly determine attention: which stimuli the organism is going to use or ignore and to what extent in its ongoing decision-making process.

This top-down (or goal-driven) attention is produced endogenously when specific information (e.g. specific types of stimuli) is actively sought out from the external or internal environment, e.g. based on the SIM memory template. The GOS actively limits the animal’s attention to information that is most relevant to the current functional and behavioural state of the organism [76,112,208]. The GOS and the arousal determine how the animal makes decisions and selects behavioural actions. The organism can predict its likely effects on the environment and itself via subjective simulation of the



**Figure 1.** Major pathways for the subjective internal model (SIM) and global organismic state (GOS) over time ( $t-1 \rightarrow t \rightarrow t+1$ ), where new sensations may enter the (blue) global broadcast area and then modify the behavioural action. The figure shows three competing (green) survival circuits in the appraisal phase and one winner in the action phase. Subjective feeling results from the dynamics of internal re-entrant activation of SIM for prediction-based decision-making and action-selection. Stress may become the long-term effect of a persisting challenge that the animal predicts will remain unresolved. The main factors not shown are the need state and prediction error. See text for explanation.

expected emotion and arousal as a common internal currency. This represents a simple mechanistic model of subjective feeling. The SIM and the GOS jointly represent the global workspace that defines the unitary subjective state of the individual (figure 1). In this perspective, the ability of the SIM to represent important aspects of the internal and external environment result from ongoing computation performed by (i) natural selection on the population gene pool (evolutionary adaptation) and (ii) by animals through individual learning. The framework is generic and allows the researcher to combine these elements in models of varying complexity. For example, one can implement a purely reactive stimulus–response organism, an organism adding a single re-entrant component (single kind of experience) linked with one GOS, or a much more complex system including re-entry for all GOS and global workspace. This would allow to depict different species and/or build simpler or more complex models for different purposes.

## 5.2. A model of subjective phenomena and elementary self-awareness

As outlined above, wellbeing is a substantially subjective (first-person) phenomenon that intimately depends on self-assessment and elements of consciousness. Direct experimental analysis of subjective feelings and experiences in animals is a daunting task. However, the use of models could help generate hypotheses and direct empirical research. The AHA cognitive architecture provides a mechanistic model for elementary forms of subjective phenomena that satisfies many definitions of sentience and consciousness.

At the simplest level, top-down attention generates a simple mechanism for both goal-directed behaviour and subjectivity. Since the GOS affects perception through the top-down selective attention, two organisms with identical genomes placed into identical environments, but differing in their current state (e.g. one slightly afraid, the other very hungry) will perceive their internal and external environments differently. Their whole pathways from perception to cognitive processing and behavioural action will be unique. Differences between the individuals accumulate over time, thereby causing diverging cognitive and behavioural trajectories. Internal parameters of these processes are inseparable from each organism (in fact, from the history of the organism–environment interactions). This satisfies our broad definition of subjective phenomena.

Elementary self-awareness is an important aspect of prediction-oriented cognition and action selection implemented in the AHA architecture. It is defined as ‘the ability of the agent to assess its own internal state and use this information for decision making and action selection’ [106]. It is implemented through re-entrant activation of the survival circuits: internal simulation of the organism’s own potential actions (or the actual actions on an animal it observes) allows to determine the option that would result in the lowest arousal for negative emotions (or highest, for positive emotions). This links wellbeing with prediction error monitoring [62,64,84]. Consistently small prediction errors may indicate that the animal copes well enough with the environmental challenges. Furthermore, self-representation and self-monitoring are the most fundamental characteristics of consciousness [24,109,141].

This simple subjective simulation machinery reflects the emerging view that simpler forms of feeling, sentience and awareness not only have continuity across species [18,19,134], but can be found even in species with simple nervous systems [209]. The AHA cognitive architecture implements subjective experience by the mechanism of re-entrant activation, which is thought also to underlie human conscious experience [132,150,210].

The AHA architecture includes the two main components of conscious computations [141]: (i) self-monitoring in the form of elementary self-awareness and (ii) global workspace in the form of a unitary set of parameters for the SIM that hold the same for both producing and predicting inferred constructs (motivations, GOS). Several philosophical approaches to the nature of consciousness agree that its most important concept is *qualia* [20,211,212]. These are private, cognitively closed experiences that cannot be easily conveyed to others. Their main properties are *unity* and *continuity* [211,212]. Intriguingly, the AHA architecture provides a simple representation of qualia. Indeed, the way perceptual information is integrated to produce the internal state is unique for each individual and differs from its previous history of interactions with the stochastic environment. It is *ineffable*: essentially non-inferable by an external observer without access to the organism’s internal data structures. The great number of the external and internal stimuli that are uniquely filtered by attention in each case and potential processing pathways (especially if such pathways can be activated recurrently) makes it impossible to derive the internal data and cognitive structures even if the observer can record (the only observable) behaviour, input and output. Even for simple finite state machines, Moore’s theorem [213] states that no amount of observation is sufficient to uniquely identify the machine. This provides a very simple model of *qualia*. The *unity* of individual experiences is based on the involvement of the same neuronal parameters for both generation and recurrent prediction of the arousal and the GOS [106]. The GOS also depicts a single central state affecting attention, cognition and behaviour at the next time steps. The *continuity* of the experience in our model is strengthened by a mechanism that tolerates small fluctuations of incoming stimuli to avoid fast GOS switching [106, p. 53].

The AHA architecture contains all the characteristic features of consciousness defined by Ginsburg & Jablonka [20,214]. (i) A *flexible value system* is represented by the GOS-linked top-down attention focus that modulates the goal depending on the internal state. (ii) *Unity and diversity through sensory binding* is implemented by the linking and integration of information between specific classes of stimuli and survival circuits. Additionally, GOS is a single unitary state. (iii) The *global availability of information* is again represented by the unitary GOS (G is for global) and by the use of the same set of parameters both for producing GOS and re-entrant simulations involved in the generation of the future action. The SIM is both global and persistent. (iv) *Temporal thickness* is equivalent to the above continuity of experience. It is implemented through an arousal-dependent motivation competition mechanism avoiding very fast switching between different GOS and behavioural states [106]. (v) *Selection* is implemented through internal motivational competition among several alternatives that gives rise to a particular GOS as well as top-down attention effects of the current GOS. (vi) The autonomous goal-driven behaviour of the AHA agent that depends on its GOS at each time point ensures *intentionality*: GOS also modulates further goal-driven actions through top-down restrictions of attention to new information. Finally, (vii) *self and embodiment* are ensured as AHA models each agent as a complete virtual organism including unique genome, physiology, cognitive architecture and behavioural actions. The agents ‘live’ in, and the evolving gene pool adapts them to, their virtual environment that contains food, predators and other agents as well as other factors the researcher may deem important for the animal and the model. Individual learning can be added on top of this, as it is of course important for adaptive behaviour in a range of animals.

We hypothesize that the subjective wellbeing can be a fundamental component of the evolved cognitive architecture because it provides the central vehicle for self-monitoring, with emotions



serving as an internal currency. Self-monitoring along with virtual processing and global availability are major elements of conscious processing. In effect, this will integrate the organism's needs, motivation, emotion and subjective feeling.

The model in figure 1 is both an abstraction and simplification of the processes in the brains and bodies of animals during decision-making. Each neuronal response function [42,195] and hormonal modulation [69,128] represents the net aggregate of a range of processes, and these aggregates are therefore not in themselves observable. Relevant parameter values can be found by evolving populations of digital organisms [196,215,216] in environments that resemble the evolutionary history of the species [42,217,218]. With this tool, we can theoretically investigate the behaviour and well-being of animals that live in a particular environment or those that are transferred to a novel situation or subjected to specific treatment procedures.

### 5.3. Model expectations

A model provides a theoretical framework that facilitates thinking about a phenomenon under study [219]. Simulation experiments can be performed that are not possible on living organisms. The cognitive architecture brings together basic building blocks from diverse fields to a complete machinery that can 'run'. This allows to study subjective processes that are highly relevant for understanding and ultimately improving animal wellbeing. Even the conceptual and graphical version of the model addresses important welfare challenges both for wild and domestic animals. Animal subjective states and wellbeing are expressed in observable behaviour: patterns and biases of decision-making and actions. Our cognitive architecture encompassing sensing, SIM, multiple competing survival circuits, global broadcast and the GOS determining top-down attention control (figure 1) can suggest certain behavioural patterns.

#### 5.3.1. The animal's response to a stimulus depends on its global organismic state

While classical state-dependent theories in behavioural ecology [220–222] describe behaviour as dependent on states such as fat reserves or territory size, the key theoretical construct of the cognitive architecture is that the GOS is the decisive internal state of the organism. It determines which survival circuit a stimulus will be processed through and which behavioural response is finally evoked. Some stimuli can be linked with different survival circuits, for instance may conspecifics be judged as unwanted competitors for food or mates and wanted protection against predators. This is consistent with the neurobiological evidence that the animal's internal state can determine whether, for example, a zebrafish responds to a specific stimulus with approach or avoidance [223,224]. Even the same neurons could be involved in diverging responses under different perceived risk [225]. Controlling the animal's GOS and the arousal level are the main ways to achieve satisfactory subjective wellbeing.

#### 5.3.2. Simultaneous pressures may lead to stress

This expectation concerns the situation when an animal simultaneously and over some time faces pressures from two or more survival circuits for control of the GOS. Frequent switching of the global state and attention without substantial reduction of the arousal would indicate inefficient decisions. High levels of neuronal activity are energetically costly [226,227] and could lead to neurotransmitter exhaustion [228]. High simultaneous recruitment of more than one survival circuit would normally translate to poor wellbeing. This agrees with the evidence that animals often try to avoid situations with many choices [229,230]. An ecological example is a series of studies by Milinski and Heller on sticklebacks [231,232]. When starved fish were exposed to food, they first prioritized feeding at a high rate in the centre of a prey swarm although they simultaneously received signals of imminent high predation risk. After short, they moved to the periphery of the swarm where feeding was both less efficient and less cognitively demanding. We interpret this as a conflict between two life-threatening factors, starvation and predation, controlled by separate survival circuits. As fish prioritized feeding, its hunger arousal fell while its fear arousal kept growing. The solution was to move to a place where it could attend to both survival circuits, but with lower efficiency. While this option was available by moving less than 1 m for the sticklebacks, it may be far less available for many animals. We interpret this as avoiding the recruitment of both hunger and defence circuits that would worsen subjective feeling and lead to stress. Parenthetically, it is instructive that similar considerations are discussed in the robotics literature [233].

### 5.3.3. Uncertainty would increase behavioural heterogeneity, but not at high arousal

In our framework, global information broadcast across several survival circuits is involved in the prediction of the best behaviour in the nearest future. The animal does this on the basis of ‘what would it feel’ if each of the available decision options is made. If there is high uncertainty as to the outcome of potential actions but the need state is not very strong (low to average arousal), one of many available survival circuits could be engaged, evoking diverse behavioural actions. This would increase the diversity and complexity of the behavioural output. However, in a situation of high need (high arousal), top-down attention control would significantly block all the stimuli not associated with the current GOS, leading to reduced behavioural complexity. Similar patterns have been documented, with stress reducing the diversity of behaviour in mammals [234–236].

### 5.3.4. High need state and stress may cause ambiguity bias

The situation of high need that is not satisfied for a long time maintains the arousal at a high level and upholds the relevant survival circuit’s command of the GOS. This results in a narrow top-down attention span that will effectively ignore or suppress signals associated with all alternative survival circuits. Thus, a significant recognition and response bias towards the currently activated GOS may be expected. For example, an animal that remains hungry may interpret ambiguous stimuli and contexts as signals of food and respond accordingly. Similarly, an animal in chronic anxiety may display a negative cognitive bias by interpreting ambiguous stimuli as signals of danger or punishment. This tends to agree with the observations that many species display negative cognitive biases under stress [89,102,237–239].

### 5.3.5. Prolonged engagement of a single survival circuit and global organismic state may facilitate spontaneous change and (irrelevant) displacement activity

If the GOS is controlled by a single survival circuit for a long time (because the need is not satisfied), it may become subject to spontaneous dissipation of arousal due to neuronal exhaustion and neurotransmitter expenditure [106,240]). Then, a different survival circuit has a chance to win the competition over the next GOS. Because such dissipation would be accompanied by broadening of the attention span, different survival circuits could win and engage as the next GOS, even one that is irrelevant to the current needs. Thus, a displacement activity may appear. However, if the original motivational need is still not satisfied, it will be recruited again. Thus, short displacement activities may be expected to separate longer periods of behaviour that is unsuccessful at reducing the arousal of the GOS. Such a pattern—higher occurrence of displacement activities separating longer motivational states—has indeed been observed in primates [241] and honeybees [242].

## 6. Computational animal welfare: the digital twin approach

Aided by the recent progress in describing physiology, brain function and behaviour in mathematical and computational terms, simulation modelling has become a common tool in medicine and psychiatry. For example, ‘computational psychiatry’ combines big data analysis methods with theoretical models that account for mental illness as dysfunctional computations of the human cognitive system [243,244]. Animal welfare science could benefit from a similar computational approach. We argue that computer simulation of the animal’s cognitive and behavioural function could provide a valuable tool to understand, monitor and improve the wellbeing status of animals in production facilities, those kept as pets as well as wild animals subject to various anthropogenic effects.

We expect that the developing computational animal welfare field should follow the emerging *digital twin* paradigm. Broadly, it involves a digital representation of a physical object through a computer-aided design and computer simulations [245]. The concept has recently been extended to biomedical engineering [246], agriculture [247] and even global climate [248]. It is considered a viable paradigm for personalized medicine [249]. The digital twin framework is a ‘disruptive trend that will have increasingly broad and deep impact over the next five years and beyond’ [250]. In our opinion, animal welfare could benefit from making use of this paradigm, especially because both health and wellbeing could be redefined in individual terms, i.e. in terms of the subjective state of an individual animal rather than the species or population norm.

## 7. Consequences for behaviour and welfare

While this computational framework is still in development, it has several important implications for how we think about animal behaviour and welfare. Computational models enable us to study specific hypotheses about the mechanics of animal cognition and behaviour before testing them experimentally. Further, challenging cognitive architecture models with new empirical data can generate novel hypotheses [219]. Even informal analyses of cognitive architecture can suggest interesting behavioural hypotheses.

The cognitive architecture models are theory-inspired, but there is a great potential in combining them with machine-learning approaches (e.g. [251]) based on big data collected in realistic (e.g. farm) settings. This is especially important at this era of digitalization in agriculture (and aquaculture) and precision livestock farming [43,44] that heavily depend on models and simulations [252]. Hybrid modelling approaches will result in improved transparency and accountability for decision-making [253,254] that is crucial for animal welfare [255]. Architectural models that implement the whole integrated phenotype [256] may be used to help monitor both the physical health and subjective well-being of animals. Such models may suggest good proxies for experimental assessment [257] and continuous monitoring [258] (e.g. using video [259]), predict indicators of deviations from good well-being state (based on indices of behavioural complexity [236]). And it can be used to run scenarios to forecast likely effects of environmental or procedural changes on animal health and the welfare status, including complex and emergent effects. In an advanced precision farm environment, a digital twin simulation can help predict various stress and welfare effects for both planned operational changes and possible perturbations. This would be cheaper and faster than using physical experimental systems and avoid unwanted animal welfare issues in the R&D process. The computational digital twin paradigm could prove useful also in the conservation ecology context. For example, it can predict effects of anthropogenic environmental interventions on the welfare of wild animals in semi-natural habitats, advancing the ecology of emotion (see [42,260–262]).

## 8. Concluding remarks

Consumers, legislators and representatives for the food production industries have a growing concern about animal welfare [2,3,7]. The welfare status of a production facility can be monitored via physiological and behavioural proxies to inner cognition, emotion and feeling that are expected to correlate with the welfare status [257,263]. We make a case for this method being complemented by computational animal welfare models.

Most researchers will agree that animal wellbeing is intrinsically linked with subjective phenomena in the broad sense, which may or may not include conscious states similar to those experienced by humans [6,9,11]. The recent decades have witnessed significant progress in neurobiological and neurocomputational mechanisms of human conscious experience [132,141,264,265]. However, we are still quite far from understanding the phenomenal consciousness and brain mechanisms of cognition in general [266]. In our opinion, one way to progress is to use functional definitions of subjective phenomena, just as the founders of ethology used to do for behaviour [53,205]. In the empirical animal welfare research, this translates to ‘asking’ animals about their motivation and emotional states—essentially what they want—through preference, learning, generalization and similar experiments [9,12,257]. A good example of such an approach is the analysis of positive and negative emotional states through optimistic or pessimistic cognitive biases when judging an ambiguous stimulus [89,103].

We think that computational models implementing functional mechanisms that account for internal subjective phenomena is a fruitful pathway. Unlike other fields such as behavioural ecology, we cannot rely on simple, elegant mathematical equations because the phenomenon of subjective cognition cannot be understood in isolation from the subject (the integrated phenotype [256]). It is complex and includes the interaction of many stochastic components, recursion, top-down causation and emergence. Agent-based simulation [267–269] with evolutionary adaptation [45,197,270] seems the most feasible option. The above discussion points to possible ways of developing a computational system that implements basic functional units of subjective phenomena: predictive, re-entrant and top-down processing, elementary self-awareness and global workspace in a simple mechanistic system.

The cognitive architecture implementing evolutionary adaptation [50,106] may then provide the basic component for larger and more complex digital twin models. Such models will help monitor and predict health, behaviour and subjective wellbeing of animals. This opens an exciting and challenging avenue for computational animal welfare science.

Ethics. This is a theoretical paper dealing with computational models aimed to develop new ways to improve animal welfare. We therefore expect no ethical issues.

Data accessibility. This is a theoretical paper that contains no data. Example computer code and documentation are available at <https://ahamodel.uib.no>.

Authors' contributions. J.G. and S.E. started the development of the theoretical ideas on the architectural models of decision-making more than 10 years ago. S.B. extended the ideas to psychology and cognition and has rewritten the computer codes. J.G. and T.S.K. then extended the framework to the animal wellbeing field. S.B. wrote the initial draft of the manuscript. J.G., S.E. and T.S.K. provided theoretical developments and contributed critically to the development of the manuscript.

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## References

- Ohl F, van der Staay FJ. 2012 Animal welfare: at the interface between science and society. *Vet. J.* **192**, 13–19. (doi:10.1016/j.tvjl.2011.05.019)
- Spedding C. 2000 *Animal welfare*. London, UK: Earthscan.
- Haynes RP. 2008 *Animal welfare: competing conceptions and their ethical implications*. New York, NY: Springer.
- Christensen T, Denver S, Sandøe P. 2019 How best to improve farm animal welfare? Four main approaches viewed from an economic perspective. *Anim. Welf.* **28**, 95–106. (doi:10.7120/09627286.28.1.095)
- Kristiansen TS, Fernø A, Pavlidis MA, Van de Vis H (eds) 2020 *The welfare of fish*. Cham, Switzerland: Springer.
- Broom DM. 2014 *Sentience and animal welfare*. Wallingford, UK: CABI.
- Fisher M. 2018 *Animal welfare science, husbandry and ethics: the evolving story of our relationship with farm animals*. Sheffield, UK: 5M Publishing.
- Serpell JA. 2019 How happy is your pet? The problem of subjectivity in the assessment of companion animal welfare. *Anim. Welf.* **28**, 57–66. (doi:10.7120/09627286.28.1.057)
- Dawkins MS. 2017 Animal welfare with and without consciousness. *J. Zool.* **301**, 1–10. (doi:10.1111/jzo.12434)
- Appley MC, Sandøe PT. 2002 Philosophical debate on the nature of well-being: implications for animal welfare. *Anim. Welf.* **11**, 283–294.
- Mendl M, Paul ES. 2004 Consciousness, emotion and animal welfare: insights from cognitive science. *Anim. Welf.* **13**, 17–25.
- Dawkins M. 2015 Animal welfare and the paradox of animal consciousness. *Adv. Study Behav.* **47**, 5–38. (doi:10.1016/bs.asb.2014.11.001)
- Proctor HS, Carder G, Cornish AR. 2013 Searching for animal sentience: a systematic review of the scientific literature. *Animals* **3**, 882–906. (doi:10.3390/ani3030882)
- Robbins J, Franks B, von Keyserlingk MAG. 2018 'More than a feeling': an empirical investigation of hedonistic accounts of animal welfare. *PLoS ONE* **13**, e0193864. (doi:10.1371/journal.pone.0193864)
- Weary DM, Robbins JA. 2019 Understanding the multiple conceptions of animal welfare. *Anim. Welf.* **28**, 33–40. (doi:10.7120/09627286.28.1.033)
- Dawkins MS. 2012 *Why animals matter: animal consciousness, animal welfare, and human well-being*. Oxford, UK: Oxford University Press.
- Bekoff M, Allen C, Burghardt GM. 2002 *The cognitive animal: empirical and theoretical perspectives on animal cognition*. Cambridge, MA: MIT Press.
- Boly M, Seth AK, Wilke M, Ingmundson P, Baars B, Laureys S, Edelman DB, Tsuchiya N. 2013 Consciousness in humans and non-human animals: recent advances and future directions. *Front. Psychol.* **4**, 625. (doi:10.3389/fpsyg.2013.00625)
- Edelman DB, Seth AK. 2009 Animal consciousness: a synthetic approach. *Trends Neurosci.* **32**, 476–484. (doi:10.1016/j.tins.2009.05.008)
- Ginsburg S, Jablonka E. 2019 *The evolution of the sensitive soul: learning and the origins of consciousness*. Cambridge, MA: MIT Press.
- Burkatt JM, van Schaik CP. 2020 Marmoset prosociality is intentional. *Anim. Cogn.* **23**, 581–594. (doi:10.1007/s10071-020-01363-6)
- Mather JA. 2008 Cephalopod consciousness: behavioural evidence. *Conscious. Cogn.* **17**, 37–48. (doi:10.1016/j.concog.2006.11.006)
- Nieder A, Wagener L, Rinnert P. 2020 A neural correlate of sensory consciousness in a corvid bird. *Science* **369**, 1626–1629. (doi:10.1126/science.abb1447)
- Paul ES, Sher S, Tamiotto M, Winkielman P, Mendl MT. 2020 Towards a comparative science of emotion: affect and consciousness in humans and animals. *Neurosci. Biobehav. Rev.* **108**, 749–770. (doi:10.1016/j.neubiorev.2019.11.014)
- Thom JM, Clayton NS. 2015 Translational research into intertemporal choice: the Western scrub-jay as an animal model for future-thinking. *Behav. Process.* **112**, 43–48. (doi:10.1016/j.beproc.2014.09.006)
- Suddendorf T, Corballis MC. 2010 Behavioural evidence for mental time travel in nonhuman animals. *Behav. Brain Res.* **215**, 292–298. (doi:10.1016/j.bbr.2009.11.044)
- Dere E, Kart-Teke E, Huston JP, De Souza Silva MA. 2006 The case for episodic memory in animals. *Neurosci. Biobehav. Rev.* **30**, 1206–1224. (doi:10.1016/j.neubiorev.2006.09.005)
- Dere E, Dere D, de Souza Silva MA, Huston JP, Zlomuzica A. 2018 Fellow travellers: working memory and mental time travel in rodents. *Behav. Brain Res.* **352**, 2–7. (doi:10.1016/j.bbr.2017.03.026)
- Templer VL, Hampton RR. 2013 Episodic memory in nonhuman animals. *Curr. Biol.* **23**, R801–R806. (doi:10.1016/j.cub.2013.07.016)
- Smith JD, Zakrzewski AC, Church BA. 2016 Formal models in animal-metacognition research: the problem of interpreting animals' behavior. *Psychon. Bull. Rev.* **23**, 1341–1353. (doi:10.3758/s13423-015-0985-2)
- Kornell N. 2014 Where is the 'meta' in animal metacognition? *J. Comp. Psychol.* **128**, 143–149. (doi:10.1037/a0033444)
- Burghardt GM. 1997 Amending Tinbergen: a fifth aim for ethology. In *Anthropomorphism, anecdotes, and animals* (eds RW Mitchell, NS Thompson, HL Miles), pp. 254–276. Albany, NY: State University of New York Press.
- Carruthers P. 2018 Comparative psychology without consciousness. *Conscious. Cogn.* **63**, 47–60. (doi:10.1016/j.concog.2018.06.012)
- Pierson LM, Trout M. 2017 What is consciousness for? *New Ideas Psychol.* **47**, 62–71. (doi:10.1016/j.newideapsych.2017.05.004)
- Clark KB. 2018 Possible origins of consciousness in simple control over 'involuntary' neuroimmunological action. *Conscious. Cogn.* **61**, 76–78. (doi:10.1016/j.concog.2018.04.002)
- Feinberg TE, Mallatt J. 2016 The nature of primary consciousness: a new synthesis. *Conscious. Cogn.* **43**, 113–127. (doi:10.1016/j.concog.2016.05.009)

37. Merker B. 2005 The liabilities of mobility: a selection pressure for the transition to consciousness in animal evolution. *Conscious. Cogn.* **14**, 89–114. (doi:10.1016/S1053-8100(03)00002-3)
38. Pettersen JM, Bracke MBM, Midtlyng PJ, Folkedal O, Stien LH, Steffenak H, Kristiansen TS. 2014 Salmon welfare index model 2.0: an extended model for overall welfare assessment of caged Atlantic salmon, based on a review of selected welfare indicators and intended for fish health professionals. *Rev. Aquac.* **6**, 162–179. (doi:10.1111/raq.12039)
39. Bracke MBM, Koene P, Estevez I, Butterworth A, de Jong IC. 2019 Broiler welfare trade-off: a semi-quantitative welfare assessment for optimised welfare improvement based on an expert survey. *PLoS ONE* **14**, e0222955. (doi:10.1371/journal.pone.0222955)
40. Collins LM, Part CE. 2013 Modelling farm animal welfare. *Animals* **3**, 416–441. (doi:10.3390/ani3020416)
41. Giske J, Eliassen S, Fiksen Ø, Jakobsen PJ, Aksnes DL, Mangel M, Jørgensen C. 2014 The emotion system promotes diversity and evolvability. *Proc. R. Soc. B* **281**, 20141096. (doi:10.1098/rspb.2014.1096)
42. Giske J, Eliassen S, Fiksen Ø, Jakobsen PJ, Aksnes DL, Jørgensen C, Mangel M. 2013 Effects of the emotion system on adaptive behavior. *Am. Nat.* **182**, 689–703. (doi:10.1086/673533)
43. Rowe E, Dawkins MS, Gebhardt-Henrich SG. 2019 A systematic review of precision livestock farming in the poultry sector: is technology focussed on improving bird welfare? *Animals* **9**, 1–18. (doi:10.3390/ani9090614)
44. Føre M *et al.* 2018 Precision fish farming: a new framework to improve production in aquaculture. *Biosyst. Eng.* **173**, 176–193. (doi:10.1016/j.biosystemseng.2017.10.014)
45. Eliassen S, Andersen BS, Jørgensen C, Giske J. 2016 From sensing to emergent adaptations: modelling the proximate architecture for decision-making. *Ecol. Model.* **326**, 90–100. (doi:10.1016/j.ecolmodel.2015.09.001)
46. Calabretta R, Di Ferdinando A, Wagner GP, Parisi D. 2003 What does it take to evolve behaviorally complex organisms? *Biosystems* **69**, 245–262. (doi:10.1016/S0303-2647(02)00140-5)
47. Begon M, Townsend CR, Harper JL. 2006 *Ecology: from individuals to ecosystems*. Oxford, UK: Blackwell.
48. Fawcett TW, Fallenstein B, Higginson AD, Houston AI, Mallpress DEW, Trimmer PC, McNamara JM. 2014 The evolution of decision rules in complex environments. *Trends Cogn. Sci.* **18**, 153–161. (doi:10.1016/j.tics.2013.12.012)
49. Bossaerts P, Murawski C. 2017 Computational complexity and human decision-making. *Trends Cogn. Sci.* **21**, 917–929. (doi:10.1016/j.tics.2017.09.005)
50. Budaev S, Jørgensen C, Mangel M, Eliassen S, Giske J. 2019 Decision-making from the animal perspective: bridging ecology and subjective cognition. *Front. Ecol. Evol.* **7**, 164. (doi:10.3389/fevo.2019.00164)
51. Heisenberg M. 2014 The beauty of the network in the brain and the origin of the mind in the control of behavior. *J. Neurogenet.* **28**, 389–399. (doi:10.3109/01677063.2014.912279)
52. Edelman S. 2016 The minority report: some common assumptions to reconsider in the modelling of the brain and behaviour. *J. Exp. Theor. Artif. Intell.* **28**, 751–776. (doi:10.1080/0952813X.2015.1042534)
53. McFarland D, Bosser T. 1993 *Intelligent behavior in animals and robots*. Cambridge, MA: MIT Press.
54. Gorostiza EA, Colomb J, Brembs B. 2016 A decision underlies phototaxis in an insect. *Open Biol.* **6**, 160229. (doi:10.1098/rsob.160229)
55. Špinko M. 2019 Animal agency, animal awareness and animal welfare. *Anim. Welf.* **28**, 11–20. (doi:10.7120/09627286.28.1.011)
56. Hogan JA. 2009 Causation: the study of behavioral mechanisms. In *Tinbergen's legacy. Function and mechanism in behavioral biology* (eds JJ Bolhuis, S Verhulst), pp. 35–53. Cambridge, UK: Cambridge University Press.
57. Toates F. 1986 *Motivational systems*. Cambridge, UK: Cambridge University Press.
58. Friend T. 1989 Recognizing behavioral needs. *Appl. Anim. Behav. Sci.* **22**, 151–158. (doi:10.1016/0168-1591(89)90051-8)
59. Dawkins MS. 1988 Behavioural deprivation: a central problem in animal welfare. *Appl. Anim. Behav. Sci.* **20**, 209–225. (doi:10.1016/0168-1591(88)90047-0)
60. Brembs B. 2011 Towards a scientific concept of free will as a biological trait: spontaneous actions and decision-making in invertebrates. *Proc. R. Soc. B* **278**, 930–939. (doi:10.1098/rspb.2010.2325)
61. Proekt A, Banavar JR, Maritan A, Pfaff DW. 2012 Scale invariance in the dynamics of spontaneous behavior. *Proc. Natl Acad. Sci. USA* **109**, 10 564–10 569. (doi:10.1073/pnas.1206894109)
62. Bubic A, von Cramon DY, Schubotz RL. 2010 Prediction, cognition and the brain. *Front. Hum. Neurosci.* **4**, 1–15. (doi:10.3389/fnhum.2010.00025)
63. McNally GP, Johansen JP, Blair HT. 2011 Placing prediction into the fear circuit. *Trends Neurosci.* **34**, 283–292. (doi:10.1016/j.tins.2011.03.005)
64. Clark A. 2015 Embodied prediction. *Open Mind* **7**, 1–21. (doi:10.15502/9783958570115)
65. Giurfa M. 2013 Cognition with few neurons: higher-order learning in insects. *Trends Neurosci.* **36**, 285–294. (doi:10.1016/j.tins.2012.12.011)
66. Haberkern H, Jayaraman V. 2016 Studying small brains to understand the building blocks of cognition. *Curr. Opin. Neurobiol.* **37**, 59–65. (doi:10.1016/j.conb.2016.01.007)
67. Pezzulo G, Rigoli F, Friston K. 2015 Active inference, homeostatic regulation and adaptive behavioural control. *Prog. Neurobiol.* **134**, 17–35. (doi:10.1016/j.pneurobio.2015.09.001)
68. Pezzulo G, Rigoli F, Friston KJ. 2018 Hierarchical active inference: a theory of motivated control. *Trends Cogn. Sci.* **22**, 294–306. (doi:10.1016/j.tics.2018.01.009)
69. Jensen CH, Weidner J, Giske J, Budaev S, Jørgensen C, Eliassen S. 2021 Hormonal adjustments to future expectations impact growth and survival in juvenile fish. *Oikos* **130**, oik.07483. (doi:10.1111/oik.07483)
70. Gallistel CR, King AP. 2010 *Memory and the computational brain: why cognitive science will transform neuroscience*. Chichester, UK: Wiley.
71. Haselgrove M. 2016 Overcoming associative learning. *J. Comp. Psychol.* **130**, 226–240. (doi:10.1037/a0040180)
72. Colas JT. 2017 Value-based decision making via sequential sampling with hierarchical competition and attentional modulation. *PLoS ONE* **12**, e0186822. (doi:10.1371/journal.pone.0186822)
73. Usher M, McClelland JL. 2001 The time course of perceptual choice: the leaky, competing accumulator model. *Psychol. Rev.* **108**, 550–592. (doi:10.1037/0033-295X.108.3.550)
74. Kermani Kolankeh A, Teichmann M, Hamker FH. 2015 Competition improves robustness against loss of information. *Front. Comput. Neurosci.* **9**, 35. (doi:10.3389/fncom.2015.00035)
75. Barberini CL, Morrison SE, Saez A, Lau B, Salzman CD. 2012 Complexity and competition in appetitive and aversive neural circuits. *Front. Neurosci.* **6**, 1–13. (doi:10.3389/fnins.2012.00170)
76. Pessoa L. 2015 Précis of the cognitive-emotional brain. *Behav. Brain Sci.* **38**, e71. (doi:10.1017/S0140525X14000120)
77. Gisek P. 2007 A parallel framework for interactive behavior. *Prog. Brain Res.* **165**, 475–492. (doi:10.1016/S0079-6123(06)60300-9)
78. Gisek P. 2012 Making decisions through a distributed consensus. *Curr. Opin. Neurobiol.* **22**, 927–936. (doi:10.1016/j.conb.2012.05.007)
79. Barker AJ, Baier H. 2015 Sensorimotor decision making in the zebrafish tectum. *Curr. Biol.* **25**, 2804–2814. (doi:10.1016/j.cub.2015.09.055)
80. Burnett CJ, Li C, Webber E, Tsaousidou E, Xue SY, Brüning JC, Krashes MJ. 2016 Hunger-driven motivational state competition. *Neuron* **92**, 187–201. (doi:10.1016/j.neuron.2016.08.032)
81. Clark A. 2013 Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behav. Brain Sci.* **36**, 181–204. (doi:10.1017/S0140525X12000477)
82. Friston KJ, Rosch R, Parr T, Price C, Bowman H. 2017 Deep temporal models and active inference. *Neurosci. Biobehav. Rev.* **77**, 388–402. (doi:10.1016/j.neubiorev.2017.04.009)
83. Friston K, Schwartenbeck P, FitzGerald T, Moutoussis M, Behrens T, Dolan RJ. 2014 The anatomy of choice: dopamine and decision-making. *Phil. Trans. R. Soc. B* **369**, 20130481. (doi:10.1098/rstb.2013.0481)
84. Schultz W, Dickinson A. 2000 Neuronal coding of prediction errors. *annu. Rev. Neurosci.* **23**, 473–500. (doi:10.1146/annurev.neuro.23.1.473)
85. Hoffmeyer J. 2008 *Biosemiotics: an examination into the signs of life and the life of signs*. Scranton, PA: University of Scranton Press.
86. LeDoux JE. 2012 Rethinking the emotional brain. *Neuron* **73**, 653–676. (doi:10.1016/j.neuron.2012.02.004)
87. Toates F. 2006 A model of the hierarchy of behaviour, cognition, and consciousness. *Conscious. Cogn.* **15**, 75–118. (doi:10.1016/j.concog.2005.04.008)
88. Alcaro A, Carta S, Panksepp J. 2017 The affective core of the self: a neuro-archetypal perspective on the foundations of human (and animal)

- subjectivity. *Front. Psychol.* **8**, 1424. (doi:10.3389/fpsyg.2017.01424)
89. Mendl M, Paul ES. 2020 Animal affect and decision-making. *Neurosci. Biobehav. Rev.* **112**, 144–163. (doi:10.1016/j.neubiorev.2020.01.025)
90. Fanselow MS. 2018 The role of learning in threat imminence and defensive behaviors. *Curr. Opin. Behav. Sci.* **24**, 44–49. (doi:10.1016/j.cobeha.2018.03.003)
91. Damasio AR. 2010 *Self comes to mind: constructing the conscious brain*. New York, NY: Pantheon Books.
92. Bach DR, Dayan P. 2017 Algorithms for survival: a comparative perspective on emotions. *Nat. Rev. Neurosci.* **18**, 311–319. (doi:10.1038/nrn.2017.35)
93. Panksepp J. 2011 The basic emotional circuits of mammalian brains: do animals have affective lives? *Neurosci. Biobehav. Rev.* **35**, 1791–1804. (doi:10.1016/j.neubiorev.2011.08.003)
94. Rolls ET. 2000 Précis of the brain and emotion. *Behav. Brain Sci.* **23**, 177–234. (doi:10.1017/S0140525X00512424)
95. LeDoux JE. 2000 Emotion circuits in the brain. *Annu. Rev. Neurosci.* **23**, 155–184. (doi:10.1146/annurev.neuro.23.1.155)
96. Calderon DP, Kilinc M, Maritan A, Banavar JR, Pfaff DW. 2016 Generalized CNS arousal: an elementary force within the vertebrate nervous system. *Neurosci. Biobehav. Rev.* **68**, 167–176. (doi:10.1016/j.neubiorev.2016.05.014)
97. Pfaff DW. 2006 *Brain arousal and information theory: neural and genetic mechanisms*. Cambridge, MA: Harvard University Press.
98. Russell JA. 1980 A circumplex model of affect. *J. Pers. Soc. Psychol.* **39**, 1161–1178. (doi:10.1037/h0077714)
99. Remington NA, Fabrigar LR, Visser PS. 2000 Reexamining the circumplex model of affect. *J. Pers. Soc. Psychol.* **79**, 286–300. (doi:10.1037/0022-3514.79.2.286)
100. Trimmer P, Paul E, Mendl M, McNamara J, Houston A. 2013 On the evolution and optimality of mood states. *Behav. Sci. (Basel)*. **3**, 501–521. (doi:10.3390/bs3030501)
101. Kittilsen S. 2013 Functional aspects of emotions in fish. *Behav. Process.* **100**, 153–159. (doi:10.1016/j.beproc.2013.09.002)
102. Paul ES, Harding EJ, Mendl M. 2005 Measuring emotional processes in animals: the utility of a cognitive approach. *Neurosci. Biobehav. Rev.* **29**, 469–491. (doi:10.1016/j.neubiorev.2005.01.002)
103. Mendl M, Burman OHP, Paul ES. 2010 An integrative and functional framework for the study of animal emotion and mood. *Proc. Biol. Sci.* **277**, 2895–2904. (doi:10.1098/rspb.2010.0303)
104. Ukhomsky AA. 1978 *Selected works*. Moscow, Russia: Nauka.
105. Zueva EY, Zuev KB. 2015 The concept of dominance by A.A. Ukhomsky and anticipation. In *Anticipation: learning from the past* (ed. M Nadin), pp. 13–35. Berlin, Germany: Springer.
106. Budaev S, Giske J, Eliassen S. 2018 AHA: a general cognitive architecture for Darwinian agents. *Biol. Inspired Cogn. Archit.* **25**, 51–57. (doi:10.1016/j.bica.2018.07.009)
107. Koolhaas JM *et al.* 2011 Stress revisited: a critical evaluation of the stress concept. *Neurosci. Biobehav. Rev.* **35**, 1291–1301. (doi:10.1016/j.neubiorev.2011.02.003)
108. Friston K, Schwartenbeck P, FitzGerald T, Moutoussis M, Behrens T, Dolan RJ. 2013 The anatomy of choice: active inference and agency. *Front. Hum. Neurosci.* **7**, 598. (doi:10.3389/fnhum.2013.00598)
109. Seth AK, Friston KJ. 2016 Active interoceptive inference and the emotional brain. *Phil. Trans. R. Soc. B* **371**, 20160007. (doi:10.1098/rstb.2016.0007)
110. Sutton RS, Barto AG. 1981 Toward a modern theory of adaptive networks: expectation and prediction. *Psychol. Rev.* **88**, 135–170. (doi:10.1037/0033-295X.88.2.135)
111. Holland PC, Schiffrino FL. 2016 Mini-review: prediction errors, attention and associative learning. *Neurobiol. Learn. Mem.* **131**, 207–215. (doi:10.1016/j.nlm.2016.02.014)
112. Buschman TJ, Miller EK. 2014 Goal-direction and top-down control. *Phil. Trans. R. Soc. B* **369**, 20130471. (doi:10.1098/rstb.2013.0471)
113. Cabanac M. 1992 Pleasure: the common currency. *J. Theor. Biol.* **155**, 173–200. (doi:10.1016/S0022-5193(05)80594-6)
114. Lorenz DM, Jeng A, Deem MW. 2011 The emergence of modularity in biological systems. *Phys. Life Rev.* **8**, 129–160. (doi:10.1016/j.plrev.2011.02.003)
115. Clune J, Mouret J-B-J, Lipson H. 2013 The evolutionary origins of modularity. *Proc. R. Soc. B* **280**, 20122863. (doi:10.1098/rspb.2012.2863)
116. Thompson DA *et al.* 2013 Evolutionary principles of modular gene regulation in yeasts. *Elife* **2013**, 1–37. (doi:10.7554/eLife.00603)
117. Meunier D, Lambiotte R, Bullmore ET. 2010 Modular and hierarchically modular organization of brain networks. *Front. Neurosci.* **4**, 200. (doi:10.3389/fnins.2010.00200)
118. Kurzban R. 2012 Modularity and decision making. In *Evolution and the mechanisms of decision making* (eds P Hammerstein, JR Stevens), Cambridge, MA: The MIT Press.
119. Sternberg S. 2011 Modular processes in mind and brain. *Cogn. Neuropsychol.* **28**, 156–208. (doi:10.1080/02643294.2011.557231)
120. Barrett LF. 2016 The theory of constructed emotion: an active inference account of interoception and categorization. *Soc. Cogn. Affect. Neurosci.* **12**, nsw154. (doi:10.1093/scan/nsw154)
121. Shettleworth SJ. 2012 Modularity, comparative cognition and human uniqueness. *Phil. Trans. R. Soc. Lond. B* **367**, 2794–2802. (doi:10.1098/rstb.2012.0211)
122. Carruthers P. 2003 Moderately massive modularity. *R. Inst. Phil. Suppl.* **53**, 67–89. (doi:10.1017/s1358246100008274)
123. Fodor JA. 1983 *The modularity of mind*. Cambridge, MA: MIT Press.
124. Tosh CR, McNally L. 2015 The relative efficiency of modular and non-modular networks of different size. *Proc. R. Soc. B* **282**, 20142568. (doi:10.1098/rspb.2014.2568)
125. Ellefsen KO, Mouret JB, Clune J. 2015 Neural modularity helps organisms evolve to learn new skills without forgetting old skills. *PLoS Comput. Biol.* **11**, e1004128. (doi:10.1371/journal.pcbi.1004128)
126. Bentkowski P, Van Oosterhout C, Mock T. 2015 A model of genome size evolution for prokaryotes in stable and fluctuating environments. *Genome Biol. Evol.* **7**, 2344–2351. (doi:10.1093/gbe/evv148)
127. Wagner A. 2011 *The origins of evolutionary innovations: a theory of transformative change in living systems*. Oxford, UK: Oxford University Press.
128. Weidner J, Jensen CH, Giske J, Eliassen S, Jørgensen C. 2020 Hormones as adaptive control systems in juvenile fish. *Biol. Open* **9**, bio046144. (doi:10.1242/bio.046144)
129. Shanahan M, Baars B. 2005 Applying global workspace theory to the frame problem. *Cognition* **98**, 157–176. (doi:10.1016/j.cognition.2004.11.007)
130. Bullinaria JA. 2007 Understanding the emergence of modularity in neural systems. *Cogn. Sci.* **31**, 673–695. (doi:10.1080/15326900701399939)
131. Godwin D, Barry RL, Marois R. 2015 Breakdown of the brain's functional network modularity with awareness. *Proc. Natl Acad. Sci. USA* **112**, 3799–3804. (doi:10.1073/pnas.1414466112)
132. Baars BJ. 1995 *A cognitive theory of consciousness*. Cambridge, UK: Cambridge University Press.
133. Baars BJ, Franklin S, Ramsay TZ. 2013 Global workspace dynamics: cortical 'binding and propagation' enables conscious contents. *Front. Psychol.* **4**, 200. (doi:10.3389/fpsyg.2013.00200)
134. Baars BJ. 2005 Subjective experience is probably not limited to humans: the evidence from neurobiology and behavior. *Conscious. Cogn.* **14**, 7–21. (doi:10.1016/j.concog.2004.11.002)
135. Doan TP, Lagartos-Donate MJ, Nilssen ES, Ohara S, Witter MP. 2019 Convergent projections from perirhinal and postrhinal cortices suggest a multisensory nature of lateral, but not medial, entorhinal cortex. *Cell Rep.* **29**, 617–627; e7. (doi:10.1016/j.celrep.2019.09.005)
136. Fore S, Palumbo F, Pelgrims R, Yaksi E. 2018 Information processing in the vertebrate habenula. *Semin. Cell Dev. Biol.* **78**, 130–139. (doi:10.1016/j.semcdb.2017.08.019)
137. Vonderschen K, Bleckmann H, Hofmann MH. 2002 A direct projection from the cerebellum to the telencephalon in the goldfish, *Carassius auratus*. *Neurosci. Lett.* **320**, 37–40. (doi:10.1016/S0304-3940(02)00022-8)
138. Watanabe K, Chiu H, Pfeiffer BD, Wong AM, Hooper ED, Rubin GM, Anderson DJ. 2017 A circuit node that integrates convergent input from neuromodulatory and social behavior-promoting neurons to control aggression in *Drosophila*. *Neuron* **95**, 1112–1128. (doi:10.1016/j.neuron.2017.08.017)
139. Kaplan HS, Nichols ALA, Zimmer M. 2018 Sensorimotor integration in *Caenorhabditis elegans*: a reappraisal towards dynamic and distributed computations. *Phil. Trans. R. Soc. B* **373**, 20170371. (doi:10.1098/rstb.2017.0371)

140. Tononi G, Koch C. 2015 Consciousness: here, there and everywhere? *Phil. Trans. R. Soc. B* **370**, 20140167. (doi:10.1098/rstb.2014.0167)
141. Dehaene S, Lau H, Kouider S. 2017 What is consciousness, and could machines have it? *Science* **358**, 484–489. (doi:10.1126/science.aan8871)
142. Sloman A, Chrisley R. 2003 Virtual machines and consciousness. *J. Conscious. Stud.* **10**, 133–172.
143. Tononi G, Boly M, Massimini M, Koch C. 2016 Integrated information theory: from consciousness to its physical substrate. *Nat. Rev. Neurosci.* **17**, 450–461. (doi:10.1038/nrn.2016.44)
144. Hessel G. 2012 The current status of the simulation theory of cognition. *Brain Res.* **1428**, 71–79. (doi:10.1016/j.brainres.2011.06.026)
145. Soylu F. 2016 An embodied approach to understanding: making sense of the world through simulated bodily activity. *Front. Psychol.* **7**, 1914. (doi:10.3389/fpsyg.2016.01914)
146. Hurley S. 2008 The shared circuits model (SCM): how control, mirroring, and simulation can enable imitation, deliberation, and mindreading. *Behav. Brain Sci.* **31**, 1–58. (doi:10.1017/S0140525X07003123)
147. Casile A, Caggiano V, Ferrari PF. 2011 The mirror neuron system: a fresh view. *Neuroscientist* **17**, 524–538. (doi:10.1177/1073858410392239)
148. Svensson H, Ziemke T. 2007 Making sense of embodiment: simulation theories and the sharing of neural circuitry between sensorimotor and cognitive processes. In *Body, language and mind. Volume 1: embodiment* (eds T Ziemke, J Zlatev, RM Frank), pp. 241–269. Berlin, Germany: Mouton de Gruyter.
149. Barsalou LW. 2008 Grounded cognition. *Annu. Rev. Psychol.* **59**, 617–645. (doi:10.1146/annurev.psych.59.103006.093639)
150. Edelman GM. 2004 *Wider than the sky: the phenomenal gift of consciousness*. New Haven, CT: Yale University Press.
151. Budaev SV, Brown C. 2011 Personality traits and behaviour. In *Fish cognition and behavior* (eds C Brown, K Laland, J Krause), pp. 135–165. Cambridge, UK: Blackwell Publishing.
152. Gosling SD, John OP. 1999 Personality dimensions in nonhuman animals: a cross-species review. *Curr. Dir. Psychol. Sci.* **8**, 69–75. (doi:10.1111/1467-8721.00017)
153. Réale D, Reader SM, Sol D, McDougall PT, Dingemans NJ. 2007 Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318. (doi:10.1111/j.1469-185X.2007.00010.x)
154. Sun R, Wilson N. 2014 A model of personality should be a cognitive architecture itself. *Cogn. Syst. Res.* **29–30**, 1–30. (doi:10.1016/j.cogsys.2014.02.001)
155. Broom DM. 1996 Animal welfare defined in terms of attempts to cope with the environment. *Acta Agric. Scand. Sect. A-Anim. Sci.* **27**, 22–28.
156. Jensen P, Toates F. 1993 Who needs 'behavioural needs'? Motivational aspects of the needs of animals. *Appl. Anim. Behav. Sci.* **37**, 161–181. (doi:10.1016/0168-1591(93)90108-2)
157. Nordenfält L. 2006 *Animal and human health and welfare: A comparative philosophical analysis*. Wallingford, CT: CABI.
158. Yeates J. 2018 Naturalness and animal welfare. *Animals* **8**, 53. (doi:10.3390/ani8040053)
159. Duncan IJ, Petherick JC. 1991 The implications of cognitive processes for animal welfare. *J. Anim. Sci.* **69**, 5017–5022. (doi:10.2527/1991.69125017x)
160. Dawkins MS. 1990 From an animal's point of view: motivation, fitness, and animal welfare. *Behav. Brain Sci.* **13**, 1–61. (doi:10.1017/S0140525X00077104)
161. Droege P, Braithwaite VA. 2014 A framework for investigating animal consciousness. In *Brain imaging in behavioral neuroscience* (eds J Lee, G Illies, F Ohl) pp. 79–98. Berlin, Germany: Springer. (doi:10.1007/7854\_2014\_278)
162. Jones RC. 2013 Science, sentience, and animal welfare. *Biol. Phil.* **28**, 1–30. (doi:10.1007/s10539-012-9351-1)
163. Boissy A *et al.* 2007 Assessment of positive emotions in animals to improve their welfare. *Physiol. Behav.* **92**, 375–397. (doi:10.1016/j.physbeh.2007.02.003)
164. Mellor DJ. 2012 Animal emotions, behaviour and the promotion of positive welfare states. *N. Z. Vet. J.* **60**, 1–8. (doi:10.1080/00480169.2011.619047)
165. Balcombe J. 2009 Animal pleasure and its moral significance. *Appl. Anim. Behav. Sci.* **118**, 208–216. (doi:10.1016/j.applanim.2009.02.012)
166. Fraser D. 2008 Understanding animal welfare. *Acta Vet. Scand.* **50**, 1–7. (doi:10.1186/1751-0147-50-51-51)
167. Hewson CJ. 2003 What is animal welfare? Common definitions and their practical consequences. *Can. Vet. J.* **44**, 496–499.
168. McEwen BS. 2007 Physiology and neurobiology of stress and adaptation: central role of the brain. *Physiol. Rev.* **87**, 873–904. (doi:10.1152/physrev.00041.2006)
169. Ulrich-Lai YM, Herman JP. 2009 Neural regulation of endocrine and autonomic stress responses. *Nat. Rev. Neurosci.* **10**, 397–409. (doi:10.1038/nrn2647)
170. Joëls M, Baram TZ. 2009 The neuro-symphony of stress. *Nat. Rev. Neurosci.* **10**, 459–466. (doi:10.1038/nrn2632)
171. Peter MCS. 2011 The role of thyroid hormones in stress response of fish. *Gen. Comp. Endocrinol.* **172**, 198–210. (doi:10.1016/j.ygcen.2011.02.023)
172. Madaro A, Olsen RE, Kristiansen TS, Ebbesson LOE, Nilsen TO, Flik G, Gorissen M. 2015 Stress in Atlantic salmon: response to unpredictable chronic stress. *J. Exp. Biol.* **218**, 2538–2550. (doi:10.1242/jeb.120535)
173. Horvath K, Angeletti D, Nascetti G, Carere C. 2013 Invertebrate welfare: an overlooked issue. *Ann. Ist. Super. Sanita* **49**, 9–17. (doi:10.4415/ANN\_13\_01\_04)
174. Chang ES. 2005 Stressed-out lobsters: crustacean hyperglycemic hormone and stress proteins. *Integr. Comp. Biol.* **45**, 43–50. (doi:10.1093/icb/45.1.43)
175. Sandi C, Haller J. 2015 Stress and the social brain: behavioural effects and neurobiological mechanisms. *Nat. Rev. Neurosci.* **16**, 290–304. (doi:10.1038/nrn3918)
176. Broom DM. 1998 Welfare, stress, and the evolution of feelings. *Adv. Study Behav.* **27**, 371–403. (doi:10.1016/S0065-3454(08)60369-1)
177. Dawkins MS. 1998 Evolution and animal welfare. *Q. Rev. Biol.* **73**, 305–328. (doi:10.1086/420307)
178. Guidolin D, Albertin G, Guescini M, Fuxe K, Agnati LF. 2011 Central nervous system and computation. *Q. Rev. Biol.* **86**, 265–285. (doi:10.1086/662456)
179. Piccinini G. 2007 Computational modelling vs. computational explanation: is everything a Turing machine, and does it matter to the philosophy of mind? *Australas. J. Philos.* **85**, 93–115. (doi:10.1080/00048400601176494)
180. Piccinini G, Scarantino A. 2011 Information processing, computation, and cognition. *J. Biol. Phys.* **37**, 1–38. (doi:10.1007/s10867-010-9195-3)
181. Bennett CH. 1982 The thermodynamics of computation—a review. *Int. J. Theor. Phys.* **21**, 905–940. (doi:10.1007/BF02084158)
182. Chu D. 2018 Performance limits and trade-offs in entropy-driven biochemical computers. *J. Theor. Biol.* **443**, 1–9. (doi:10.1016/j.jtbi.2018.01.022)
183. Piccinini G, Shagrir O. 2014 Foundations of computational neuroscience. *Curr. Opin. Neurobiol.* **25**, 25–30. (doi:10.1016/j.conb.2013.10.005)
184. O'Reilly RC, Munakata Y. 2000 *Computational explorations in cognitive neuroscience: understanding the mind by simulating the brain*. Cambridge, MA: MIT Press.
185. Pylyshyn ZW. 1984 *Computation and cognition*. Cambridge, MA: MIT Press.
186. Minsky M. 1986 *The society of mind*. New York, NY: Touchstone Books.
187. Miłkowski M. 2018 From computer metaphor to computational modeling: the evolution of computationalism. *Minds Mach.* **28**, 515–541. (doi:10.1007/s11023-018-9468-3)
188. Boden MA. 2006 *Mind as machine: a history of cognitive science*. Oxford, UK: Clarendon Press.
189. Lucentini DF, Gudwin RR. 2015 A comparison among cognitive architectures: a theoretical analysis. *Procedia Comput. Sci.* **71**, 56–61. (doi:10.1016/j.procs.2015.12.198)
190. Anderson JR. 2007 *How can the human mind occur in the physical universe?* Oxford, UK: Oxford University Press.
191. Newell A. 1994 *Unified theories of cognition*. Harvard, MA: Harvard University Press.
192. Sun R. 2004 Desiderata for cognitive architectures. *Phil. Psychol.* **17**, 341–373. (doi:10.1080/0951508042000286721)
193. Vernon D, Von Hofsten C, Fadiga L. 2016 Desiderata for developmental cognitive architectures. *Biol. Inspired Cogn. Archit.* **18**, 116–127. (doi:10.1016/j.bica.2016.10.004)
194. Pezzullo G, Barsalou LW, Cangelosi A, Fischer MH, McRae K, Spivey MJ. 2013 Computational grounded cognition: a new alliance between grounded cognition and computational modeling. *Front. Psychol.* **3**, 612. (doi:10.3389/fpsyg.2012.00612)
195. Andersen BS, Jørgensen C, Eliassen S, Giske J. 2016 The proximate architecture for decision-making in fish. *Fish Fish.* **17**, 680–695. (doi:10.1111/faf.12139)

196. Huse G, Giske J. 1998 Ecology in Mare Pentium: an individual-based spatio-temporal model for fish with adapted behaviour. *Fish. Res.* **37**, 163–178. (doi:10.1016/S0165-7836(98)00134-9)
197. Strand E, Huse G, Giske J. 2002 Artificial evolution of life history and behavior. *Am. Nat.* **159**, 624–644. (doi:10.1086/339997)
198. Giske J, Mangel M, Jakobsen P, Huse G, Wilcox C, Strand E. 2003 Explicit trade-off rules in proximate adaptive agents. *Evol. Ecol. Res.* **5**, 835–865.
199. Budaev S. 2018 Source code: sbudaev/AHA-R1: The AHA Model: Reference Model R1, release 1.0. See <https://github.com/sbudaev/AHA-R1>. (doi:10.5281/zenodo.1215790)
200. Theoretical Ecology Group. 2020 The AHA Model. See <https://ahamodel.uib.no/> (accessed 8 October 2020).
201. Huse G, Strand E, Giske J. 1999 Implementing behaviour in individual-based models using neural networks and genetic algorithms. *Evol. Ecol.* **13**, 469–483. (doi:10.1023/A:1006746727151)
202. Ruxton GD, Beauchamp G. 2008 The application of genetic algorithms in behavioural ecology, illustrated with a model of anti-predator vigilance. *J. Theor. Biol.* **250**, 435–448. (doi:10.1016/j.jtbi.2007.10.022)
203. Ng YK. 1995 Towards welfare biology: evolutionary economics of animal consciousness and suffering. *Biol. Phil.* **10**, 255–285. (doi:10.1007/BF00852469)
204. Dennett D. 2017 *From bacteria to Bach and back: the evolution of minds*. New York, NY: W. W. Norton & Company.
205. Lorenz KZ. 1974 Science as a source of knowledge. *Science* **185**, 229–234. (doi:10.1126/science.185.4147.229)
206. Hebb DO. 1946 Emotion in man and animal: an analysis of the intuitive processes of recognition. *Psychol. Rev.* **53**, 88–106. (doi:10.1037/h0063033)
207. LeDoux JE. 2014 Coming to terms with fear. *Proc. Natl Acad. Sci. USA* **111**, 2871–2878. (doi:10.1073/pnas.1400335111)
208. Norman DA, Shallice T. 1986 Attention to action: willed and automatic control of behavior. In *Consciousness and self regulation* (eds RJ Davidson, GE Schwartz, D Shapiro), pp. 1–18. Boston, MA: Plenum Press.
209. Barron AB, Klein C. 2016 What insects can tell us about the origins of consciousness. *Proc. Natl Acad. Sci. USA* **113**, 4900–4908. (doi:10.1073/pnas.1520084113)
210. Seth AK, Baars BJ. 2005 Neural Darwinism and consciousness. *Conscious. Cogn.* **14**, 140–168. (doi:10.1016/j.concog.2004.08.008)
211. Blackmore S. 2005 *Consciousness: a very short introduction*. Oxford, UK: Oxford University Press.
212. Searle JR. 2000 Consciousness. *Annu. Rev. Neurosci.* **23**, 557–578. (doi:10.1146/annurev.neuro.23.1.557)
213. Moore EF. 1956 Gedanken-experiments on sequential machines. In *Automata studies* (eds CE Shannon, J McCarthy), pp. 129–153. Princeton, NJ: Princeton University Press.
214. Bronfman ZZ, Ginsburg S, Jablonka E. 2016 The transition to minimal consciousness through the evolution of associative learning. *Front. Psychol.* **7**, 1954. (doi:10.3389/fpsyg.2016.01954)
215. Giske J, Huse G, Fiksen Ø. 1998 Modelling spatial dynamics of fish. *Rev. Fish Biol. Fish.* **8**, 57–91. (doi:10.1023/A:1008864517488)
216. Gras R, Devaurs D, Wozniak A, Aspinall A. 2009 An individual-based evolving predator-prey ecosystem simulation using a fuzzy cognitive map as the behavior model. *Artif. Life* **15**, 423–463. (doi:10.1162/artl.2009.Gras.012)
217. Evers E, De Vries H, Spruijt BM, Sterck EHM. 2014 The EMO-model: an agent-based model of primate social behavior regulated by two emotional dimensions, anxiety-FEAR and satisfaction-LIKE. *PLoS ONE* **9**, e87955. (doi:10.1371/journal.pone.0087955)
218. MacPherson B, Mashayekhi M, Gras R, Scott R. 2017 Exploring the connection between emergent animal personality and fitness using a novel individual-based model and decision tree approach. *Ecol. Inform.* **40**, 81–92. (doi:10.1016/j.ecoinf.2017.06.004)
219. Hilborn R, Mangel M. 1997 *The ecological detective: confronting models with data*. Princeton, NJ: Princeton University Press.
220. Mangel M, Clark C. 1986 Towards a unified foraging theory. *Ecology* **67**, 1127–1138. (doi:10.2307/1938669)
221. McNamara JM, Houston AI. 1986 The common currency for behavioral decisions. *Am. Nat.* **127**, 358–378. (doi:10.1086/284489)
222. Houston A, Clark C, McNamara J, Mangel M. 1988 Dynamic models in behavioural and evolutionary ecology. *Nature* **332**, 29–34. (doi:10.1038/332029a0)
223. Filosa A, Barker AJ, Dal Maschio M, Baier H. 2016 Feeding state modulates behavioral choice and processing of prey stimuli in the zebrafish tectum. *Neuron* **90**, 596–608. (doi:10.1016/j.neuron.2016.03.014)
224. Horstick EJ, Mueller T, Burgess HA. 2016 Motivated state control in larval zebrafish: behavioral paradigms and anatomical substrates. *J. Neurogenet.* **30**, 122–132. (doi:10.1080/01677063.2016.1177048)
225. Ito B *et al.* 2019 Intense threat switches dorsal raphe serotonin neurons to a paradoxical operational mode. *Science* **363**, 538–542. (doi:10.1126/science.aau8722)
226. Niven JE. 2016 Neuronal energy consumption: biophysics, efficiency and evolution. *Curr. Opin. Neurobiol.* **41**, 129–135. (doi:10.1016/j.conb.2016.09.004)
227. Ames A. 2000 CNS energy metabolism as related to function. *Brain Res. Rev.* **34**, 42–68. (doi:10.1016/S0165-0173(00)00038-2)
228. Christoffersen GRJ. 1997 Habituation: events in the history of its characterization and linkage to synaptic depression. A new proposed kinetic criterion for its identification. *Prog. Neurobiol.* **53**, 45–66. (doi:10.1016/S0301-0082(97)00031-2)
229. Reed DD, Kaplan BA, Brewer AT. 2012 Discounting the freedom to choose: implications for the paradox of choice. *Behav. Process.* **90**, 424–427. (doi:10.1016/j.beproc.2012.03.017)
230. Hayes SC, Kapust J, Leonard SR, Rosenfarb I. 1981 Escape from freedom: choosing not to choose in pigeons. *J. Exp. Anal. Behav.* **36**, 1–7. (doi:10.1901/jeab.1981.36-1)
231. Milinski M, Heller R. 1978 Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature* **275**, 642–644. (doi:10.1038/275642a0)
232. Heller R, Milinski M. 1979 Optimal foraging of sticklebacks on swarming prey. *Anim. Behav.* **27**, 1127–1141. (doi:10.1016/0003-3472(79)90061-7)
233. Lewis M, Canamero L. 2016 Hedonic quality or reward? A study of basic pleasure in homeostasis and decision making of a motivated autonomous robot. *Adapt. Behav.* **24**, 267–291. (doi:10.1177/1059712316666331)
234. Alados CL, Escos JM, Emlen JM. 1996 Fractal structure of sequential behaviour patterns: an indicator of stress. *Anim. Behav.* **51**, 437–443. (doi:10.1006/anbe.1996.0040)
235. Seuront L, Cribb N. 2017 Fractal analysis provides new insights into the complexity of marine mammal behavior: a review, two methods, their application to diving and surfacing patterns, and their relevance to marine mammal welfare assessment. *Mar. Mamm. Sci.* **33**, 847–879. (doi:10.1111/mms.12399)
236. de Oliveira CGL, Miranda JGV, Japyassú HF, El-Hani CN. 2018 Using Zipf–Mandelbrot law and graph theory to evaluate animal welfare. *Phys. A Stat. Mech. Appl.* **492**, 285–295. (doi:10.1016/j.physa.2017.08.127)
237. Enkel T, Gholizadeh D, von Bohlen und Halbach O, Sanchis-Segura C, Hurlmann R, Spanagel R, Gass P, Vollmayr B. 2010 Ambiguous-cue interpretation is biased under stress and depression-like states in rats. *Neuropsychopharmacology* **35**, 1008–1015. (doi:10.1038/npp.2009.204)
238. Bateson M, Desire S, Gartside SE, Wright GA. 2011 Agitated honeybees exhibit pessimistic cognitive biases. *Curr. Biol.* **21**, 1070–1073. (doi:10.1016/j.cub.2011.05.017)
239. Burman O, McGowan R, Mendl M, Norling Y, Paul E, Rehn T, Keeling L. 2011 Using judgement bias to measure positive affective state in dogs. *Appl. Anim. Behav. Sci.* **132**, 160–168. (doi:10.1016/j.applanim.2011.04.001)
240. Landsrød LK. 2017 Decision-making in a proximate model framework: how behaviour flexibility is generated by arousal and attention. MSc thesis, Department of Biological Sciences, University of Bergen, Norway. See <http://bora.uib.no/handle/1956/16385>.
241. Buckley V, Semple S. 2012 Evidence that displacement activities facilitate behavioural transitions in ring-tailed lemurs. *Behav. Process.* **90**, 433–435. (doi:10.1016/j.beproc.2012.04.009)
242. Root-Bernstein M. 2010 Displacement activities during the honeybee transition from waggle dance to foraging. *Anim. Behav.* **79**, 935–938. (doi:10.1016/j.anbehav.2010.01.010)
243. Huys QJM, Maia TV, Frank MJ. 2016 Computational psychiatry as a bridge from neuroscience to clinical applications. *Nat. Neurosci.* **19**, 404–413. (doi:10.1038/nn.4238)
244. Adams RA, Huys QJM, Roiser JP. 2015 Computational psychiatry: towards a mathematically informed understanding of



- mental illness. *J. Neurol. Neurosurg. Psychiatry* **87**, 53–63. (doi:10.1136/jnnp-2015-310737)
245. El Saddik A. 2018 Digital twins: the convergence of multimedia technologies. *IEEE Multimed.* **25**, 87–92. (doi:10.1109/MMUL.2018.023121167)
246. Geris L, Lambrechts T, Carlier A, Papanitiou I. 2018 The future is digital: in silico tissue engineering. *Curr. Opin. Biomed. Eng.* **6**, 92–98. (doi:10.1016/j.cobme.2018.04.001)
247. Monteiro J, Barata J, Veloso M, Veloso L, Nunes J. 2018 Towards sustainable digital twins for vertical farming. In *13th Int. Conf. on Digital Information Management (ICDIM)*, Berlin, Germany 24–26 September, pp. 234–239. (doi:10.1109/ICDIM.2018.8847169)
248. Voosen P. 2020 Europe is building a 'digital twin' of Earth to revolutionize climate forecasts. *sciencemag.org*. (doi:10.1126/science.abf0687)
249. Bruynseels K, de Sio FS, van den Hoven J. 2018 Digital twins in health care: ethical implications of an emerging engineering paradigm. *Front. Genet.* **9**, 31. (doi:10.3389/fgene.2018.00031)
250. Pettey C. 2017 Prepare for the impact of digital twins. *Gartner*. See <https://www.gartner.com/smarterwithgartner/prepare-for-the-impact-of-digital-twins>.
251. Schmidhuber J. 2015 Deep learning in neural networks: an overview. *Neural Netw.* **61**, 85–117. (doi:10.1016/j.neunet.2014.09.003)
252. Black JL. 2014 Brief history and future of animal simulation models for science and application. *Anim. Prod. Sci.* **54**, 1883–1895. (doi:10.1071/an14650)
253. de Fine Licht K, de Fine Licht J. 2020 Artificial intelligence, transparency, and public decision-making: why explanations are key when trying to produce perceived legitimacy. *AI Soc.* **35**, 917–926. (doi:10.1007/s00146-020-00960-w)
254. Rotsidis A, Theodorou A, Bryson JJ, Wortham RH. 2019 Improving robot transparency: an investigation with mobile augmented reality. In *28th IEEE Int. Conf. on Robot and Human Interactive Communication (RO-MAN)*, New Delhi, India, 14–18 October. (doi:10.1109/RO-MAN46459.2019.8956390)
255. Sandøe P, Corr SA, Lund TB, Forkman B. 2019 Aggregating animal welfare indicators: can it be done in a transparent and ethically robust way? *Anim. Welf.* **28**, 67–76. (doi:10.7120/09627286.28.1.067)
256. Murren CJ. 2012 The integrated phenotype. *Integr. Comp. Biol.* **52**, 64–76. (doi:10.1093/icb/ics043)
257. Kirkden RD, Pajor EA. 2006 Using preference, motivation and aversion tests to ask scientific questions about animals' feelings. *Appl. Anim. Behav. Sci.* **100**, 29–47. (doi:10.1016/j.applanim.2006.04.009)
258. Brando S, Buchanan-Smith HM. 2018 The 24/7 approach to promoting optimal welfare for captive wild animals. *Behav. Process.* **156**, 83–95. (doi:10.1016/j.beproc.2017.09.010)
259. Roberts SJ, Cain R, Dawkins MS. 2012 Prediction of welfare outcomes for broiler chickens using Bayesian regression on continuous optical flow data. *J. R. Soc. Interface* **9**, 3436–3443. (doi:10.1098/rsif.2012.0594)
260. Laundre JW, Hernandez L, Ripple WJ. 2010 The landscape of fear: ecological implications of being afraid. *Open Ecol. J.* **3**, 1–7. (doi:10.2174/1874213001003030001)
261. Bleicher SS. 2017 The landscape of fear conceptual framework: definition and review of current applications and misuses. *PeerJ* **5**, e3772. (doi:10.7717/peerj.3772)
262. Gallagher AJ, Creel S, Wilson RP, Cooke SJ. 2017 Energy landscapes and the landscape of fear. *Trends Ecol. Evol.* **32**, 88–96. (doi:10.1016/j.tree.2016.10.010)
263. Baciadonna L, McElligott AG. 2015 The use of judgement bias to assess welfare in farm livestock. *Anim. Welf.* **24**, 81–91. (doi:10.7120/09627286.24.1.081)
264. Lou HC, Changeux JP, Rosenstand A. 2017 Towards a cognitive neuroscience of self-awareness. *Neurosci. Biobehav. Rev.* **83**, 765–773. (doi:10.1016/j.neubiorev.2016.04.004)
265. Banks W (ed.). 2009 *Encyclopedia of consciousness*. New York, NY: Academic Press.
266. Uttal WR. 2011 *Mind and brain a critical appraisal of cognitive neuroscience*. Cambridge, MA: MIT Press.
267. Railsback SF, Grimm V. 2019 *Agent-based and individual-based modeling. a practical introduction*. Princeton, NJ: Princeton University Press.
268. Stillman RA, Railsback SF, Giske J, Berger UT, Grimm V. 2015 Making predictions in a changing world: the benefits of individual-based ecology. *Bioscience* **65**, 140–150. (doi:10.1093/biosci/biu192)
269. DeAngelis DL, Diaz SG. 2018 Decision-making in agent-based modeling: a review and future prospectus. *Front. Ecol. Evol.* **6**, 237. (doi:10.3389/FEVO.2018.00237)
270. Adami C, Schossau J, Hintze A. 2016 Evolutionary game theory using agent-based methods. *Phys. Life Rev.* **19**, 1–26. (doi:10.1016/j.plrev.2016.08.015)

## Brief glossary

<b>Agent</b>	an autonomous entity that is capable of adaptive, goal-directed behaviour.
<b>Awareness</b>	a cognitive state that results in the representation of an environmental or an internal object as a whole so as to create an isomorphism between this object and its subjective representation.
<b>Consciousness</b>	awareness of the agent's own existence and relationships with its environment.
<b>Experience</b>	a subjective process by which an agent perceives its external and internal environment through awareness. Note that we consider experience a broader concept than feeling that also includes intellectual experience, belief, etc.
<b>Feeling</b>	specific state of awareness closely linked with subjective experience, this can include sensory feelings and emotional feelings.
<b>Mind</b>	an intelligent computing system that implements learning, cognition and behavioural control. Mind can include a capacity for awareness and is supplemented by numerous automatic processing modules.
<b>Sentience</b>	the capacity to experience subjective feelings.
<b>Subjective</b> (processes/ states)	internal processes and states of the organism that exist from the first-person point of view; their existence is inseparable from and cannot be defined independently of the experiencing organism.